Advances in
MARINE BIOLOGY

VOLUME
50

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A J Southward, C M Young
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525 B Street, Suite 1900, San Diego, California 92101-4495, USA
84 Theobald's Road, London WC1X 8RR, UK

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ISBN-13: 978-0-12-026151-2
ISBN-10: 0-12-026151-0

PRINTED IN THE UNITED STATES OF AMERICA
06 07 08 09 9 8 7 6 5 4 3 2 1

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Biology and Ecology of the Hydrocoral *Millepora* on Coral Reefs

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ADVANCES IN MARINE BIOLOGY VOL 50

0065-2881/06 $35.00
DOI: 10.1016/S0065-2881(05)50001-4

Millepores are colonial polypoidal hydrozoans secreting an internal calcareous skeleton of an encrusting or upright form, often of considerable size. Defensive polyps protruding from the skeleton are numerous and highly toxic and for this reason millepores are popularly known as "stinging corals" or "fire corals." In shallow tropical seas millepore colonies are conspicuous on coral reefs and may be locally abundant and important reef-framework builders. The history of systematic research on the Milleporidae and the sister family Stylasteridae is rich and full with the works of early naturalists beginning with Linnaeus. Seventeen living millepore species are recognised. Marked phenotypic variation in form and structure of colonies is characteristic of the genus Millepora. The first published descriptions of the anatomy and histology of millepores were by H. N. Moseley in one of the Challenger Expedition reports. These original, detailed accounts by Moseley remain valid and, except for recent descriptions of the ultrastructure of the skeleton and skeletogenic tissues, have not needed much modification.

Millepores occur worldwide on coral reefs at depths of between 1 and 40 m and their distribution on reefs is generally zoned in response to physical factors. Colonies may be abundant locally on coral reefs but usually comprise <10% of the overall surface cover. Growth rates of colonies are similar to the measured rates of branching and platelike scleractinian corals. Millepores are voracious zooplankton feeders and they obtain part of their nutrition from autotrophic sources, photosynthetic production by symbiotic zooxanthellae.

Reproduction in millepores is characterised by alternation of generations with a well-developed polypoid stage that buds off planktonic medusae. Sexual reproduction is seasonal for known species and the medusae have a brief planktonic life. Asexual production is achieved by sympodial growth, the production of new skeleton and soft tissue along a growing edge or branch tip, and by the reattachment, regeneration and repair of damaged or broken colony fragments.

The physiological and ecological responses of species of millepores are similar to those of the species of scleractinian corals over a broad range of natural and anthropogenic disturbances. Severe damage to colonies may occur during major storms. Delicately branching species are more susceptible than massive and bladed species. The ability of broken fragments to regenerate can ameliorate the extent of damage. Widespread bleaching and mortality of millepores has been reported during mass bleaching events that have affected many coral reefs. Millepores are often the first to recover after short-term bleaching events. Harmful effects of oil spills, chronic oil pollution and oil-spill detergents have been widely reported for millepores.

Although the hydrozoan coenosarc, with its fiercely stinging zooids, does not appear to be an attractive substratum for attachment and settlement of epizooans, a number of sessile and errant forms commonly occur on millepores. These include barnacles, amphipods, tanaid and alpheid crustaceans,

polychaetes and gastropods. Burrowing molluscs, polychaetes and crustacea also abound. Many of these species or their close relatives also occur on scleractinian corals. A variety of predators, grazers and fouling organisms occur on millepores. These include errant polychaetes, several coral-feeding fish and a gastropod mollusc. Various invasive green, red and brown algae are widespread, growing on dead branches of millepores and overgrowing live coral tissue. Various "band diseases" associated with microorganisms that appear to cause lesions on millepores and loss of tissue have been documented but are not of widespread occurrence. Infestations of endolithic algae and fungi growing within the skeletons have been reported in a number of millepore species.

1. INTRODUCTION

Millepores (family Milleporidae, class Hydrozoa, phylum Cnidaria) are colonial, polypoid hydrocorals secreting a calcareous skeleton of an encrusting or upright form, often of considerable size (Boschma, 1948). Feeding and defensive polyps protrude through pores in the skeleton. The defensive polyps are numerous and highly toxic, and for this reason, millepores are often called "stinging corals" or "fire corals" (Hyman, 1940; Boschma, 1948; Barnes, 1980). Medusae are formed in special cavities (the ampullae) in the skeleton and are shed freely in the water (Hyman, 1940; Boschma, 1948).

In shallow tropical seas, they are among the most conspicuous of the skeleton-forming animals on coral reefs. Millepores may be locally abundant and important calcareous reef framework builders, second only to the Scleractinia (stony corals). Their ecological importance may be considerable at high densities if significant numbers of plankton prey are consumed (Lewis, 1992a). From the viewpoint of evolutionary ecology, they may offer insights into complex hydrozoan life cycles (Schuchert, 1996). Yet, in spite of their ecological and geological importance, millepores have received relatively little attention in comprehensive reef studies, compared to the preeminent stony corals. Standard textbooks in invertebrate zoology generally devote limited space to the taxon despite detailed monographic work from the late nineteenth century.

A sister hydrocoral family, the Stylasteridae (the "lace corals"), superficially resemble the millepores, forming upright, calcareous, fragile, usually small uniplanar or slightly arborescent colonies, coloured orange, red, blue or violet (Hyman, 1940; Cairns, 1984). In contrast to the Milleporidae, the young escape as planula larvae. Though reported as occurring on coral reefs, they are most abundant and diverse at depths of 200–500 m in all ocean basins (Cairns, 1984) and appear to lack the ecological importance of millepores in shallow tropical waters.

The purpose of this review is to focus attention on millepores in order to broaden interest and stimulate further study, to bring together disparate aspects of their biology scattered throughout the literature, and to comment on and evaluate recent information on the biology and ecology of the group. Because millepores are members of the coral reef constructor guild (Fagerstrom, 1987) and are frequently included under the general rubric of "hard corals" in reef surveys (e.g., Lang, 2003), attention is drawn to the morphological and ecological similarities with the scleractinians. A review of existing knowledge of hydrocorals can help to support management strategies necessary to reduce the decline of coral reefs in the current global crisis (Hughes *et al.*, 2003).

2. SYSTEMATICS AND HISTORY

The two families of hydrocorals, the Milleporidae and the Stylasteridae, secrete a calcareous skeleton but differ in details of skeletal structure, polyp morphology and reproduction (Hyman, 1940; Boschma, 1956; Barnes, 1980; Schuchert, 2005). The family Milleporidae comprises a single living genus, *Millepora,* which has a worldwide marine distribution (Boschma, 1948, 1956). The Stylasteridae contain 23 genera (Cairns, 1983). The affinity of the Milleporidae with the hydroids was first demonstrated by Louis Agassiz (1858) and that of the Stylasteridae by Moseley (1879). For a long time the two families were considered closely allied and were combined in a single order called the *Hydrocorallina* (Hyman, 1940; Boschma, 1956; Barnes, 1980) but were subsequently assigned to the orders Milleporina and Stylasterina (Boschma, 1956). However, their systematic position within the class Hydrozoa has been a subject of prolonged debate (Cairns, 1984; Calder, 1988; Schuchert, 1996).

Although the use of the orders Milleporina and Stylasterina is still common in standard textbooks (Hyman, 1940; Barnes, 1980), in field identification guides (Humann, 1993) and other treatises (Veron, 2000), it has been argued by Petersen (1979), Bouillon (1985) and Schuchert (1996) that the family Milleporidae resides within the order Capitata and the Stylasteridae are separated in the order Filifera. The Capitata can be divided into three suborders, the Moerisiida (the most primitive group), the Tubulariida and the Zancleida (Petersen, 1979). The latter contains the family Milleporidae.

The Filifera are assumed to have evolved from forms close to the primitive Moerisiida, but the phylogeny is more difficult to trace than that of the Capitata because the morphology of the polyp has undergone fewer changes within the order (Petersen, 1979; Bouillon, 1985). Two evolutionary lines can be traced from primitive stolonal Filifera. One line leads to the

Hydractiniodea (containing the Stylasteridae), which develop polymorphic colonies with a calcareous skeleton, and the Bougainvillioidea and Pandeoidea, both of which form racemose colonies.

Further refinements in classification define the Filifera and Capitata as suborders in the order Anthomedusae (Schuchert, 2005). The definitions of the two families as reported by Schuchert (2005) are as follows:

Family Stylasteridae: "Hydroid colony erect, branched, usually flabellate, more rarely encrusting, with a thick calcareous exoskeleton (coenosteum); polyps polymorphic and retractile; gastrozooids with one whorl of filiform tentacles, exceptionally without tentacles; bottom of gastric cavity with or without an upright pointed or rounded toothed spine (gastrostyle); dactylozooids filiform, without tentacles, with or without dactylostyle; gastrozooids and dactylozooids retractable into special skeletal depressions; gastropores and dactylopores; gastrozooids and dactylozooids either irregularly distributed over the colony, or limited to certain regions of the colony, or often arranged in circles (cyclosystems) where one gastrozooid is surrounded by several dactylozooids; gonophores are reduced fixed sporosacs and developed inside vesicles (ampullae) covered by or buried in coenosteum."

Family Milleporidae: "Hydroid colony forming massive calcareous exoskeletons (coenosteum) of varied shape; coenosteum with an internal complex network of coenosarcal tubes and covered externally by a thin ectodermal layer, coenosteal surface perforated by pores; margins of pores not elevated; large gastropores surrounded by smaller dactylopores, forming indistinct cyclosystems; polyps polymorphic; gastrozooids relatively short and stout, with an oral whorl of four to seven short capitate tentacles, arising from gastropores; dactylozooids long, slender, mouthless, with scattered capitate tentacles, arising from dactylopores; cnidome with stenoteles and macrobasic mastigophores; gonophores arising from coenosarc within chambers embedded entirely in the coenosteum. Medusae free swimming eumedusoids with exumbrellar nematocyst patches, radial and circular canals present, without tentacles and sense organs; gonads occupying the place of an indistinct manubrium."

The history of systematic research on millepores (and of the stylasterids) is full and rich with the work of early naturalists, beginning with Linnaeus. The genus *Millepora* Linnaeus, 1758 originally included a number of species, but only *Millepora alcicornis* is referred to the genus as it is presently understood (Boschma, 1948). Although there is some uncertainty as to the true identity of the original *M. alcicornis,* which may have been a scleractinian coral, the definition by Linnaeus almost certainly refers to the current genus *Millepora* (Calder, 1988). Nevertheless, the genus *Millepora* in Linnaeus (1767) contained a heterogeneous group of organisms.

The subsequent history of the genus involved many of the early taxonomic authorities responsible for the nomenclature of other taxa of invertebrates, but particularly of the Coelenterata (Cnidaria). Prominent among them were P. S. Pallas, E. J. C. Esper, J. B. P. A. de M. Lamarck, P. Duchassaing, J. Michelotti, H. Milne Edwards and A. E. Verrill. These and others described a number of species and varieties of millepores, mainly based on differences in growth forms. The material on which these descriptions were based included specimens from museums and those collected on international expeditions or first hand by the naturalists themselves.

Pallas (1766) included a number of madrepores (various stony corals) and nullipores (lime-secreting coralline algae) in the genus along with *M. alcicornis* of which he distinguished five varieties. Esper (1790) also included species belonging to the nullipores and foraminiferans in the genus and assigned names to several varieties of *Millepora.* These varieties later came to have specific value. Lamarck (1816) recognised *Millepora squarrosa* and *Millepora complanata* as well as *M. alcicornis* but still included nullipores in the genus. Although these heterogeneous taxa that bear no relation to the millepores were excluded by Duchassaing and Michelotti (1860) and by Milne Edwards (1860), a new problem arose: an excess of species. Duchassaing and Michelotti (1860, 1864) listed seven West Indian species and later distinguished as many as 24 species from the same region, based on minor differences in form. Similarly, Milne Edwards (1860) diagnosed 16 species and presented notes on four other forms. Verrill (1868) added new species and varieties from Brazil. Problems of specific relationships among the numerous species and varieties of forms were addressed by Klunzinger (1879), who designated species with their correct names or placed them in synonymy.

In response to the reports of so many species by Milne Edwards (1860) and Duchassaing and Michelotti (1864), species limits in the genus *Millepora* were considered by Hickson (1898a,b) who concluded that all the described species were growth forms of one extremely variable species *M. alcicornis.* Thus arose the "species problem" in *Millepora* dealt with by Boschma (1948).

Hilbrand Boschma (1893–1976), a former director of the Rijkmuseum at Leiden, was foremost among the investigators of hydrocorals. Between 1948 and 1970, he published some 70 papers dealing with the three orders of hydrocorals (named Milleporina, Axoporina and Stylasterina) of which the Milleporidae were dealt with in 15 (Vervoort and Zibrowius, 1981). The bulk of Boschma's work was taxonomic in nature, based on an exhaustive analysis of the literature, on samples sent to him by individual scientists and from specimens in museums that he visited worldwide. He had few opportunities to collect hydrocorals himself or to observe millepores in the field. He visited Indonesia in 1922 with the Danish zoologist Dr. Th. Mortensen and again in 1929 and 1930 as a biologist with the Snellius Expedition (Vervoort, 1977). In 1949 he visited Fiji where he made detailed observations on the distribution and ecology of millepores on shallow reefs. In the seminal publication entitled "The Species Problem in Millepora," Boschma (1948) recognised 10 species, defined by distinct characters based on peculiarities of their growth forms, surface polyp pore distributions and ecology.

Both Milleporidae and Stylasteridae are recognised in tertiary deposits (Moore *et al.*, 1952), but although many fossils have been assigned to *Millepora*, Boschma (1956) recognised only two species, *Millepora tornquisti* from Eocene rocks of Madagascar and *M. alcicornis* in Pleistocene deposits in the Panama Canal zone (Vaughan, 1919). Many other fossils commonly regarded as species of *Millepora* were rejected by Boschma (1951). Branching milleporids were reported from the Upper Cretaceous in northern Spain (Rehfeld and Ernst, 1998).

There still remain taxonomic problems in the genus *Millepora* (de Weerdt, 1981, 1984; Estalella, 1982). Although some 50 species of millepores have been described (Veron, 2000), 11 extant species of *Millepora* from the Pacific and six from the Atlantic are recognised (de Weerdt and Glynn, 1991; Cairns *et al.*, 1999). A difficulty lies in the variable phenotypic forms of colonies of each species with no apparent stable morphological characteristics of taxonomic value as well as a lack of unambiguous morphological diagnostic characteristics between species. Examples of variations in growth forms of *M. alcicornis* are illustrated in Figure 1. Structural details of the skeleton such as size, shape, number and distribution of zooid pores are variable in each species and were rejected by Boschma (1948) as being of doubtful taxonomic value. However, combinations of dactylopore sizes and densities were found to be species-specific characters in four species of Atlantic millepores (de Weerdt, 1984; Amaral *et al.*, 2002), and a description of a new species was based on such surface structural details and on colony growth forms and ecology (de Weerdt and Glynn, 1991). Millepore phenotypic variability has a dynamic aspect since colony morphology varies temporally with changing environmental conditions. Vago *et al.* (1998) found that *Millepora dichotoma* in the Gulf of Elat (Red Sea) exhibited four main morphotypes whose distribution varied with depth but whose depth dependencies were modified by sediment levels and colony damage. Modification of colony form was demonstrated from tomography studies in which delicately branching coralla were found embedded in the skeletons of more massive colonies, indicating a transition in colony morphotypes over time (Vago *et al.*, 1994).

Morphological changes and plasticity were also demonstrated by de Weerdt (1981) in *M. complanata* by transplanting colonies of a particular morphotype to different depths and sites on reefs. She found that delicate branching forms from low-energy areas at 15 m became sturdier in appearance when transplanted to sites where turbulent water motion prevailed in the surf zone. Bladed morphotypes transplanted from depths of 5 m to the surf zone demonstrated a more rapid growth rate than control colonies

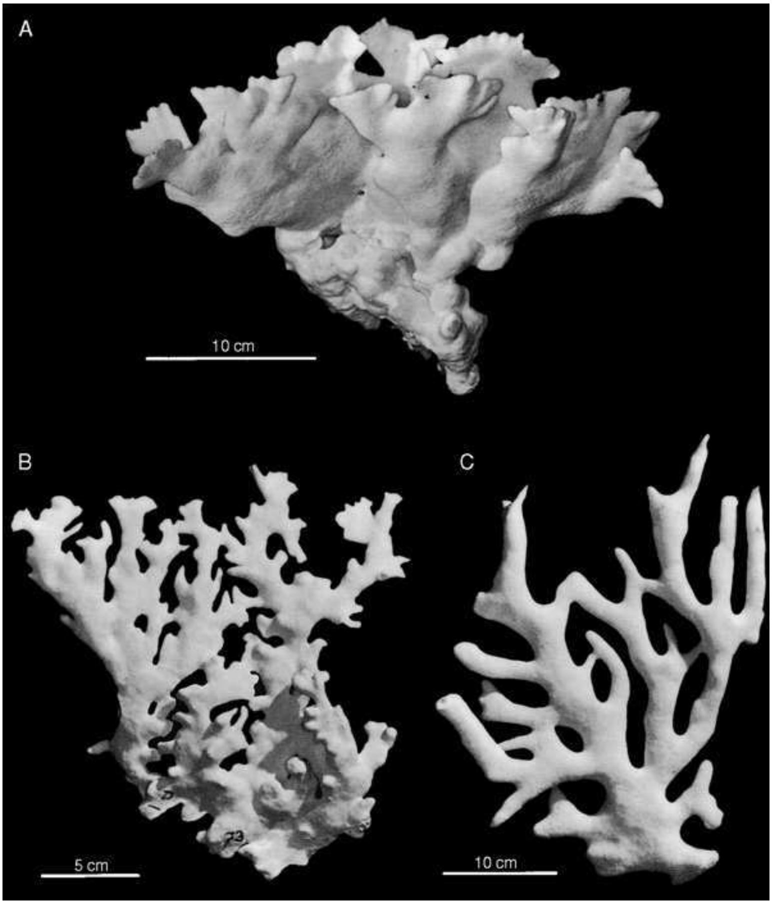

Figure 1 Growth forms of colonies of *Millepora alcicornis*. (A) Coarse branching. (B) Bushy branching. (C) Fine branching. (From de Weerdt, 1981.)

and developed lateral outgrowths. Bladed colonies transplanted to 15 m developed delicate branchlike outgrowths. Changes in growth rates and form were probably the result of a combination of changes in intensity of wave action, water turbulence and to varying light conditions.

Meroz-Fine *et al.* (2003) recognised branching and encrusting morphs of *M. dichotoma* in the Red Sea and suggested that differences in biological and molecular data warranted separation of the morphs into two species. They found that experimental field manipulation of the two morphs resulted in separate growth rates and differences in growth plasticity. There were also statistically significant differences in nematocyst capsule sizes between the two groups. Molecular data from cellular sequencing of DNA demonstrated that the two morphs differed considerably. Further molecular evidence (RNA) from the symbiotic zooxanthellae showed a different pattern of clades in the hosts.

Given the aforementioned, it is likely that studies involving molecular systematics may be required to confirm species identifications (Manchenko *et al.*, 1993; Cairns *et al.*, 1999; Collins, 2000; Meroz-Fine *et al.*, 2003). The use of only growth form and attributes of gastropores and dactylopores is unlikely to be sufficient (Amaral *et al.*, 2002). Work on the genetic structure of populations of hydrozoans has the potential to distinguish more readily between species. Liu and Chen (1992) examined allelic differences between enzyme loci in three species of millepores from Taiwan and concluded that *Millepora tenella* probably represents a varied growth form of *M. dichotoma*. Alloimmune responses and histocompatibility reactions occurring in response to physical contacts between colonies may also come to have value in distinguishing between species possessing alloimmune recognition systems (Müller *et al.*, 1983; Frank and Rinkevich, 1994). Identical histocompatability alleles may allow related colonies to fuse, but unrelated colonies will repel one another. Molecular methods using DNA fingerprinting techniques may also aid in species definitions. In preliminary analyses, diagnostic DNA markers that distinguished between *M. alcicornis* and *M. complanata* have been identified and there may exist hybrids of the two species (C. S. Tepper, personal communication, ctepper@cornellcollege.edu).

Thus, although a "species problem" may remain for millepores, it is surely remarkable that a Family of worldwide distribution, with a long geological history and apparent ecological success, is represented by <20 species. Amaral *et al.* (2002) attributed this to difficulties associated with taxonomy and distinction among the various species.

3. ANATOMY, MORPHOLOGY AND HISTOLOGY

Colonies of *Millepora* occur as upright, leaflike, platelike and variously shaped branching structures that may reach 30–60 cm in height. They also occur as lumpy rounded growths and frequently as encrustations over corals and other hard surfaces. They are usually yellow or brown in colour. Examples of three species of *Millepora* from the Caribbean are shown in Figures 2 and 3.

The skeleton of the colony is composed of fine porous calcareous deposits with numerous interconnecting canals or passageways. A classic description of the calcareous mass or coenosteum of *Millepora* and the internal anatomy was published with illustrations (Figure 4) by Moseley (1880). In spite of

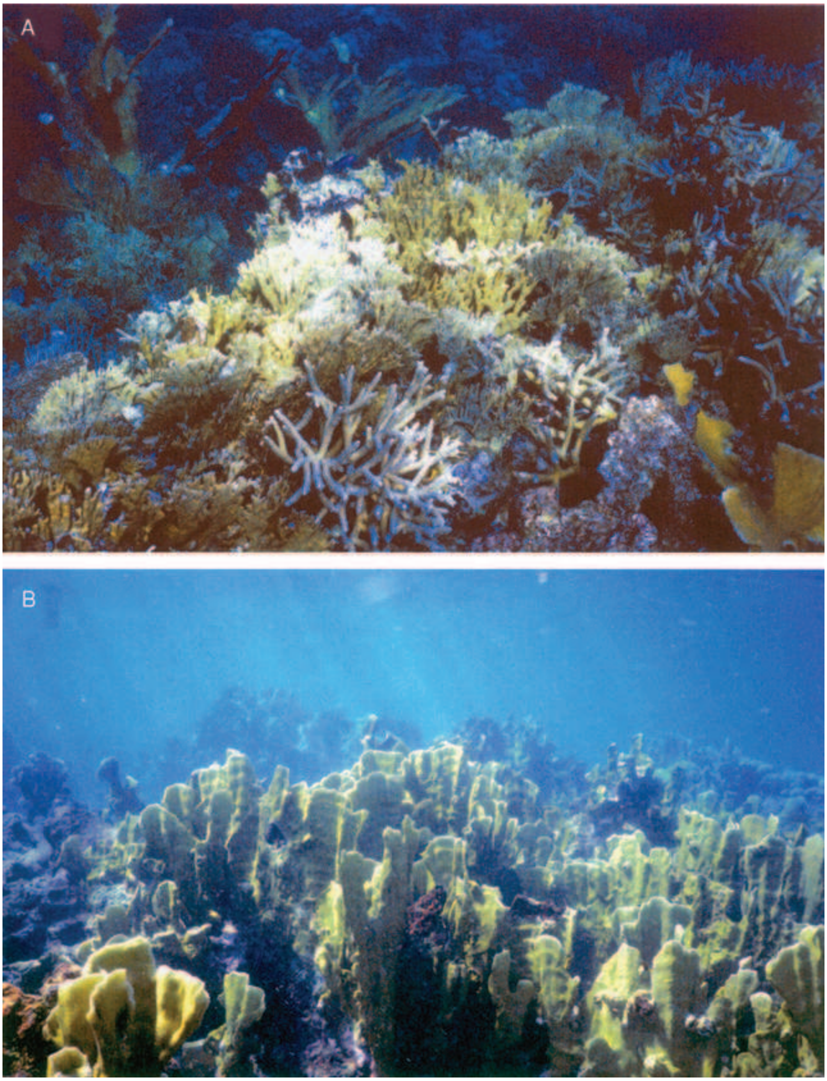

Figure 2 Underwater photographs of millepore colonies. (A) Densely packed colonies of *Millepora alcicornis,* British Virgin Islands, depth 7–8 m. A branching colony of the coral *Acropora cervicornis* 1 m in diameter appears in the bottom foreground. (B) Densely packed colonies of *Millepora complanata* on a fringing reef at Barbados, depth 2 m. The five colonies grouped at the bottom left are 10 cm in height.

limitations of the former histological techniques, the detailed descriptions of Moseley remain valid, and except for minor changes, the original descriptions have not needed much amendment. Line drawings and figures of the sections

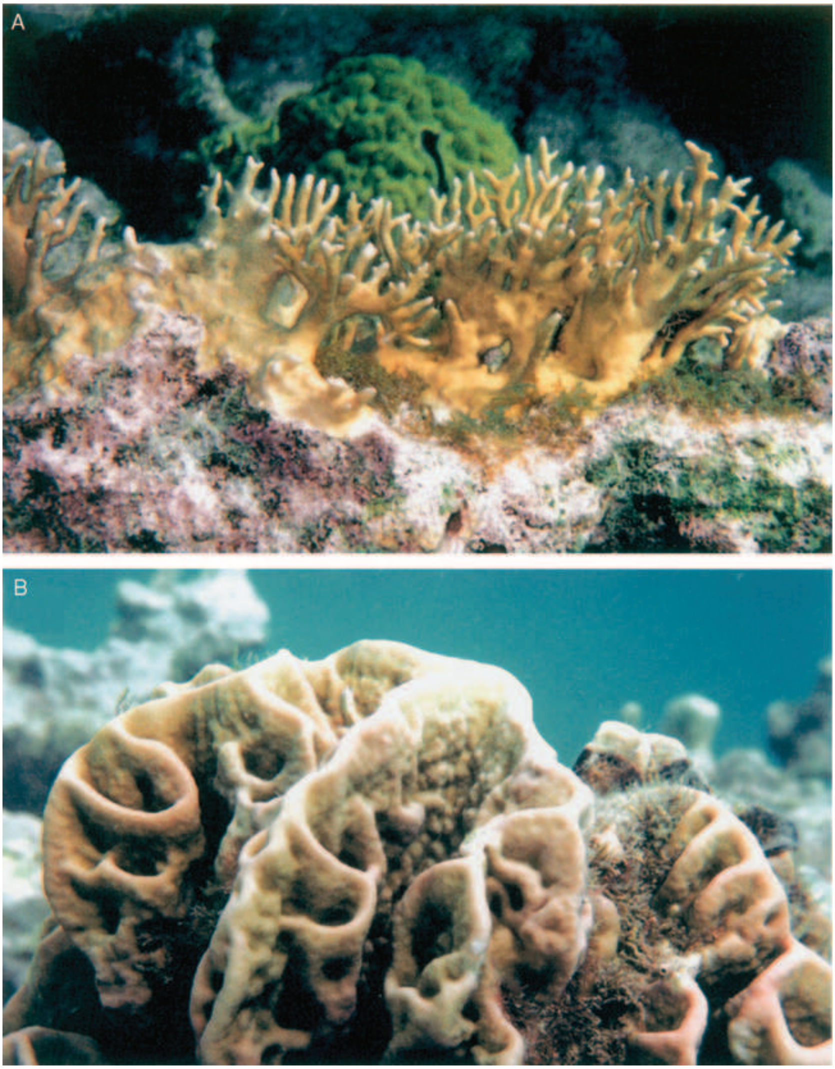

Figure 3 Underwater photographs of millepore colonies. (A) Closeup of colony of *Millepora alcicornis*, British Virgin Islands, depth 1 m. Colony is 20 cm in width. (B) Closeup of colony of *Millepora squarrosa* on a fringing reef at Barbados, depth 1 m. Colony is 15 cm in width.

of the coenosteum offered by Moseley have been copied into most recent textbooks of invertebrate zoology or slightly modified as in Moschenko (1993). Thus, there is an opportunity for improving our knowledge of the anatomy of millepores using modern microscope technologies.

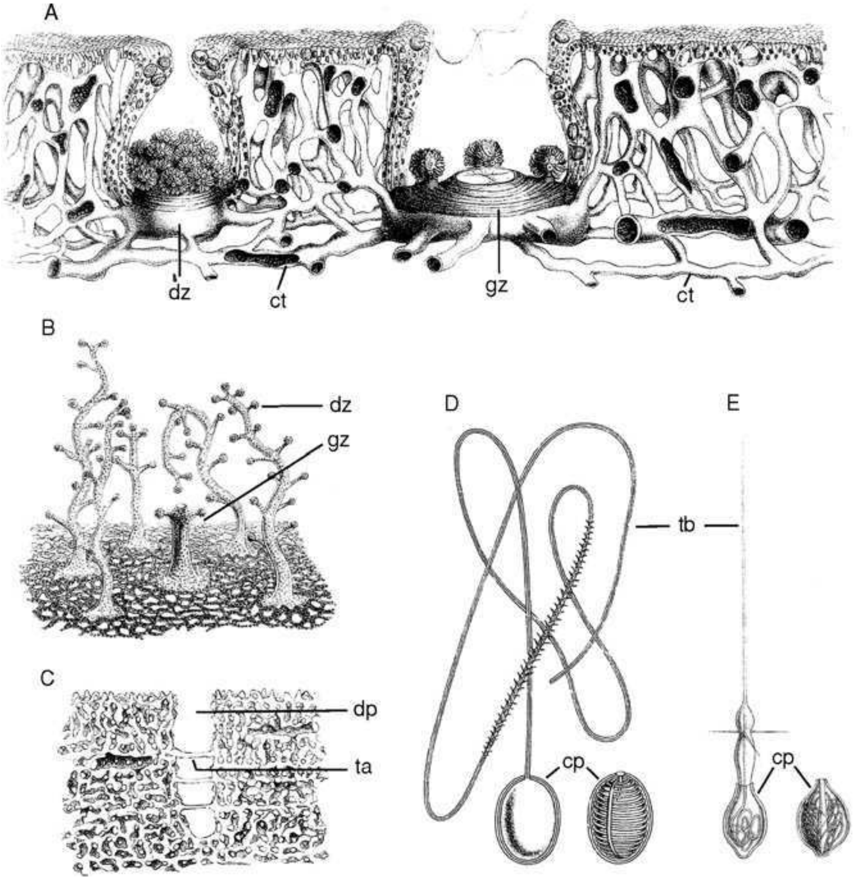

Figure 4 Anatomy and histology of *Millepora*. (A) Cross section of decalcified skeleton. ct: branch of coenosteum, dz: dactylozooid, gz: gastrozooid. (B) Gastrozooids and dactylozooids expanded. dz: dactylozooid, gz: gastrozooid. (C) Cross section of skeleton showing dactylopore and tabulae. dp: dactylopore, ta: tabula. (D) Discharged and undischarged capsules of macrobasic mastigophore nematocyst type. cp: capsule, tb: tube. (E) Discharged and undischarged capsules of stenotele nematocyst type. (From Moseley, 1880. Courtesy Blacker Wood Library of Biology, Rare Books and Special Collections Division, McGill University Libraries, Montreal, Quebec, Canada.)

The skeletal surface has a nodular or fascicular appearance. Each nodule is composed of a bundle of rounded crystalline needles (dactylostyles) (Le Tissier, 1991). The main mass of the coenosteum is composed of trabeculae of dense fibrocrystalline calcareous matter arranged in lamellae, the fibres of which cross one another at all angles. This fibrous hard tissue terminates towards a cavity in the coenosteum in a series of sharp points, suggesting it is made up from rodlike elements. Chemical analysis of the coenosteum indicates that the composition is not significantly different from other hard corals and the fundamental cellular mechanism of calcification is the same in both groups (Le Tissier, 1991). Carotenoproteins containing zeaxanthin, canthaxanthin and astaxanthin have been extracted from the calcareous skeletons of eight millepores from the Caribbean (Czeczuga *et al.*, 1999).

The surface of the colony is pitted with pinhole-sized pores, which lead into canals at right angles to the surface and are crossed at intervals by horizontal plates or tabulae (Figure 4C). The larger of the pores (gastropores) house the gastrozooids, cylindrical polyps with a central mouth. The smaller pores (dactylopores) contain the dactylozooids, which are long slender polyps without a mouth. The surface of the coenosteum is uneven and often covered with slightly rounded elevations. The pores are dispersed over the entire surface of the skeleton except along the distal edges and tips of branches of colonies where skeleton growth takes place. They are scattered or arranged in irregular groups or cyclosystems of a large gastropore surrounded by five to eight smaller dactylopores frequently occupying separate small rounded prominences.

The canals and spaces within the coenosteum (Figure 4A) are occupied by a network of soft tissue, which ramifies through the skeleton and unites the body cavities of the zooids. This, together with a thin layer of tissue covering the surface of the corallum, constitutes the coenosarc. Thus, the histological structure of the coenosarc consists of an ectodermal layer with a membranous layer, the mesoderm, developed beneath it and an endodermal lining. The ectodermal layer consists for the most part of tall fusiform cells with oval nuclei, clothing the surface and dipping down into the pores where it becomes continuous with the zooid bases. In the calicoblastic ectoderm are large, dense membrane-bound granules of the type generally associated with waste products or storage. Nematocysts are also often present (Le Tissier, 1991). Canals or tubes of coenosarc ramify in a complicated network throughout the coenosteum and have numerous connections with the surface and with the polyps. The canals are living only near the surface however, and the polyps extend only to the top tabula of the tubes of the coenosteum. The canals of the coenosarc secrete the coenosteum, which corresponds to the periderm of hydroids. Coenosteum tubes are often densely infested with endolithic algae (Bellamy and Risk, 1982) and fungal hyphae (Kendrick *et al.*, 1982; Te Strake *et al.*, 1988).

De Kruijf (1975) reported that in their fully expanded state, both gastrozooids and dactylozooids of *M. alcicornis* and *M. complanata* are about 2.5 mm in length. Gastrozooids are 0.06–0.16 mm in diameter at the base and dactylozooids 0.06–0.10 mm in diameter. The oral disk of a gastrozooid is surrounded by three to seven capitate tentacles that are reduced to nematocyst knobs

(Hyman, 1940). Dactylozooids lack a mouth and oral disk and are covered with numerous capitate tentacles arranged in circles of three or four along the whole tapering polyp stalk (Figure 4B). Both types of polyps are semi-transparent and can be fully retracted into the pores in the skeleton. Although they are not readily visible in the field, the hairlike zooids may be expanded both day and night and have the appearance of white felt on the coenosteum (Lewis, 1989). Zooids are apparently similar in morphology in most species of millepores (Moschenko, 1993).

The occurrence of nematocysts with their stinging properties is well known for the Cnidaria (Russell, 1965, 1984). Millepores have several kinds of nematocysts (Hyman, 1940) of the types described by Weill (1934) and Mariscal (1974). There are stenoteles, isorhizas (in at least some species) on the polyps and microbasic and macrobasic mastigophores on the zooids and on the general coenosarc (Figure 4D and E). Stenoteles are penetrant nematocysts and are limited to the class Hydrozoa. They occur in hydras, millepores and siphonophores but not in stylasterids (Schuchert, 2005). They have a rounded or oval capsule with a lid, a short butt and a long slender tube bearing spines. Mastigophores consist of a small capsule and a spiny, cylindrical butt or shaft followed by a slender tube. The microbasic type has a short shaft, less than three times the capsule length. In macrobasic mastigophores the shaft is longer, more than three times the length of the shaft (Mariscal, 1974), although Östman (2000) has identified an intermediate length of discharged shafts between microbasic and macrobasic. Macrobasic mastigophores are found only in the millepores and constitute one reason for placing them in a separate suborder. Calder (1988) has reported that the gastrozooids of *M. alcicornis* also contain microbasic mastigophores 30.0–31.9 × 24.5–26.3 μm. There are stenoteles of several sizes: (small) 8.3–8.9 × 5.7–6.6 μm; (medium) 15.9–17.6 × 12.9–14.2 μm and large stenoteles 21.6–24.7 × 15.9–18.7 μm. Dactylozooids contained small stenoteles 8.3–8.6 × 5.9–6.5 μm.

The powerful nematocysts of millepores are noted for producing an intense burning sensation in man, exceeding the irritation produced by contacts with most scleractinian coral colonies. Darwin (1839) remarked during a visit of the Beagle to the Cocos-Keeling Islands that "I was a good deal surprised by finding two species of the coral of the genus *Millepora*, possessed of the property of stinging. The sensation was as bad as that from a nettle, but more like that caused by the Portuguese man-of-war (*Physalia*)."

Swimmers on reefs soon learn to avoid the "fire coral" because of the painful stings it can inflict. Although envenomation by contact generally causes only local symptoms of skin irritation and burning followed by erythema and urticaria over 1–2 weeks, Moats (1992) has reported systemic symptoms of generalised malaise, fever and significant burning pain. Sagi *et al.* (1987) described a case of deep, full skin burns from *M. dichotoma*.

Extracts of whole colonies of *M. alcicornis* and of *M. tenera* contain neurotoxins causing convulsions, respiratory distress and rapid death in mice (Mariscal, 1974). Isolated nematocyst venoms are lethal to mice and display variable haemolytic, vasopermeable and dermonecrotic properties (Radwan, 2002). Nematocyst venoms purified by gel filtration chromatography possess prominent proteins of molecular weights 35 and 31 kDa and their fraction could be inactivated using known anti-haemolytic agents (Radwan, 2002). Diphenylamine was considered the toxic agent in tissue extracts of two species of millepores in the Red Sea by Al-Lihaibi *et al.* (2002). Rojas *et al.* (2002) found that crude tissue extracts of *M. complanata* contained peptides and proteins that stimulated contraction of smooth muscle via an increase in calcium permeability. Wittle and Wheeler (1974) showed that purified toxins from millepores came from their nematocysts and displayed haemolitic and dermonecrotic activities with a rash that lasted several days.

4. DISTRIBUTION, ABUNDANCE AND RECRUITMENT

Millepores occur worldwide in tropical seas and are a frequent component of coral reefs at depths of between 1 and ~40 m (Boschma, 1948). Geographic distributions of the currently recognised species are shown in Table 1. Robust, platelike and rounded massive colonies are generally found on the shallow edges of reefs where there is strong, turbulent water movement. Platy species such as *M. complanata* are often oriented with their flat sides facing the direction of the prevailing waves or currents (Stearn and Riding, 1973; Bak, 1975). Delicate branching forms and thin leafy colonies flourish in deeper water and on more sheltered reefs. Encrusting growths, which may occur at all depths, appear to be the initial stage of growth of every growth form and often cover the dead surface of other corals (Scoffin *et al.*, 1980; Shinn *et al.*, 1981).

In common with scleractinian corals, the distribution of millepores on reefs is frequently distinctly zoned (Lewis, 1960, 1989) in response to physical factors. Within zones, however, the spatial distribution of millepores is unevenly spaced or patchy. An analysis of spatial pattern of millepore colonies of two species in Barbados (*M. complanata* and *M. squarrosa*) indicated clumped or contagious distributions (Lewis, 1996). Explanations for the causes of colony aggregations differed for the two species, however. It was proposed that the patchy distribution of *M. complanata* was due to stolonal growth from the base of colonies and to breakage, displacement and reattachment of colony branches. There was a high survival rate of fragments trapped between existing densely packed colony branches (Lewis,

Table 1 Distribution of *Millepora* species on coral reefs

Species and locality	Growth forms	Depth (m); reef zone	Water movement	References
M. alcicornis Linnaeus, 1758 Caribbean, American seas	Bushy branches, encrusting, lacy flat plates	0–50; fore reef, lagoon patch reefs, surf zone, reef flat	Intense to light water movement	Squires (1958); Newell *et al.* (1959); Hoffmeister and Multer (1968); Garrett *et al.* (1971); Mergner (1972); Goreau and Goreau (1973); Stearn and Riding (1973); Adey *et al.* (1977); Dunne and Brown (1979); Cairns (1982); Ramsaroop (1982); Rützler and Macintyre (1982)
M. exaesa Forskal, 1775 Aldabra, Red Sea, Seychelles	Robust branches or rounded mass	0–10; reef front, reef flats	Turbulent to moderate water movement	Barnes *et al.* (1971); Rosen (1971); Mergner (1977)
M. dichotoma Forskal, 1775 Red Sea, Seychelles	Fans, branches, vertical plates	0–5; reef crest, below algal ridge	Turbulent swell, breaking waves	Taylor (1968); Loya and Slobodkin (1971); Mergner (1971, 1977); Stoddart (1973)
M. squarrosa Lamarck, 1816 Caribbean	Thick plates united in box complex	0–20; reef crest, reef front, reef flat, all zones	Turbulent to heavy wave action, currents	Roos (1971); Roberts (1972); Stearn and Riding (1973); Kuhlmann (1974); Ott (1975); Dunne and Brown (1979)

M. complanata Lamarck, 1816 Caribbean, American seas	Vertical plates, blades	0.5–10; surf zone, reef crest, reef flat, inner spur and groove zone	Strong to heavy wave action, surf, turbulent water movement and swell	Squires (1958); Mergner (1972); Goreau and Goreau (1973); Stearn and Riding (1973); Kuhlmann (1974); Scatterday (1974, 1977); Adey (1975); Geister (1975); Raymont *et al.* (1976); Adey *et al.* (1977); Morelock *et al.* (1977); Cairns (1982); Ramsaroop (1982); Rützler and Macintyre (1982); Dustan and Halas (1987); Lewis (1989)
M. platyphylla Hemperick and Ehrenberg, 1834 Moorea, Red Sea Indo-Pacific	Blades, plates, fans, branches	0–10; surf zone, reef crest, spur and groove zone seaward reef flat	Strong to heavy wave action, surf, swell	Taylor (1968); Barnes *et al.* (1971); Loya and Slobodkin (1971); Mergner (1971); Pichon (1971); Rosen (1971); Stoddart (1973); Maragos (1974a,b); Morton (1974); Done (1982); Galzin and Pointier (1985); Hamelin-Vivien (1985)
M. intricata Milne Edward, 1857 Pacific	Compact masses of slender branches			Boschma (1948)
M. striata Duchassaing and Michelotti, 1864 Caribbean	Loosely connected plates			de Weerdt (1984)
M. braziliensis Verrill, 1868 Brazil	Robust branches	1–5; reef front	Moderate to heavy wave action	Boschma (1961,1962); Laborel (1969a,b)

(Continued)

Table 1 (Continued)

M. nitida Verrill 1868, Brazil	Rounded clumps of short branches	1–5; back reef	Moderate wave action	Laborel (1969a,b)
M. murrayi Quelch, 1884 Indo-Pacific, Taiwan	Thin slender branches, clumps	1–10		Boschma (1948); Soong and Cho (1998)
M. tenera Boschma, 1948 Maldives, Taiwan	Fans, branches and plates	0–10; reef crest, exposed slopes	Medium to strong water movement	Boschma (1950); Davies *et al.* (1971); Maragos and Jokiel (1986); Liu and Chen (1992)
M. latifolia Boschma, 1848 Java Sea	Plates, fused branches			Boschma (1948)
M. foveolata Crossland, 1952 Indo-Pacific, Red Sea	Encrusting small branches			Crossland (1952); Boschma (1966)
M. tuberosa Boschma, 1966 Mauritius	Compact masses, short branches	1–2; encrusting on sea grass	Moderate water movement	Boschma (1966)
M. xishaensis Zou, 1978 China				Zou (1978)
M. boschmai de Weerdt and Glynn, 1991 Pacific Panama	Encrusting base with irregular plates	2–18; fore reef slope, deep outer reef slope	Strong to moderate wave action	de Weerdt and Glynn (1991)

1991a). Because of its more wave-resistant rounded coralla morphology, the distribution of *M. squarrosa* was more likely due to settlement preferences and differential survival of recruits.

Millepores may be abundant locally but over whole reefs usually cover <10% of the substratum. From a broad survey of 302 coral reef sites in the western Atlantic, the relative abundance of millepores compared to scleractinians was 8% on shallow reefs and only 2% on deeper reefs below 5 m (Kramer, 2003). Surveys of benthic cover on reefs at 18 sites around the Caribbean (CARICOMP, 1997) reported percent cover data for millepores of between 0.1 and just >9%. Percent cover was highest on near-continent reefs, reaching 8.0% at Curacao and 9.1% at Margarita Island, Venezuela. In reef communities on the Pacific coast of Panama, *Millepora* spp. comprised 0.9% of the total cover of photosymbiotic corals in the lower forereef slope at Uva Island reef (Glynn and de Weerdt, 1991). Other examples of low abundance (<5% of benthic surface) in deeper water include *M. alcicornis* in Florida (Dustan and Halas, 1987) and *Millepora platyphylla* in Australia (Done, 1982). Liddle and Ohlhorst (1981) reported *M. alcicornis* in Jamaica comprise only 1–2% of total coral cover. Salvat and Richard (1985) reported that 1.6–17% of total coral cover at Takapoto Atoll in the Pacific was composed of millepores.

It should be noted, however, that plan view estimates of millepore cover may seriously underestimate living surface area cover on reefs because of the vertical growth of both branched and bladed colonies. Dahl (1973) and Lewis (1989) recommended that plan view area estimates should be multiplied by factors of between five and seven to include areas of vertical dimension.

Exceptions to low abundances include *M. dichotoma*, which may cover up to 36% of the reef surface in the Red Sea (Loya and Slobodkin, 1971) and *M. complanata* covering up to 48% in Florida (Dustan and Halas, 1987). *Millepora dichotoma* monopolised space on the midregion of reefs in the Red Sea (the *Millepora* zone) where it was regarded as an opportunistic species and a rapid colonizer (Loya, 1976). An encrusting form of *M. platyphylla*, together with the stony coral *Acropora palmerae*, covered up to half the area of the midridge zone on reefs at Eniwetok Atoll in the Pacific (Odum and Odum, 1955). Dense concentrations of *M. alcicornis* occur on some reefs in Barbados (Figure 5A) and were observed by the author on a number of reefs in the British Virgin Islands and Cayman Islands (Figures 2 and 3).

Although millepore coverage is generally less than that of scleractinian corals, Tougas and Porter (2002) found that the former consistently recruited more often and grew faster than their scleractinian counterparts on reefs of the Florida Keys. Recruitment of hydrocorals was nearly eight times that of the scleractinians and was directly related to the relative abundance of hydrocorals in the adult population on different reefs. Millepores were among the dominant

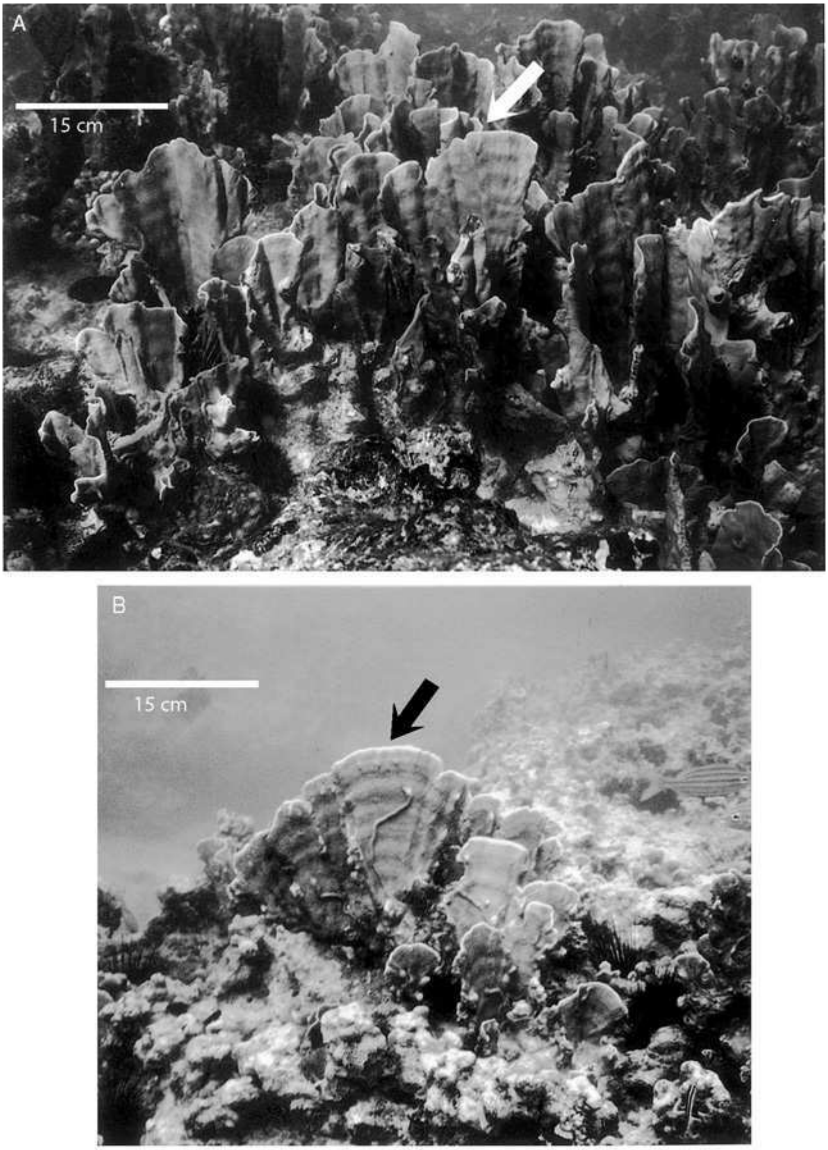

Figure 5 Underwater photographs of banded colonies of *Millepora complanata* at Barbados. (A) Colony with five growth bands. (B) Colony with six growth bands. (From Lewis, 1991b.)

species of corals at shallow sites where recruitment was strong and absent at other sites where recruitment was low. Recruitment was greatest at intermediate depths of 4–6 m on all reefs. As was the case with the Scleractinia, experimental millepore recruitment was higher on down-facing test panels than on vertical or upper surfaces where sedimentation rates were high. Although settlement rates varied from year to year, it appears that millepore recruitment was more successful than for scleractinians on Florida reefs. However, Rogers *et al.* (1984) reported that millepore settlement comprised only 7% of total coral recruitment. Suitable available space for settlement and growth is, of course, required by *Millepora* for successful colonisation of reefs, as for scleractinian corals and other sessile invertebrates.

Boschma (1948) remarked on the fusion of adjacent colonies of millepores (and of Madreporaria) and regarded the phenomenon as a result of competition for space. The basal part of a colony of *Millepora murrayi* was covered by a thin layer of a neighbouring colony of *M. platyphylla* that formed a distinct ridge at its growing edge. Similarly, a platelike growth of *Millepora latifolia* was united with a strongly branched, more delicate colony of *M. intricata* where the two colonies were growing next to each other. In both cases Boschma considered that the weaker of two colonies was treated by the stronger as a foreign object and was enveloped by the dominant colony. He perceived relationships between neighbouring millepore colonies, such as were later found amongst the Scleractinia, and this led to expanded concepts and study of competition, aggression and historecognition phenomena. Boschma (1948) also noted evidence of competition for space between colonies of millepores with corals (*Pocillopora* spp.) and algae (*Laurencia* spp. and *Amphiroa* spp.).

Competition for space among coral reef algae and animals has been reviewed by a number of authors (Karlson, 1999) and takes many forms. Overgrowth of several species of Caribbean gorgonids by millepores has been recorded by Wahle (1980) and of scleractinians by Chornesky (1991). In contrast, millepores have been overgrown in the Red Sea by a sponge, a scleractinian and an alcyonarian (Rinkevich *et al.*, 1993). In encounters between scleractinians and millepores, the former caused tissue destruction and bleaching, although in some cases the hydrocoral effectively destroyed the scleractinian. Millepores were reported to kill three species of scleractinians by overgrowth (Müller *et al.*, 1983), but usually contact with other species caused necrosis, callus formation and finally formation of a contact barrier.

In cases of physical contact between colonies of the same species, millepores, like other cnidarians, possess an allorecognition system that precisely discriminates between "self" and "nonself" tissues. When two colonies of *M. dichotoma* come into tissue contact, one of the genotypes is usually overgrown by the other (Frank and Rinkevich, 2001). This type of response appears to be genetically controlled. Not only the type and direction but also the intensity of the allogenic response are repeatable and indicate an alloimmune memory. In contacts with clone mates, millepore colonies may have an almost unlimited capacity to fuse with each other (Frank and Rinkevich, 1994). Non–clone mates have limited ability to fuse depending on regions of the colonies in contact. There is a gradient of fusion success depending on the number of polyps present. The base or foot region of a corallum has the fewest zooids and hence the greatest incidence of fusion. In xenogeneic encounters, four types of incompatible responses were noted: tissue necrosis, abnormal growth patterns, barriers and overgrowth (Frank and Rinkevich, 1994).

5. AGE AND GROWTH

There are only a few reports of growth rates of millepore colonies. Witman (1988) measured field branch tip vertical growth of 8.0 mm yr in *M. complanata* in Florida. Strömgren (1976) recorded branch length annual increments of 5.4–19.8 mm in specimens held in aquaria at Jamaica. A mean growing edge increment of platy colonies in Curacao was reported as 16.8 mm yr by de Weerdt (1981). Areal growth rates of colonies of *M. dichotoma* using an *in situ* photographic method (Rahav *et al.*, 1991) were estimated at about 130 cm^2 in 1 yr. The mean linear growth rate of marked colonies of *M. complanata* on reefs in Barbados was 22.4 ± 2.7 mm yr (Lewis, 1991b). Prominent dark and light alternating horizontal bands formed by vertical sinusoidal growth observed on vertical plates (Figure 5A and B), correlated with annual growth increments and provided an independent method of aging colonies. Comparison of band widths from colonies on several reefs indicated that growth rates varied from year to year and between reefs. A mean population age of between 5 and 6 yr was estimated from band counts in a sample of 102 undamaged colonies on four reefs, with the largest colonies attaining an age of 10 yr and 25–30 cm in blade height. Mean age estimates of a population may be modified by the frequency of breakage and fragmentation of colonies.

Comparative growth rate data of branching hermatypic corals in the western Atlantic region (Glynn, 1973b) indicate that annual linear growth of millepores noted earlier lies within the range reported for acroporids. Annual increments for *Acropora cervicornis* varied between 4.5 and 26.6 cm and *Porites porites* increased between 3.7 and 4.1 cm per annum. On a geological scale, millepores are slower in terms of reef accretion than acroporid corals (Adey, 1978) presumably because of their lower abundance.

6. FEEDING AND NUTRITION

Millepores are reported to be voracious plankton feeders (Abe, 1938; de Kruijf, 1975; Lewis, 1992a). Feeding behaviour and responses to chemical stimuli of zooids of *M. alcicornis* and *M. complanata* were found to be similar to those of other hydrozoans (de Kruijf, 1975). Spontaneous behaviour of distended millepore gastrozooids and dactylozooids consists of both slow and fast swaying and retraction or contraction in what appears to be search behaviour. Retraction of zooids is a graded movement, depending on stimulus strength and nutritional status. Upon presentation of food, gastrozooids react by wide mouth opening, random swaying and closing of the mouth when prey touches the oral disk. Mouth opening can also be elicited by mechanical and electrical stimulation. Contact of prey by dactylozooids may involve entrapment by nematocysts or rejection and subsequent ingestion by gastrozooids upon random touching. However, de Kruijf (1975) did not find any coordinated movement between dactylozooids and gastrozooids for either search or feeding behaviour (i.e., no deliberate passing of food between zooids). Search behaviour by dactylozooids likely serves a defensive function.

M. complanata responded positively to the presence of crushed and live brine shrimp with vigorous feeding responses (de Kruijf and de Kruijf, 1980). Weak responses were elicited by 2 of 22 amino acids tested, L-asparagine and L-leucine, and by reduced glutathione. Several protein substances such as bovine albumen also elicited strong feeding responses. It was proposed that the hydrocoral has an unspecified receptor for proteins of rather high molecular weight.

Spontaneous electrical activity over the surface of the coenosteum of *M. complanata* has been recorded by means of suction electrodes placed on gastrozooids and dactylozooids (de Kruijf, 1976). Contraction of both types of polyps was accompanied by bursts of electrical pulses of short duration (20–50 ms duration). Expansion of gastrozooids is accompanied by electrical pulses of longer duration. Coordination between polyps appears to be restricted to contractions. Large numbers of zooids can retract at once, but the entire colony does not retract simultaneously. There was evidence that there are at least two strongly linked conducting systems in a colony, a dactylozooid and a gastrozooid system.

Copepods were the chief prey items (63% of diet) of *M. complanata* (Lewis, 1992a) and field zooplankton catch rates were reported as a mean of 7.1 ± 4.1 prey items cm^{-2} colony surface d^{-1}. Rates of digestion of food by *M. complanata* indicated 36% completed in 6 h and 91% in 24 h. These are substantially slower than rates reported for octocorals, which digested zooplankton in 4–6 h (Sebens and Koehl, 1984), and scleractinian coral rates, which varied between 3 and 13 h (Yonge and Nicholls, 1931a; Porter, 1978). The slow digestion by *M. complanata* may be partly due to the small size of the zooids (0.2–0.3 mm oral disk diameter), which would be expected to contain relatively less digestive tissue than the larger polyps of scleractinians. The large prey size (1–2 mm for the copepod *Oithona* spp.) relative to the small zooids would also be expected to slow ingestion and digestion. The daily food consumption of *M. complanata* can be estimated from the mean daily catch rate and average adult copepod dry weights as 7.10 prey $\text{cm}^{-2}\ \text{d}^{-1} \times$ mean adult copepod dry weight of 20.60 $\mu\text{g} = 0.15$ mg dry weight or 0.59 J $\text{cm}^{-2}\ \text{d}^{-1}$ (Lewis, 1992a). This rate is higher than the values for scleractinian corals (Johannes and Tepley, 1974; Porter, 1974). Thus, the daily food consumption of millepores may be higher than it is for scleractinians. It is worth noting that production of mucus by the epithelium of millepores is low (de Kruijf, 1976) (an observation also recorded by Darwin, 1839), and thus, mucus suspension feeding, which is common in scleractinian corals (Lewis and Price, 1975), probably does not occur in hydrocorals.

Like stony corals, millepores are inhabited by symbiotic dinoflagellates, called *zooxanthellae.* Published estimates of the densities of zooxanthellae in millepores are generally lower than estimates for scleractinian corals (Stimson *et al.*, 2002). The symbiotic dinoflagellate *Gloeodinium viscum* was reported from *M. dichotoma* (Banaszak *et al.*, 1993). Autotrophic nutrition in millepores might be expected to be similar to the strategies of scleractinian corals in that carbon, photosynthetically produced by the zooxanthellae, is translocated to the hydrocoral host. Primary production by the zooxanthellae and their contribution to the coral host have been investigated by a number of authors, beginning with the first experiments of Yonge and Nicholls (1932) on the Great Barrier Reef of Australia. In most cases it was found that rates of oxygen production by the zooxanthellae exceeded the rates of consumption by the host, signifying a net contribution to the coral (McCloskey *et al.*, 1978). Once measured, oxygen fluxes were converted to carbon equivalents by standard conventions, thus facilitating the estimation of a total energy budget.

Schonwald *et al.* (1997) were able to construct a diel carbon budget for *M. dichotoma* based on a combination of oxygen electrode and radiotracer methodologies. They found that just >70% of the carbon fixed photosynthetically by the zooxanthellae was translocated to the animal host, but that photosynthesis alone could not satisfy the carbon demands (respiration, growth and excretion) needed by the coral. It was concluded that the deficit must have been obtained either heterotrophically by the capture of zooplankton or by digestion of the zooxanthellae, although no conclusive evidence for the latter exists for any cnidarian. Thus, as with the scleractinian corals, autotrophic energy sources may fall short of total energy requirements (Porter, 1985; Szmant, 1991). The millepore–zooxanthellae association obtains its carbon from a variety of sources, and as is generally held for reef corals, success is based on the mutualistic relationship of the association but with strong evidence for the importance of heterotrophic nutrition.

Oxygen production by endolithic algae, which may heavily infest millepore skeletons, was reported by Bellamy and Risk (1982). Gas bubbling up from broken branches of several species of millepores suggested that substantial volumes of gas may be trapped in the porous skeletons. Volumes of gas were low in the early morning and increased in the late afternoon, suggesting photosynthetic oxygen production during the day and consumption by respiration at night. Odum and Odum (1955) estimated the standing crop of filamentous algae in millepores and found that filaments comprised a significant proportion of the dry weight of total algae including zooxanthellae in the skeletons of *M. platyphylla* and *M. murrayi.* Standing crops of algae in millepores were of similar magnitude as estimates from scleractinian corals. Oxygen production by endoliths may, thus, influence estimates of whole reef productivity.

7. REPRODUCTION

Both asexual and sexual modes of reproduction occur in millepores. Asexual reproduction comprises the modes by which the hydroid stage colonies increase in size and new zooids are formed. This is accomplished by sympodial growth, the production of new skeleton and soft tissue along a growing edge or branch tip and by the reattachment, regeneration and repair of damaged or broken colony fragments (Lewis, 1991a; Edmunds, 1999). Simple encrustations expand by stolonal growth.

The quantitative importance of fragmentation as a method of asexual reproduction in *M. alcicornis* has been considered as a consequence of breakage of colonies during hurricanes and other disturbances. Following a hurricane in the U.S. Virgin Islands in 1988, 79% of all branches of *M. alcicornis* were broken off (Edmunds, 1999). Of these, 4% of broken branches were found reattached to the rock substratum and 64% of fragments landing on millepore substratum fused to the underlying tissue. Encrusting colony bases on vertical surfaces were less susceptible to storm damage than colonies on horizontal substrata. In Barbados, there was a high reattachment rate (35%) of broken fragments of *M. complanata* following storms. Thus, broken branches appear to act as effective asexual propagules, as was also the case in the stony corals (Tunnicliffe, 1981). Regeneration of damaged colonies may also be an important form of asexual reproduction. Storm-damaged millepores in the Caribbean recovered rapidly (Stoddart, 1974), as did *M. dichotoma* damaged by low tides in the Red Sea (Fishelson, 1973a).

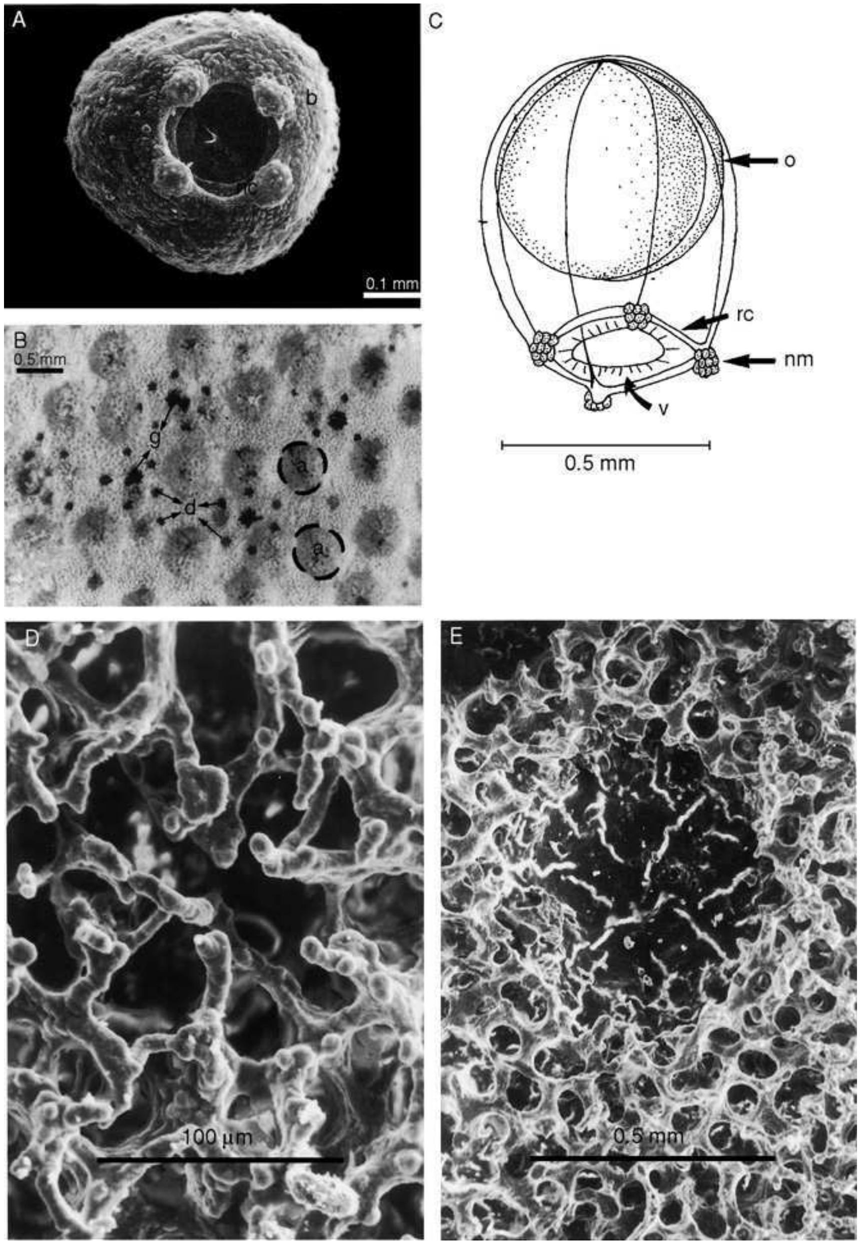

Figure 6 Ampullae and medusae of *Millepora*. (A) SEM photograph of oral view of medusa *Millepora platyphylla*. b: bell, nc: nematocyst cluster. (B) Surface of colony of *M. platyphylla*. a: ampullae, g: gastropore, d: dactylopore. (C) Medusa of

Sexual reproduction in millepores is by means of a well-developed sessile polypoid generation and the budding off of planktonic medusae. The medusae of millepores were first described by Hickson (1891, 1900) and the earliest description of the ampullae (the receptacles bearing the medusae) appears to have been that of Quelch (1884). Other descriptions and illustrations of medusae (Figure 6A and C) and ampullae (Figure 6B, D and E), as well as reports on spawning and other reproductive activity, have been provided by de Weerdt (1984), Lewis (1991c) and Soong and Cho (1998). The gonophores, the reproductive zooids of the colony, are free, but reduced medusae are budded off from the coenosarc tubules within ampullae in the coenosteum. Medusae disintegrate after shedding sex cells (Soong and Cho, 1998), presumably spend a short time in the plankton (Hyman, 1940) and, thus, have low dispersal ability. Four clusters of nematocysts of the macrobasic mastigophore type surround the opening of the subumbrellar cavity and are scattered over the surface of the swimming bell.

Millepora colonies are gonochoristic and sexual reproduction is seasonal, commencing with the appearance of ampullae and release of medusae in April and May in Taiwan, between April and July in Barbados and from June to March in Curacao. Ampullae first become visible as small white blisters on the surface of colonies. These are cavities with flat or slightly concave surfaces covered with a dense network of trabeculae, which contain the developing medusae. As the medusae become larger, the covering trabeculae begin to disintegrate. Just before the release of the medusae, the ampullae appear as swollen rounded bodies partly covered by remnants of the trabeculae (Figure 6D). Following liberation of medusae, only an empty cavity remains (Figure 6E), which subsequently becomes filled with regenerated colony skeleton.

Medusae escape from open ampullae by means of pulsations of the bell and swim for a brief time (Soong and Cho, 1998) during which release of the sexual products is achieved. Three to five eggs are released by pulsations of the bell before the female medusa sinks to the bottom. Male medusae have a single sperm sac, attached to the manubrium, which releases sperm to the subumbrellar cavity and thence into the water. Male medusae may remain actively pulsating for 6–12 h after sperm discharge.

Synchronisation of medusa release occurred between colonies, but there was no evidence of correlation with lunar cycles in Taiwan (Soong and Cho, 1998). Medusa release began before dark and continued for several hours. Colonies

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Millepora complanata. o: ovum, nm: nematocyst cluster, rc: ring canal, v: velum. (D) Ampulla with loose covering of radiating trabeculae and central pore. E: empty ampulla after release of medusa. (A and B: From Soong and Cho, 1998. C, D, and E: From Lewis, 1991c.)

began releasing male medusae before female medusae. Spawning dates of three species were separated, thus preventing possible hybridisation proposed in some stony corals (Harrison *et al.*, 1984). Swimming behaviour in medusae suggested a negative geotaxis resulting in aggregation at the water surface.

The diameters of medusae vary between 0.5 and 1.0 mm. Eggs average between 0.30 and 0.35 mm in diameter. There does not appear to exist a description of a planula of millepores, although the planulae of the related stylasterids are well known (Fritchman, 1974). Fertilisation of eggs of millepores has been achieved in the laboratory but embryos only lived 24 h (Soong and Cho, 1998).

8. EFFECTS OF NATURAL AND ANTHROPOGENIC DISTURBANCES

There is a strong perception amongst coral reef biologists of a worldwide degradation and decline of reefs and related ecosystems over the past several decades (Grigg and Dollar, 1990; Smith and Buddemeier, 1992; Wilkinson, 1993; Brown, 1997a) caused by increases in natural and anthropogenic environmental disturbances (Buddemeier and Smith, 1999; Done, 1999; Karlson, 1999; Hughes *et al.*, 2003). Symptoms of reef decline may include skeleton damage, loss of live coral cover, changes in community composition with decrease of species diversity, reduction in reproductive output and recruitment, disease and death (Connell, 1997; Done, 1999; Wilkinson, 1999).

Insofar as millepores share common traits with scleractinian corals (carbonate skeleton, zooxanthellae, autotrophic and heterotrophic nutrition), they might be expected to respond in a similar manner to at least some of the environmental stresses affecting reefs. Although the evidence is not abundant and is often qualitative, from all accounts the physiological and ecological responses of *Millepora* are similar to those of the Scleractinia over a wide range of disturbances, large and small. An early report, however, noted that some populations of millepores exposed to unfavourable conditions survived longer than other corals (Crossland, 1927). The most frequent disturbances known to have acute effects or cause significant declines in millepore cover and abundance are tropical storms, bleaching episodes and pollution.

8.1. Storms and hurricanes

Mechanical destruction during tropical storms was regarded by Stoddart (1969) as a major cause of catastrophic coral mortality on reefs. Obviously, the degree of damage depended on storm intensity, duration and frequency and the extent to which reefs are exposed or protected.

Millepores and scleractinian corals respond similarly to storms and hurricanes. In cases of extreme physical disturbances such as hurricanes, Woodley *et al.* (1981) reported that in Jamaica, whole millepore colonies were sheared off at their attachment bases, as were other corals. Mass expulsion of zooxanthellae from millepores was also observed following hurricanes, but it was noted that bleached corals still had functioning nematocysts (Goreau, 1964). Tropical cyclones in French Polynesia devastated most reef corals and caused loss and partial destruction of *M. platyphylla* down to depths of 20 m (Laboute, 1985). Three major storms within a period of 27 mo (1992–1994) in Florida greatly reduced the cover of millepores and branching scleractinian corals (Lirman and Fong, 1997). Stoddart (1974) reported severe damage to millepores and other corals from hurricanes on Belize reefs but noted that extensive new growth occurred over a 2-yr posthurricane period and that platy forms of millepores were more resilient than branching species. Wave-resistant morphologies of the bladed *M. complanata* and massive *M. squarrosa* fared better than the branching *M. alcicornis.* Less severe effects were reported elsewhere. In the U.S. Virgin Islands Rogers *et al.* (1983) found no significant effect on areal cover by millepores, although severe damage occurred to the branching coral *Acropora palmata*. In Florida, Dustan (1985) reported that storms contributed to a decrease in mean colony size in *M. alcicornis* and *M. complanata*. Mah and Stearn (1986) found that although there was a decrease in total coral cover on reefs in Barbados after a hurricane, there was no apparent decrease in prehurricane and posthurricane cover of *Millepora*. Witman (1992) reported that *M. alcicornis,* which dominated shallow exposed sites on reefs in the Virgin Islands, displayed strong resistance to damage from an extreme hurricane. Heavily calcified colony bases rapidly regenerated and broken fragments reattached to the substratum. Indeed, such fragmentation may have a selective advantage because of the high survival rate of fragments. Large colonies in a population are likely to be at greatest risk of breakage (Lewis, 1991a).

8.2. Bleaching

Bleaching of reef corals, the whitening of colonies due to the loss of their symbiotic zooxanthellae and photosynthetic pigments, was first described by Yonge and Nicholls (1931b). Although incidental bleaching of coral colonies was apparently observed as early as 1870, some 60 major bleaching events occurred between 1979 and 1990 in many coral reef regions. Many more events were reported in the 1990s and mass bleaching events around the world are generally regarded as a serious threat to coral reefs everywhere

(Brown, 1997b; Hoegh-Guldberg, 1999; Glynn *et al.*, 2001; Coles and Brown, 2003). Coral bleaching may be caused by a variety of stressors but is most frequently attributed to increases in seawater temperatures associated with El Niño-Southern Oscillation (ENSO) warming events (Glynn, 1984).

Bleaching of milleporids occurred in 1997–1998 during a worldwide mass bleaching event that affected the entire Caribbean (Williams and Bunkley-Williams, 1990). Widespread bleaching and mortality of milleporids occurred in Belize, the Cayman Islands, Cuba, Mexico and Puerto Rico, and there was minor damage in Columbia, Florida and the Virgin Islands. In Venezuela 50–60% of *Millepora* colonies bleached: Colonies of *M. alcicornis* totally bleached, whereas *M. complanata* only partially bleached. High percentages of *M. alcicornis* died during the same events in Columbia. Bleaching occurred in the same year in Taiwan and the Maldives where *M. platyphylla* was severely damaged. Bleaching of corals in Panama was first observed in 1983 (Lasker *et al.*, 1984). *M. alcicornis* and *M. complanata* were the first species in which massive bleaching was observed; bleaching began at the tips of branches and spread down to the base. All colonies recovered within 5 mo and there were no signs of prior bleaching (Gleason, 1993). Glynn (1993) reported that millepores were often the first corals to bleach on reefs in the Caribbean and Indo-Pacific regions, and they suffered local extinctions from bleaching in the eastern Pacific (Glynn and de Weerdt, 1991). Extensive coral bleaching and mortality was reported during 1982/83 and 1997/98 ENSO events (Glynn *et al.*, 2001). Although scleractinian coral species responses varied between localities, tissue death was especially high in *Millepora* spp. *M. intricata* suffered 100% mortality in shallow water (1–10 m) in Panama and *M. platyphylla* was eliminated in deep water (12–18 m). No living colonies of *Millepora boschmai* were found after the 1997/98 event and it has been suggested that the species may now be locally extinct (Glynn and de Weerdt, 1991). On the other hand, the continued growth of millepores that survived a 1982 bleaching event on the Great Barrier Reef quickly increased coral cover (Fisk and Done, 1985). Mass bleaching and discolouration of *M. complanata* was observed in Florida, caused by thermal stress, although the colonies still had functioning nematocysts and regained colour after 6–8 wk (Jaap, 1979). *Millepora alcicornis* was the most severely affected of several species suffering loss of zooxanthellae on a Bermuda reef, following an incident of unusually high temperature (Cook *et al.*, 1990) but was also the first to recover. Williams and Bunkley-Williams (1990) also noted that millepores in the Caribbean were among the first to recover following short-term bleaching events. Although scleractinian corals were heavily damaged by bleaching in Moorea, French Polynesia, the millepores showed no evidence of bleaching other than occasional mild discolouration (Gleason, 1993).

8.3. Oil pollution

Oil spills are a common anthropogenic pollutant in many remote areas of coral reefs. The effects of oil pollution are varied, ranging from smothering of organisms in direct contact with the oil to decreases in coral cover or reduction of reproductive potential on reefs and little effect where the oil is floating above the substratum. Detailed reports of oil spills on reefs with millepores come from the Red Sea and from Panama. Loya (1975) reported that surface cover of *M. dichotoma* (an important framework builder on reef flats in the Red Sea) was reduced by 16% following an oil spill. Chronic oil spills occurring between 1969 and 1973 reduced the cover of *M. dichotoma* by 90% and the number of colonies by 69% (Loya, 1975) with little sign of recolonisation, thus altering the composition of the coral community. However, Fishelson (1973b) found that *M. dichotoma* was less affected by chronic oil pollution than were scleractinian corals. An oil spill in Panama over shallow water coral patch reefs had little effect on *M. complanata* populations examined ~2 mo later, possibly because the corals were not in direct contact with the oil (Rützler and Sterrer, 1970). Oil inflow onto the adjacent sand beach, however, dramatically reduced meiofauna populations. After a second oil spill in Panama, Jackson *et al.* (1989) reported high mortality of *Millepora* spp. and severe reduction of the population upon contact with the oil. In contrast, Neff and Anderson (1981) exposed *Millepora* sp. to fuel oil and found no impact on polyp retraction, expulsion of zooxanthellae or calcium deposition, whereas four species of scleractinian corals showed signs of stress. In conclusion, although there are few specific references to millepores, it appears that the generally harmful effects of oil spills and chronic oil pollution on scleractinian corals, as outlined by Brown (1996), can be applied to millepores. The same negative effects can also be expected from the detergents used for oil spill "cleanups" (Grigg and Dollar, 1990).

8.4. Eutrophication, sedimentation and miscellaneous damage

Eutrophication from sewage and agricultural runoff, resulting in the deterioration of water quality, has become a serious problem for coral reefs with examples from both the Atlantic and the Pacific (Pastorok and Bilyard, 1985). Reports of damage to reefs generally include millepores with the stony corals. In Barbados, where eutrophication was caused by the combined action of nutrient enrichment, sedimentation and groundwater discharge, percentage cover of both millepores and Scleractinians was lower on highly affected reefs than on less eutrophic reefs (Tomascik and Sander, 1987).

Sedimentation from bottom dredging and coastal runoff is one of the greatest potential causes of coral reef degradation as a result of smothering of reef organisms and reduction of available light for photosynthesis (Rogers, 1990). Millepores are apparently unable to tolerate high levels of suspended sediments (Graus and Macintyre, 1989). Morelock *et al.* (1983) reported smothering of corals (including *M. alcicornis*) by silt and reduction of coral cover in Puerto Rico. Coastal mining and processing activities may also release metal contaminants into reef ecosystems (Johannes, 1975). Anchoring and boat damage have become serious threats to the health of corals on many reefs (Dustan and Halas, 1987). Diver and anchor damage was as apparent on vertical blades of *M. complanata* as it was on the elkhorn coral *Acropora palmata* on reefs in Florida (Dustan and Halas, 1987). Abnormally high temperatures caused by exposure at low tide or excessive heating in shallow-water pools often causes bleaching and mortality of millepores. Loya (1975) reported that shallow reef flats dominated by millepores in the Gulf of Eilat suffered 90% mortality of corals from an exceptionally low tide but subsequently showed strong recovery (Loya, 1976). *M. alcicornis* was extensively bleached following elevated water temperatures on Bermudan reefs but showed significant recovery following the return of normal temperatures (Cook *et al.*, 1990).

8.5. Diseases

The first reports of symptomatic diseases of scleractinian corals, millepores and gorgonians appeared in the 1970s on reefs off Belize, Bermuda and in the Caribbean (Garrett and Ducklow, 1975; Antonius, 1977). These are generally known as "band diseases": black band disease, white band disease and yellow blotch disease. Most band diseases have been associated with microorganisms that contribute to the development of lesions and loss of bands or strips of coral tissue. Black band disease has been documented on millepores (Rützler and Santavy, 1983; Santavy and Peters, 1997) but does not appear to be widespread. *Millepora* was not susceptible to artificial infection of black band disease in a series of aquarium experiments (Antonius, 1981). A form of white band disease or "white plague" was reported on millepores in Florida (Richardson, 1998). Peters (1996) noted that the occurrence of these diseases might be caused by exposure to widespread anthropogenic pollution and habitat degradation, as well as by pathogens and parasites. Incidences of band diseases are generally low on reefs, <2% of all corals (including millepores) were infected in Barbados and Jamaica, but as much as 10% of colonies in Trinidad (Hoetjes *et al.*, 2002).

9. SYMBIONTS AND COMMENSALS

Although the hydrozoan coenosteum with its fiercely stinging zooids does not appear to be an attractive substrate for attachment or settlement of epiphytes or epizooans, a number of sessile organisms are commonly found in association with millepores. Hickson (1891) remarked that "worms, molluscs, barnacles, and others may be seen on every species [of millepore] that is examined." Many of the same epizooans have also been reported living on scleractinian corals. Settlement on a millepore substrate is advantageous to epizooans because they are generally free of sediment and provide protection from predation and grazing. Infaunal forms also abound in millepores but typically gain entry by boring into dead skeleton and living within tunnel systems. Crustaceans and worms appear to be the most common millepore commensals. Brander *et al.* (1971) recorded 11 species of polychaetes and 7 species of crustaceans on millepores on Aldabra Atoll in the Indian Ocean.

9.1. Barnacles

There is a considerable amount of literature dealing with sessile barnacles associated with reef corals (references in Patton, 1976). Three species of coral-inhabiting barnacles are known to occur upon *Millepora* spp.: the pyrgomatine *Savignium milleporae* and two balanines, *Megabalanus stultus* and *Megabalanus ajax* (Ross and Newman, 1973). *Savignium milleporae* occurs in the Indo-Pacific region and has been recorded on nine species of millepores (Soong and Changlai, 1992). Darwin was the first to describe the symbiotic barnacles *Balanus stultus* and *B. ajax* on millepores (Ross, 1999). *M. stultus* occurs in the western Atlantic and has been recorded upon *M. alcicornis* and *M. complanata* (Ross, 1999). *M. ajax* is found in the western Pacific on *M. platyphylla* (Ross, 1999). Barnacles of the subfamily Pyrgomatinae are obligatory epizooans on hydrocorals, living within the host skeleton (Pasternak *et al.*, 2001). *S. milleporae* like other pyrgomatids bores a tube in the coral skeleton and its opercular plates lie flat and even with the coral surface. The base of *M. stultus* lies flush with the surface of the coral and the plates are covered with layers of coral tissue and protrude above the coral surface (Figure 7A).

The nature of the relationship between coral-inhabiting barnacles and their hosts is still uncertain. Lewis (1992b) described the association of *M. stultus* with *M. complanata* in Barbados, West Indies, and found that 9% of the colonies examined were colonised, that there was a mean of 2.58 barnacles per colony and that adult barnacles were clumped or aggregated

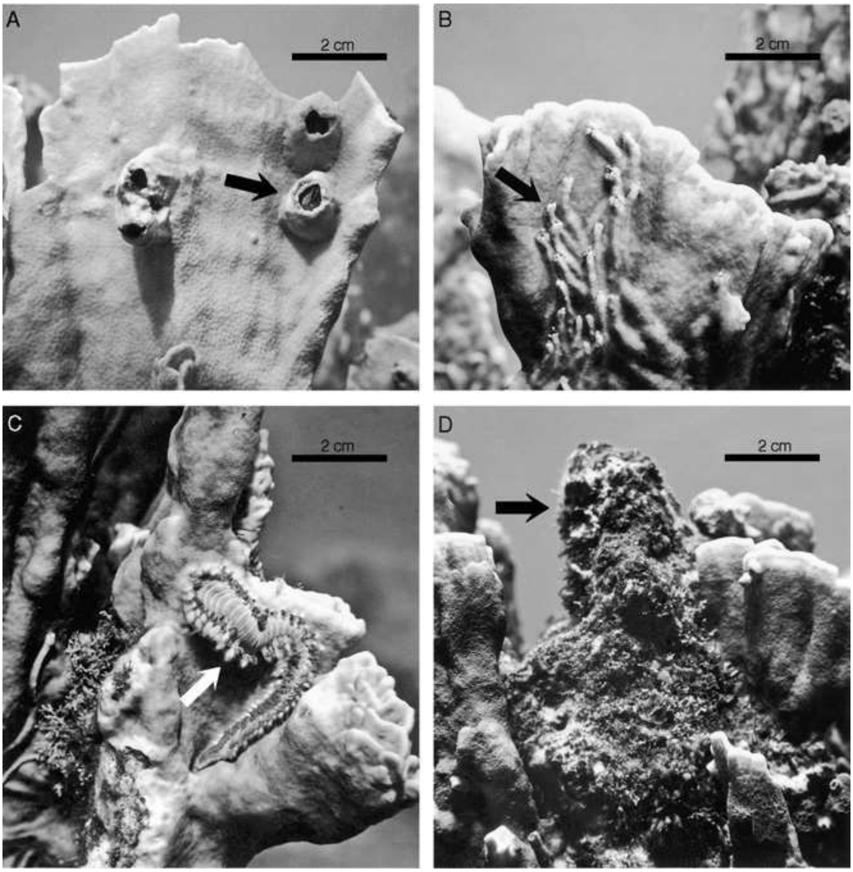

Figure 7 Underwater photographs of epizooans and epiphytes on *Millepora complanata* (arrows). (A) The barnacle *Megabalanus stultus.* (B) The serpulid worm *Spirobranchus polycerus.* (C) The amphinomid polychaete *Hermodice carunculata.* (D) Algae.

on the host branches. A positive correlation between the abundance of millepore colonies on reefs and the frequency of colonies bearing barnacles indicated that barnacle larvae were attracted to reef settlement sites or that postsettlement survival occurred in proportion to density of the host millepore colonies. About 75% of barnacle recruits settled along the distal edge of recently formed branches where density of predatory zooids was least. Juvenile barnacles were subject to smothering by rapidly growing millepore tissue and dead barnacles became overgrown by host skeleton. The millepore substrate provided a refuge habitat for the barnacles, and the latter had no apparent effect upon the host at low densities. However, barnacles at high densities can distort colony growth (Boschma, 1948) and *S. milleporae* can cause skeleton deformation in *M. dichotoma* (Vago *et al.*, 1994).

A number of authors have investigated the possibility of mutual nutritional benefits between millepores and barnacles. Although Cook *et al.* (1991) found no evidence of translocation of photosynthate from host to barnacles, hydrocorals bearing barnacles accumulated significantly more ^{14}C and ^{32}P than those with no barnacles. The hydrocorals were possibly recycling substances excreted by the barnacles, and Achituv and Mizrahi (1996) also suggested that phosphorus and nitrogen excreted by the associated barnacles could be absorbed by the hydrocoral zooxanthellae, thus enhancing photosynthetic activity. Ross and Newman (1973), however, suggested that the sites of intimate contact were more likely to facilitate the barnacle's physiological control of growth of the coral than to provide a route for supplementation of the barnacle nutrition, thus confirming the opinion of Cook *et al.* (1991).

9.2. Other crustacea

9.2.1. Amphipoda

Stenothoe valida Dana is a small (2–4mm) marine amphipod, cosmopolitan in the tropics and often associated with Cnidarians (Barnard, 1970). It is abundant on colonies of *M. complanata* in Barbados and occurs on the other species, *M. alcicornis* and *M. squarrosa* (Lewis, 1992c). Individuals of *Stenothoe* live singly on the living surface of millepores as well as nestling in dead empty shells of barnacles and in other small cavities. In the laboratory, juveniles were active and moved rapidly and unharmed over the host surface when the millepore zooids were retracted. Adults, on the other hand, were seldom observed free on the millepore blade surfaces but were aggregated and confined to empty barnacle shells (Lewis, 1992c). Thus, *Stenothoe* appears to derive protection from predators within a concealed habitat and/or on the surface of millepore colonies. Although there is no obvious benefit to the host colony, it is possible that the crustacean may feed upon detritus landing on the coralla surface and thus help keep it clean.

9.2.2. Tanaidae

Leptochelia savignyi (Kroyer) is a small (2–3mm) tanaid crustacean that is nearly cosmopolitan in the north Atlantic and tropical seas (Holdich and Jones, 1983). It is common in the sublittoral, living in tubes that it constructs in crevices and among seaweeds. In Barbados, *Leptochelia* was found exclusively at the distal ends of burrows excavated by the spionid polychaete *Dipolydora armata* in living and dead branches of *M. complanata* (Lewis, 1998a). Within the spionid bore holes, *Leptochelia* spins a simple or branched tube, about 0.4 mm in diameter and 10 mm in length, composed of fine threads of a silk-like material. Burrows were restricted to areas of dead coral skeleton where the holes were unlikely to be overgrown by living millepore tissue and were out of reach of the host zooids. In the laboratory, individual tanaids emerged from their burrows and underwent short foraging excursions. Thus, millepore colonies provide a refuge for tanaids but do not appear to derive any benefit or suffer harm from the association.

9.2.3. Alpheidae

The snapping shrimp *Alpheus obesomanus* Dana was found in cavities and tunnels in most of the colonies of *M. platyphylla* examined in the Pacific by Kopp (1987). Most of the surfaces of the bored corals consisted of dead skeleton, often covered with coralline or filamentous algae. Some of the tunnel ports, however, were surrounded by living millepore tissue. It seems likely that shrimp settle on dead skeleton or among fouling organisms and endoliths such as vermetid molluscs, which are common in bored colonies. The association of shrimp tunnels with empty vermetid tubes suggests that the shrimp invades the millepore through the vermetid tube and that the association may be just a chance occurrence. Alpheids are also commonly found in tubes in scleractinian corals (Kopp, 1987) and may contribute to weakening of skeletons by initiating or enlarging tunnels.

9.3. Polychaetes

9.3.1. Serpulidae

Two serpulid worms of the genus *Spirobranchus* are obligate associates of living coral (Hunte *et al.*, 1990). *Spirobranchus giganteus* and *Spirobranchus polycerus* have been reported on living *Millepora* (Hunte *et al.*, 1990; Marsden, 1992). Whereas *S. giganteus* occurs on some nine species of scleractinian corals, *S. polycerus* is most common on *M. complanata* in Barbados and occurs only occasionally on scleractinian coral (Marsden, 1992). These worms do not bore into or excavate holes in millepores but build their tubes on the surface of the corals (Figure 7B). As the tubes increase in length (up to 10 cm on large branches), they become covered with living host skeleton and soft tissue except for the openings. Tubes of *Spirobranchus* may occur singly on blades of *Millepora* or in groups and clusters.

Millepora blades provide a substratum for *Spirobranchus* and protection from predators. Marsden (1993) has suggested that the reproductive biology of *S. polycerus* is constrained by adaption to a commensal habitat characterised by discontinuous distribution of the host and a short life span of the worm. On the other hand, suspension feeding by the coral may be reduced by the spread of the branchial crown in the opening of the worm tube where densities of zooids are low. Skeleton deformation may also result from growth of worm tubes when their density is high.

9.3.2. Spionidae

Dipolydora armata (Langerhans) is a small (4–5 mm) spionid polychaete found burrowing in *M. complanata* on coral reefs in Barbados (Blake, 1996; Lewis, 1998b). It excavates networks of interconnecting burrows in the skeleton of the coral. Burrow openings on the living surface of the millepores develop distinctive, often long calcareous erect spines caused by combined growth of the worm tube and host tissue (Figure 8A). Examination of the functional relationships between the worm and its host (Lewis, 1998b) suggests that intensive burrowing, especially at the base of the branches, might contribute to weakening and breakage of the coral (Figure 8B). Millepore zooids were absent in the vicinity of the tube openings, so the potential feeding surface of the coral was reduced in heavily colonised branches.

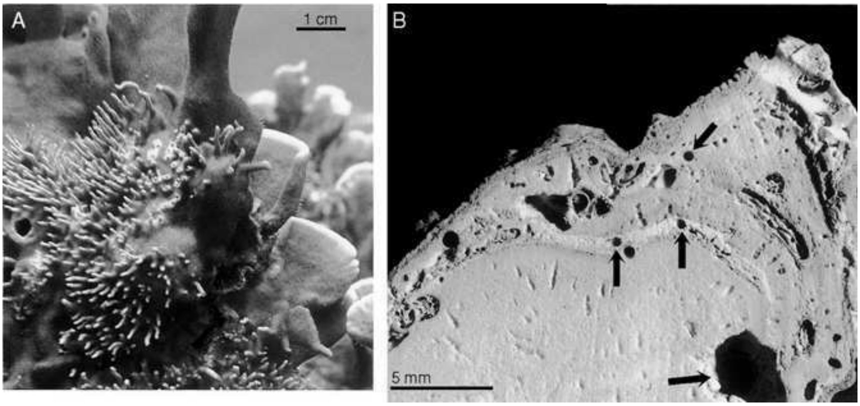

Figure 8 The spionid polychaete *Dipolydora armata* on *Millepora complanata.* (A) Cluster of worms tubes on corallum. (B) Cross section of branch showing cavities bored by worms. Large cavity at bottom right resulted from burrowing by vermetid mollusc or snapping shrimp. (From Lewis, 1998b.)

While it would be expected that *Dipolydora* would derive protection from grazers such as fish, there are also a number of features of the reproductive and larval development that appear to be of adaptive significance and favour its association with *Millepora*. The presence of larvae living free in the burrows, the possession of spermatophores, a protracted breeding cycle and complete metamorphosis and larval development within the burrow would favour colonisation and recruitment to the host coral.

10. PREDATORS, GRAZERS AND FOULING ORGANISMS

The variety of predators and grazers that feed upon living corals has been reviewed by Carpenter (1996), and there are some quantitative data on the importance of these consumers. Invertebrate and vertebrate predators and grazers on corals have generally been considered with respect to the damage they cause on reefs. It appears that millepores are less susceptible to predation and grazing than the hermatypic corals and that preference for the former is limited. For example, *Millepora* is generally avoided by the ‘‘crown of thorns’’ starfish *Acanthaster planci* (Endean, 1973; Glynn, 1973a, 1990), although ~9% of a *Millepora* population was consumed during a starfish outbreak in Samoa in 1979 (Glynn, 1990).

10.1. Polychaetes

The Amphinomidae are a family of worms common in warm tropical waters. Their ecological habits are varied. Two species, *Eurythoe complanata* (Pallas) and *Hermodice carunculata* (Pallas), have been reported living on coral reefs in Barbados (Marsden, 1960). *Eurythoe* is generally cryptic but has been observed in crevices on millepore colonies. The errant amphinomid worm *Hermodice* ranges in length from 4 to 18 cm in the Caribbean and is a common predator on coral reefs where it grazes on millepores (Figure 7C), as well as upon zooanthids, anemones and scleractinian corals. *Hermodice* lives openly on the reef surface during the day with a diurnal foraging cycle and a peak of activity in the late afternoon. It may also be found secreted in crevices (Lewis and Crooks, 1996). *Hermodice* feeds by eversion of a muscular pharynx, which sucks off coral tissue and leaves a white scar behind (Marsden, 1962). Feeding scars on millepores and scleractinians may develop into lesions that fail to regenerate new tissue and provide a base for attachment of fouling organisms and access for burrowing symbionts. Predation by *Hermodice* caused permanent damage to millepores dominating a fringing reef in the U.S. Virgin Islands (Witman, 1988) but was not regarded as a serious coral predator in Barbados (Ott and Lewis, 1972). However, excessive damage may affect the general health of the corals or alter the composition of the reef communities (Witman, 1988).

10.2. Molluscs

In the central Pacific and western Australia, the corallivorous snail *Drupella* develops population densities that result in serious loss of their coral prey. McClanahan (1997) reported a 50% difference in *Millepora* cover between sheltered and wave-exposed reefs was possibly due to outbreaks of *Drupella*. Another coral-feeding gastropod *Coralliophila abbreviata* also feeds occasionally on *M. complanata* in Barbados (Lewis, 1992b).

10.3. Fishes

The predominant fish corallivores are the butterfly fishes (Chaetodontidae). These are known to graze on coral polyps, although there are only a few species that feed entirely on corals (Hixon, 1991). Millepores generally appear to escape such predation, possibly because of their powerful nematocysts or simply because of the small size of the polyps. However, juveniles of the common Caribbean damselfish (*Microspathodon chrysurus*) frequently feed on *Millepora* in Florida (Ciardelli, 1967) and both juveniles and adults regularly consume *M. complanata* in Panama (Glynn, 1973b). Other fish that regularly consume corals include the filefish (Balistidae) and parrotfish (Scaridae), which scrape or break off pieces of colonies with their beaklike mouths. Fragments of *M. alcicornis* were found in the stomachs of the filefish *Alutera scripta* and *Cantherines macrocerus* (Randall, 1967). Stoddart (1969) suggested that a number of scarids damaged colony surfaces while seeking other food associated with millepores.

10.4. Fouling organisms

Numerous taxa of fouling organisms have been observed on bare skeletons of scleractinian corals and millepores wherever settlement and colonisation is favoured (review by Patton, 1976). Foulers may include epiphytes, hydrozoans, ascidians and sponges. Dead millepore skeleton thus provides a basis for a complex fouling community.

The settlement and growth of algae on damaged or broken branches of millepores (Figure 7D) is widespread. Lesions or scars that result from feeding by *Hermodice* initiate a sequence of rapid algal colonisation

(Witman, 1988). On reefs in the U.S. Virgin Islands, 97% of the bare space on the hydrocoral that resulted from worm predation was colonised within 1 mo by crustose coralline algae, green microalgae and red filamentous algae. Millepore branch tips were primarily colonised by the coralline alga *Neogonolithon* sp., and other bare areas became heavily pigmented with pale green microalgae within 17 d. Other algal species commonly colonising bare space included the blue-green alga *Calothrix crustacea*, a complex of red filamentous algae including *Centroceras clavulatum, Herposiphonia* sp., *Polysiphonia havaneusis*, and *Ceramium byssoideum*, as well as the brown alga *Lobophora variegata*. Several algal species commonly found on reef rock subtrata such as *Dictyosphaeria, Padina, Dictyota* and *Laurencia* were occasional millepore colonisers.

It is apparent, therefore, that numerous algal species are able to colonise damaged millepore skeletal surfaces and may limit branch growth (Witman, 1988). Heavy colonisation may completely cover colonies, allow attachment of other fouling organisms or entry of boring organisms and thus weaken or destroy the hydrocoral skeleton.

11. CONCLUSIONS

It can readily be concluded that there are many morphological and ecological similarities between the hydrocoral *Millepora* and the stony corals, the Scleractinia. These similarities are at least partly a consequence of the habitat qualities of coral reefs. Both groups consist of upright or encrusting colonies with calcareous skeletons that contribute to the reef bulk structure. Cellular mechanisms of calcification are similar. Like stony corals, millepores occur worldwide in tropical oceans and are distributed or zoned on reefs in response to environmental factors. Nutrition in both groups is derived heterotrophically from zooplankton and autotrophically from the symbiotic zooxanthellae in the coral tissue. Asexual reproduction by budding and regeneration of fragments occurs in both groups. Both show susceptibility to damage from severe storms, to bleaching during excessive sea temperature increase and to various forms of pollution, but there is some evidence of more rapid recovery in millepores. A short colony life and ready regeneration of coralla fragments suggest a superior ability to recover from severe disturbances. Like the stony corals, millepores are associated with and attract a variety of symbionts and commensals and thus help to maintain diversity on coral reefs. They are also affected by a number of potentially damaging predators, grazers and fouling organisms. Thus, the consequences of unfavourable environmental changes and the pattern of global deterioration or recovery on reefs are likely to be the same for *Millepora* as for the Scleractinia.

There are, however, also a number of notable differences between *Millepora* and the Scleractinia. There are fewer species of millepores, whereas the stylasterid hydrocorals are relatively species rich. Millepore colonies are generally less abundant on reefs and there are no large long-lived colonies such as the great massive hermatypic corals that often dominate reefs. Millepores differ from scleractinians in possessing two distinct types of polyps: feeding zooids and defensive zooids with powerful nematocysts. Stenotele nematocysts are limited to the class Hydrozoa and macrobasic mastigophores are unique to the millepores. Feeding strategies depend upon the effectiveness of these toxic nematocysts in prey capture, for apparently mucus suspension feeding, common in scleractinian corals, does not occur in millepores. Sexual reproduction in millepores involves alternation of generations and a planktonic medusa with a short pelagic life, in contrast to more variable reproductive modes and the planula larvae of stony corals. Stylasterid hydrocorals are an exception, however, in that they also release planulae. The more conservative reproductive traits of millepores may be a disadvantage limiting speciation. However, how these general differences affect the relative ecological success of millepores compared to the stony corals is not obvious.

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The Functional Value of Caribbean Coral Reef, Seagrass and Mangrove Habitats to Ecosystem Processes

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ADVANCES IN MARINE BIOLOGY VOL 50 0065-2881/06 $35.00

DOI: 10.1016/S0065-2881(05)50002-6

Caribbean coral reef habitats, seagrass beds and mangroves provide important goods and services both individually and through functional linkages. A range of anthropogenic factors are threatening the ecological and economic importance of these habitats and it is vital to understand how ecosystem processes vary across seascapes. A greater understanding of processes will facilitate further insight into the effects of disturbances and assist with assessing management options. Despite the need to study processes across whole seascapes, few spatially explicit ecosystem-scale assessments exist. We review the empirical literature to examine the role of different habitat types for a range of processes. The importance of each of 10 generic habitats to each process is defined as its "functional value" (none, low, medium or high), quantitatively derived from published data wherever possible and summarised in a single figure. This summary represents the first time the importance of habitats across an entire Caribbean seascape has been assessed for a range of processes. Furthermore, we review the susceptibility of each habitat to disturbances to investigate spatial patterns that might affect functional values.

Habitat types are considered at the scale discriminated by remotely-sensed imagery and we envisage that functional values can be combined with habitat maps to provide spatially explicit information on processes across ecosystems. We provide examples of mapping the functional values of habitats for populations of three commercially important species. The resulting data layers were then used to generate seascape-scale assessments of "hot spots" of functional value that might be considered priorities for conservation. We also provide an example of how the literature reviewed here can be used to parameterise a habitat-specific model investigating reef resilience under different scenarios of herbivory. Finally, we use multidimensional scaling to provide a basic analysis of the overall functional roles of different habitats. The resulting ordination suggests that each habitat has a unique suite of functional values and, potentially, a distinct role within the ecosystem.

This review shows that further data are required for many habitat types and processes, particularly forereef and escarpment habitats on reefs and for *seagrass beds and mangroves. Furthermore, many data were collected prior to the regional mass mortality of* Diadema *and* Acropora*, and subsequent changes to benthic communities have, in many cases, altered a habitat's functional value, hindering the use of these data for parameterising maps and models. Similarly, few data exist on how functional values change when environmental parameters, such as water clarity, are altered by natural or anthropogenic influences or the effects of a habitat's spatial context within the seascape. Despite these limitations, sufficient data are available to construct maps and models to better understand tropical marine ecosystem processes and assist more effective mitigation of threats that alter habitats and their functional values.*

1. INTRODUCTION

Caribbean coral reef habitats, seagrass beds and mangrove stands provide many important ecosystem goods and services such as coastal defence, sediment production, primary production, fisheries and the maintenance of high species diversity (Moberg and Folke, 1999). Furthermore, all three systems often occur in close proximity and many physical and ecological processes transcend individual habitats. For example, estuarine mangroves trap riverine sediments (e.g., Ogden, 1997) that might otherwise discharge onto reefs and cause mortality through sedimentation (e.g., Torres *et al.*, 2001). Ecological linkages among habitats include the migration of organisms on either an ontogenetic or a diurnal basis. Many snapper, grunts and parrotfish species, for example, undertake ontogenetic shifts in habitat use from seagrass beds or mangroves to their adult coral reef habitat (McFarland *et al.*, 1985; Lindeman *et al.*, 1998; Cocheret de la Morinière *et al.*, 2002; Mumby *et al.*, 2004a). Abiotic and ecological links frequently underpin key economic resources such as the Western Central Atlantic fishery for lobster (*Panulirus argus*), which was worth an estimated US$500 million in 1998 (Cochrane and Chakalall, 2001). The coastal zone also generates significant revenue from tourism (e.g., US$21 million annually in Bonaire, Birkeland, 1997), much of which is focused on shallow marine habitats.

The economic and ecological importance of tropical marine habitats is threatened by fundamental changes to their ecology, including increases in macroalgal cover and concomitant decreases in coral cover on reefs (e.g., Hughes, 1994; Gardner *et al.*, 2003), reductions in the biomass of fish assemblages (e.g., Roberts, 1995) and species extinctions (e.g., Caribbean monk seal; Leboeuf *et al.*, 1986). Changes to marine ecosystems in the Caribbean have been attributed to a suite of anthropogenic factors, including pollution, coastal development, overfishing, El Niño and introduced pathogens (e.g., Lessios *et al.*, 1984; Tomascik and Sander, 1987; Richardson *et al.*, 1998;

Landsea *et al.*, 1999; Aronson and Precht, 2001; Jackson *et al.*, 2001). Furthermore, the recovery rates of coral populations on reefs in the western Atlantic are lower than in the Indo-Pacific (Connell, 1997). Given the connectivity among tropical marine habitats, their great ecological and economic importance and the suite of threats to their health, it is important to understand how ecosystem processes function across whole seascapes. A better understanding of processes will illuminate the ecological and societal consequences of both natural and anthropogenic disturbances to the ecosystem. Furthermore, greater understanding of processes would enable the effects of potential management options, perhaps aimed at enhancing coral reef resilience, to be mapped, modelled and compared.

Understanding processes at the scale of seascapes is limited by the disparate nature of tropical marine research, with many studies focusing on a single reef zone or habitat. Here, we use the framework of processes described by Hatcher (1997a) to categorise available literature and assess the "functional value" of Caribbean marine habitats. Functional value indicates the importance of a particular habitat to a particular process. For example, we document that a seagrass bed has a higher (more important) functional contribution to primary production than, say, a sand flat. Wherever possible, we use direct measures of a process, but proxies were used where necessary. For example, the density of herbivores and piscivores was used as a proxy for secondary and tertiary production because few data are available to convert biomass to rates of production. This need to integrate static data on states with data on rates reflects the lack of empirical observations for many processes in many habitats. In addition to assigning functional values, we also assess the susceptibility of habitats to impacts from hurricanes, coral bleaching and disease. Because each of these disturbances is habitat specific, this analysis aims to indicate possible changes to the functional value of marine habitats.

Habitats represent an appropriate scale for reviewing functional values and susceptibility because, by definition, they are relatively homogeneous areas that might be expected to have a consistent contribution to a given process or response to a particular impact. Perhaps more importantly, the areal coverage, pattern and context of reef ecosystem habitats can now be mapped over a continuum of spatial scales using airborne and satellite remote sensing (e.g., Green *et al.*, 1996). Access to spatial information on reef ecosystems is expanding rapidly, particularly through the proliferation of high-resolution satellite sensors (Mumby and Edwards, 2002). Costs of imagery acquisition have fallen and image handling is now easily accomplished on a desktop personal computer rather than a workstation. Resulting habitat maps subsequently provide a means of linking communities to their functional values at multiple scales across a seascape, producing spatially-explicit perspectives of ecosystem processes.

We review and summarise a diverse literature to provide a habitat-scale perspective of processes across seascapes and identify research gaps. Beyond providing a resource of literature, we anticipate that this review will foster the construction of large-scale static maps of reef ecosystem processes. Maps of processes, with each habitat recoded to represent its functional value, provide a very different perspective of a tropical marine seascape than a traditional habitat map. We use this concept to provide a putative management application (see Section 6.1) by showing how a computer algorithm, generating "windows" of a size equivalent to a putative marine reserve, highlights "hot spots" of functional value that could be considered priorities for conservation, particularly if combined with equivalent maps of susceptibility to impacts likely to reduce functional values. More sophisticated uses of maps of reef ecosystem functional values might include translating a single habitat map into several overlapping layers, each pertaining to a different process, and multiple layers could then be invoked to address particular ecological and management questions. For example, layers representing calcification, bioerosion and sediment production and settlement could be linked with bathymetry to model reef growth under different scenarios of sea-level change. Spatial representations of processes will also facilitate the creation of habitat-scale ecological models, which are gaining momentum worldwide (Atkinson and Grigg, 1984; Preece and Johnson, 1993; McClanahan, 1995; Kleypas *et al.*, 1999b; Langmead and Sheppard, 2004; Wolanski *et al.*, 2004; Wooldridge and Done, 2004; Mumby and Dytham, 2005) and an example of this application is also provided (see Section 6.2).

2. ASSIGNING FUNCTIONAL VALUES TO HABITAT TYPES

The term "habitat" means different things to different people; a sponge taxonomist, for example, may refer to smaller-scale habitats than someone working with remotely-sensed imagery. However, because this chapter aims to provide a framework for generating maps of processes, we focus on the level of habitat resolution achievable from high-resolution optical remote sensing. Remote sensing instruments differ widely in their spectral and spatial configuration, and these differences profoundly affect the types of habitat that can be discriminated (Mumby *et al.*, 2004b). To highlight the general capabilities of remote sensing technologies to discriminate habitats and provide a guide to the spatial scale that we believe will be best suited to putative maps of ecosystem processes, at least in the near future, we present a systematic community and geomorphological classification proposed by Mumby and Harborne (1999) (Tables 1 and 2). The geomorphological label describes the habitat structure, whereas the benthic class indicates the biotic

Table 1 Hierarchical classification scheme, and quantitative characteristics, for the geomorphological zones typically found on Caribbean coral reefs

First tier		Second tier	
Label	Characteristics	Label	Characteristics
Back reef			
Reef crest			
Spur and groove		Low relief spurs and grooves	Spurs <5 m in height
		High relief spurs and grooves	Spurs >5 m in height
Forereef	Reef with <45-degree slope		
Escarpment	Either reef or lagoon with >45-degree slope		
Patch reef		Dense patch reef	Aggregated coral colonies (living or dead) where colonies cover >70% of the benthos
		Diffuse patch reef	Dispersed coral colonies (living or dead) where colonies cover <30% of the benthos
Lagoon floor	Lagoon floor with <45-degree slope	Shallow lagoon floor	Depth <12 m
		Deep lagoon floor	Depth >12 m

Source: Redrawn from classification scheme developed by Mumby and Harborne (1999) with permission from Elsevier.

Table 2 Hierarchical classification scheme and quantitative characteristics for the benthic communities typically found on Caribbean coral reefs

First tier		Second tier	
Label	Characteristics	Label	Characteristics
Coral classes	>1% hard coral cover; relatively high rugosity	Branching corals	*Acropora* spp. visually dominate
		Sheet corals	*Agaricia* spp. visually dominate
		Ribbon and fire corals with green calcified algae	*Agaricia tenuifolia* visually dominant
		Montastraea reef	*Montastraea annularis* visually dominates
Algal dominated	>50% algal cover; 1% hard coral cover	Green algae	
		Fleshy brown algae and sparse gorgonians	$\sim$3 gorgonians m^{-2}
		Lobophora	Monospecific *Lobophora* beds
		Euchema and *Amphiroa*	Rare assemblage dominated by red algae with encrusting sponges
Bare substratum dominated	Dominated by bare substratum; <1% hard coral; low rugosity	Bedrock/rubble and dense gorgonians	>3 gorgonians m^{-2} (usually >8 m^{-2}) and $\sim$30% algal cover
		Bedrock/rubble and sparse gorgonians	$\sim$3 gorgonians m^{-2} and little algal cover
		Rubble and sparse algae	No gorgonians
		Sand with sparse algae	>90% sand
		Mud	
		Bedrock	No gorgonians
Seagrass dominated	>10% seagrass cover; low rugosity	Sparse seagrass	Standing crop 1–10 g m^{-2}; cover <30%
		Medium density seagrass	Standing crop 11–80 g m^{-2}; cover 30–70%
		Dense seagrass	Standing crop >80 g m^{-2}; cover >70%
		Seagrass with distinct coral patches	Seagrass visually dominant, coral cover may reach 3%, gorgonians may be present

Source: Redrawn from classification scheme developed by Mumby and Harborne (1999) with permission from Elsevier.

and abiotic composition of that structure, so each habitat has two descriptors (e.g., "reef crest + branching corals"). Tables 1 and 2 also provide a context for those readers unfamiliar with the components of Caribbean tropical marine ecosystems. Furthermore, the labels used are by no means novel and represent synonyms derived from a huge body of literature devoted to describing and explaining the zonation of Caribbean coral reefs and the tables provide a general summary of reef zonation literature. The classification is not exhaustive and additional terms could be used (e.g., "transitional reefs," in relatively marginal reefs such as those in Florida; Sullivan *et al.*, 1994a). Similarly, there is a strong case for indicating whether stands of *Acropora palmata* are living or dead because populations have declined in much of the region (Sheppard *et al.*, 1995).

Each of 10 generic habitat types, forming a schematic profile of a Caribbean marine ecosystem, is assigned a functional value for each process reviewed (Figure 1). Making such generalisations is fraught with difficulties because of, among other factors, the lack of data for many habitats, methodological differences, lack of specific habitat descriptions in empirical studies, the effects of marine reserves, biogeographical variations within the Caribbean and ecological changes over time (e.g., caused by *Diadema antillarum* mortality, coral bleaching and diseases and overfishing). Therefore, functional values of each habitat are simply placed into one of four semiquantitative categories ("none," "low," "medium" or "high") to reflect the implicit problems. Assigning a functional value to each habitat is achieved using the relevant empirical data reviewed in the text and the rationale for each is made in a concluding paragraph at the end of each section. Wherever possible, such decisions are made using interpretation of quantitative data (e.g., rates of process X in habitat Y greater than the rate in habitat Z). Furthermore, where such data are available and reviewed in the text, they are also included in Figure 1 as a range of reported values for a given habitat. In cases in which the functional value is not clear (usually empirical data for a particular habitat were not found in the literature), a putative functional value is assigned based on circumstantial evidence or the authors' observations.

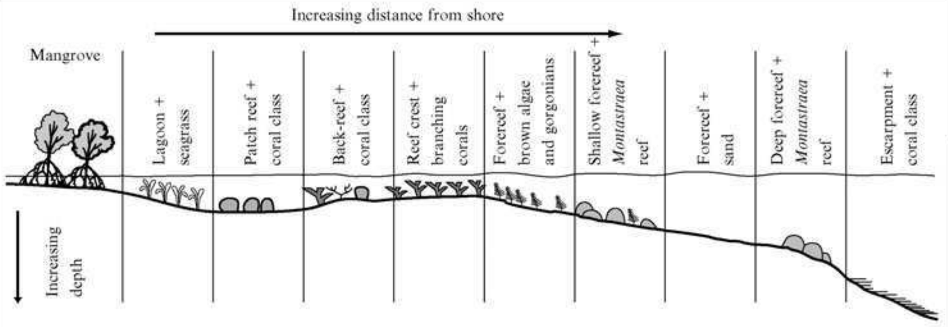
3. FUNCTIONAL VALUES OF TROPICAL MARINE HABITATS

3.1. Modification of wave and current patterns

Waves and currents do not travel passively across a reef and are significantly modified by benthic habitats such that wave refraction and energy dissipation produce wave height and energy gradients (e.g., Sheppard, 1982; Sebens, 1997). Perhaps the most obvious example of energy dissipation across a reef is the creation of lagoons to the leeside of coral reefs that have suitably calm conditions for seagrass beds and mangroves (e.g., Moberg and Rönnbäck, 2003). Hubbard (1997) describes the feedback mechanism between the reef and oceanographic processes as a key feature of true reefs.

A significant proportion of oceanic water does not actually cross reefs but is deflected through passages (Hamner and Wolanski, 1988). Wave heights of water that does cross reefs are reduced, and data from Grand Cayman showed attenuation, from the shelf margin (at ~22 m) to the forereef (at ~8 m) to be 20% (causing wave-induced flow) and tidal current speeds were also reduced by 30% (Roberts *et al.*, 1977). In Puerto Rico, the height of waves generated by both trade and local winds decreased as they travelled across the forereef by 19.5% from a depth of 20 to 10 m and 26% from 20 to 5 m. There was a concomitant reduction in wave energy of 35% from 20 to 10 m and 45% from 20 to 5 m (Lugo-Fernández *et al.*, 1994). Roberts *et al.* (1977) also showed in Grand Cayman that strong rectilinear (reversing) tidal currents dominated the deep shelf margin, but these were transformed into weak directionally variable currents on the shallow terrace margin. Tidal current transformation was caused by frictional effects resulting from strong interactions between the water body and a topographically complex zone of coral spurs and sediment grooves. The change from tidal currents (shelf) to multidirectional flow (terrace) was associated with a 60–70% speed reduction, which further weakens towards the reef crest. The frictional interaction with the spurs and grooves further increased the roughness of the zone and established a feedback loop, so there was a change from current-dominated zones (>18 m) to wave-dominated zones (<18 m) and the crossover point represented a sediment reservoir.

Water movement is altered significantly as it flows across the forereef, but the reef crest also has a vital role in the hydrodynamics of a reef ecosystem. For example, Suhayda and Roberts (1977) studied water movement across the reef crest and showed that wave height and period were typically reduced by ~50% and that this varied with water depth. Roberts *et al.* (1992) reviewed four studies and indicated that wave energy decay between the forereef and lagoon in the Caribbean ranged from 72 to 97%. Lugo-Fernández *et al.* (1994) showed that wave heights decrease by an average of 82% across the reef crest, with a simultaneous 97% energy loss, and this leads to the formation of strong across-reef currents capable of moving coarse sediment. If the crest is at or above the water level, it becomes a "high-pass" filter controlled by wave overtopping (water carried over the crest top). Conversely, if the crest is deeper than 1 m, it functions as a "low-pass" filter controlled by wave dissipating mechanisms. Suhayda and Roberts (1977) highlighted that wave-driven currents flowed onshore continuously over the reef crest and had the greatest velocity at low tide when wave breaking was most intense. The hydrological functioning of many reef



Ecosystem process (Section in text) (Units)	Mangrove	Lagoon + seagrass	Patch reef + coral class	Back-reef + coral class	Reef crest + branching corals	Forereef + brown algae and gorgonians	Shallow forereef + *Montastraea* reef	Forereef + sand	Deep forereef + *Montastraea* reef	Escarpment + coral class
Wave energy dissipation (3.1) (%)			?	?	72–97 (5)	?	45[a] (1)	?	?	?
Nitrogen fixation (3.2.1) (nmol N_2 g afdw^{-1} h^{-1})	?	?[b]	15.3 (1)	?	71.9 (1)	?	47.5 (1)	?	?	?
Gross community primary productivity (3.3.2) (g O_2 m^{-2} d^{-1})	?	2.9–3.2 (1)	5.4 (1)	62.0 (1)	15.7–44.0 (4)	?	5.4 (1)	<1.8 (1)	?	?
Density of *Sparisoma viride* (3.4.2) (Fish 100 m^{-2})	0.0–0.7 (3)	0.0–2.6 (6)	1.0–16.7 (4)	0.8–35.0 (4)	0.6–21.0 (6)	0.3–1.8 (3)	1.1–9.4 (9)	0.0 (1)	0.3–2.6 (7)	0–0.6 (2)
Density of Acanthuridae (3.4.3) (Fish 100 m^{-2})	0.4–1.7 (3)	0.1–1.4 (4)	11.7–65.3 (5)	18.0–97.5 (4)	9.8–51.4 (7)	?	2.0–19.3 (16)	0.0 (1)	0.5–4.5 (5)	1.0 (1)
Density of *Stegastes planifrons* (3.4.4) (Fish 100 m^{-2})	0.0–0.1 (4)	0.0–0.01 (4)	0.0–800.0 (4)	0.0–375.0 (3)	0.0 (1)	?	0.0–47.0 (5)	?	3.3–28.8 (4)	?
Density of *Diadema* (<1983) (3.4.5) (Individuals m^{-2})	?	0.0–2.8 (4)	6.7–72.8 (2)	0.1–3.9 (4)	2.4–25.8 (5)	0.5–4.5 (1)	3.5–18.0 (6)	0.0 (1)	0.1–1.7 (5)	?
Density of *Diadema* (>1983) (3.4.5) (Individuals m^{-2})[c]	<1	<1	<1	<1	<1	<1	<1	0	<1	0

Figure 1 (Continued)

Density of planktivores (3.5.1) (Fish 100 m^{-2})	0.0 (4)	0.0 (4)	?	?	?	?	18.3–128.9 (3)	?	90.1–138.3 (2)	?
Density of *Haemulon flavolineatum* (3.5.2) (Fish 100 m^{-2})	6.0–99.8 (5)	0.5–32.1 (6)	4.5–51.0 (2)	110–130 (1)	21.0 (1)	?	2.4–5.8 (4)	?	1.2–2.2 (3)	0.3 (1)
Density of *Epinephelus striatus* (3.5.3) (Fish 100 m^{-2})	0.0–212.0 (2)	0.0–? (2)	0.1–4.0 (2)	?	?	0.1–0.3 (1)	0.1–0.4 (1)	?	?	0.04 (1)
Density of *Panulirus argus* (3.6.1) (Individuals ha^{-1})	247.0–642.0 (1)	5.5–263.0 (4)	32.1–900.0 (3)	?	?	2.0–10.0 (2)	6.0–15.2 (2)	0.0 (1)	?	38.3 (1)
Density of *Strombus gigas* (3.6.2) (Individuals ha^{-1})	?	0–20000 (7)	11.7–15.8 (1)	0.0–111.0 (2)	?	24.0–31.0 (1)	?	2.0–310[d] (4)	?	?
Gross community calcification (3.7.2) (kg $CaCO_3$ m^{-2} yr^{-1})	?	0.1–0.2[e] (1)	?	3.5–3.8 (1)	1.5–10.0 (2)	?	1.6–10.3 (5)	0.9 (1)	1.9–4.7 (2)	0.3–1.0 (3)
Community bioerosion (3.8.2) (kg $CaCO_3$ m^{-2} yr^{-1})			?	?	?	?	≈0.4–3.3 (3)		?	?
Coral recruitment (3.9.2) (Juveniles m^{-2})	?	?	0.8–24.0 (1)	?	?	?	2.2–21.1 (4)		12.9 (1)	3.0–18.0 (3)
Scleractinian diversity (3.10.1) (Shannon diversity index)	?	?	1.56–2.09 (2)	0.35–1.62 (3)	0.01–1.4 (3)	0.48–1.36 (2)	0.75–2.20 (5)	?	1.54–2.12 (4)	1.26–1.81 (3)

[a] 45% dissipation of energy across a forereef (from a depth of 20 m to 5 m) but data not habitat specific.

[b] 0.03–140 mg N m^{-2} d^{-1}.

[c] At least seven studies have documented post-mortality densities of <1 individuals m^{-2} in a range of habitats.

[d] Aggregations of up to 2793 adults ha^{-1} documented.

[e] Net calcification rate measured by hydrochemical techniques.

crest zones currently found on Caribbean reefs is likely to have been significantly altered following the dramatic reduction in *Acropora* populations because of white band disease (see Section 5.3), but few data are available.

Across an entire reef there is a characteristic gradient from high-velocity flow in shallow zones, induced by waves, to unidirectional or directionally variable currents of lower velocity in the deeper reef and lagoonal habitats (Sebens, 1997). The exact characteristics of water flow across the depth gradient can be modified by reef topography. Spur and groove zones are particularly important because strong on-shelf flow can be entrapped and advected up deep grooves at the shelf margin, and subsequently over the reef crest, and these areas typically have high levels of turbulence (Roberts *et al.*, 1977). Under particular conditions of reef topography and significant wave action, it is also possible that water levels on the outer edge of reef flats may be raised ("set up") by up to 20% of the incident wave height above the mean water level just seaward of the reef (Tait, 1972). Such wave setup can significantly affect circulation and can drive flow into lagoonal areas and out through reef channels.

3.1.1. Habitat functional values (Figure 1)

Reef crests clearly have a high functional value for dissipating wave energy (72–97%). Wave energy is also dissipated across the forereef (45% from a depth of 20–5 m; Lugo-Fernández *et al.*, 1994), but there appear to be no data on the role of different habitats, so each is assigned a putative medium functional value. Currents dominate water flow along the shelf margin (Roberts *et al.*, 1977), so in the absence of quantitative data, the escarpment is proposed as having a low functional value. Data are also scarce for the back reef and patch reef, but some wave energy crosses the reef crest and the rugosity of these habitats presumably dissipates some of the remaining energy (low functional values). Seagrass beds and mangroves require calm conditions (Moberg and Rönnbäck, 2003) and are assigned no functional value.

Figure 1 Functional values of habitats for ecosystem processes across a schematic profile of a Caribbean tropical marine seascape, derived from empirical literature reviewed in the text. Black, dark grey, light grey and no shading indicate high, medium, low and no functional values, respectively. Figures represent range of published values. The number of studies (some of which may contribute more than one value) used to derive the ranges are in parentheses. ? indicates a putative class, but quantitative data have not been found in the literature. The two sets of functional values for the density of *Diadema antillarum* refer to the mass mortality of the urchin in 1983. The shallow *Montastraea* reef is regarded as being at a depth of ~5–12 m and the deep *Montastraea* reef ~12–20 m. The mangrove habitat includes creeks.

3.2. Biogeochemical cycling

Section 3.3 (Primary productivity) focuses on carbon cycling (the "currency" of community biogeochemistry, Kinsey, 1985), and here, we consider how different reef ecosystem habitats are involved in nutrient (primarily nitrogen) cycling. The process of nitrogen cycling on reefs is described by D'Elia and Wiebe (1990) and Downing *et al.* (1999), but neither contains information on how the component pathways (e.g., ammonification and nitrification) vary between habitats. Indeed, it is clear from the literature that there is very little spatially-explicit data on nutrient cycling, and available data are generally restricted to soft-sediment habitats or shallow Indo-Pacific reefs. For example, lagoons are likely to be areas of high denitrification (loss of fixed nitrogen) because there is a low redox potential close to the surface of the sediments and a large input of organic matter to lagoonal sediments (D'Elia and Wiebe, 1990). Because of the lack of data, we limit our discussion of habitat functional values in reef biogeochemistry to nitrogen fixation.

3.2.1. Nitrogen fixation

Like other aspects of reef biogeochemistry, much of the research on nitrogen fixation has been undertaken in the Indo-Pacific and on a limited number of habitats (e.g., Wiebe *et al.*, 1975), but it is possible to discern general trends. Nitrogen fixation is a function of the abundance of nitrogen fixing biota, particularly cyanobacteria (Adey and Steneck, 1985) and their hydrodynamic environment. The hydrodynamic regimen is important because nitrogen fixation is generally positively correlated with water-flow speed (Williams and Carpenter, 1998 and references therein). Shallow reef areas, therefore, provide an optimal environment for nitrogen fixation. D'Elia and Wiebe (1990) list the sites of major nitrogen fixation as windward forereef and "spur and groove" zones, particularly those with extensive algal turfs. The presence of *Diadema* can also increase chlorophyll-specific acetylene reduction (a measure of nitrogen fixation) in shallow water, although fixation only supported $<2\%$ of the nitrogen required by an algal turf community in St. Croix (Williams and Carpenter, 1997).

In shallow (<6 m) water in the Bahamas, Goldner (1980) examined nitrogen fixation rates by epiphytic cyanobacteria (e.g., found on seagrasses and macroalgae) and epilithic cyanobacteria (e.g., found on rock, sand and coral rubble). Nitrogen fixation rates were firstly found to be most active on intertidal beach rock (423.0 nmol N_2 g ash-free dry weight^{-1} [afdw^{-1}] h^{-1}), *Thalassia* (173.9 nmol N_2 g afdw^{-1} h^{-1}) and the macroalga *Acanthophora* (145.4 nmol N_2 g afdw^{-1} h^{-1}). Secondly, rates varied between habitats and were 71.9 nmol N_2 g afdw^{-1} h^{-1} in an *A. palmata* zone, 47.5 nmol

N_2 g afdw^{-1} h^{-1} on a forereef and 15.3 nmol N_2 g afdw^{-1} h^{-1} on a small patch reef. Goldner (1980) then suggested that nitrogen fixation rates may be correlated with surface area of the substratum; patch reefs had lower nitrogen fixation rates than the reef crest and had a smaller surface area available for algal colonisation. Goldner (1980) further concluded that the highly variable fixation rates probably reflected the patchy distribution of cyanobacteria. The patchy distribution of cyanobacteria is partly caused by spatial patterns of herbivore densities (see Section 3.4). Damselfishes have particularly important effects on cyanobacterial cover, and Brawley and Adey (1977) showed that Caribbean damselfishes increase cyanobacteria abundance in the turf algae within their territories by reducing grazing pressure. Data from the Great Barrier Reef (Sammarco, 1983) suggest that nitrogen fixation is positively correlated to fish grazing (higher outside damselfish territories), but it is unclear whether this is a systematic difference between regions or reflects a complex interaction between cyanobacteria and damselfishes that varies between species and habitats.

Nitrogen fixation in seagrass beds is accomplished by bacteria in the sediment around roots, known as the rhizosphere, and epiphytes on the leaves and stems, known as the phyllosphere. Nitrogen fixation rates in seagrass beds are sufficient to frequently make phosphorus the limiting nutrient (Fourqurean *et al.*, 1992). There has been some debate on the relative contributions of fixation by the rhizosphere and phyllosphere, and there is significant variation in results between sites and the effect of nitrogen fixation on primary productivity (summarised by Welsh, 2000). However, empirical evidence indicates that in the absence of significant nutrient inputs, both the phyllosphere and the rhizosphere are important sites of nitrogen fixation in *Thalassia* communities (Goering and Parker, 1972; Capone *et al.*, 1979). Rates of nitrogen fixation in the Caribbean vary from 0.03 to 140 mg N m^{-2} d^{-1} in six studies using a variety of techniques (summarised by Welsh, 2000). Variations in fixation rates across seagrass beds of different densities appear to have received little attention, but the close relationship between photosynthetic activity of plants and bacterial fixation in the rhizosphere indicates that fixation is likely to be tightly correlated to seagrass biomass. In mangrove stands, there seems to be some nitrogen fixing by root associated bacteria, but tidal influx is likely to be a more important source of nutrients (Hogarth, 1999).

3.2.2. Habitat functional values (Figure 1)

There are few habitat-specific data measuring nitrogen fixation using comparable techniques. However, seagrass beds and reef crests appear to have optimal conditions (high functional values) for nitrogen fixation because of the combined effects of the rhizosphere and phyllosphere (0.03–140 mg N m^{-2} d^{-1}) and high water movement and rugosity (71.9 nmol N_2 g $afdw^{-1}$ h^{-1}) in shallow water, respectively. Other available data indicate medium functional values for shallow *Montastraea* reefs (47.5 nmol N_2 g $afdw^{-1}$ h^{-1}) and low functional values for patch reefs (15.3 nmol N_2 g $afdw^{-1}$ h^{-1}). Nitrogen fixation appears to be correlated to surface area (Goldner, 1980), so we assign a low functional value for gorgonian-dominated habitats. Fixation rates are likely to be low on deep *Montastraea* reefs and escarpments because of decreased light levels, and we have assigned low functional values. Though supporting depauperate benthic communities, sand habitats are likely to have some cyanobacteria present and are assessed as having a low functional value. Back reefs presumably have lower fixation rates than reef crests because of differences in hydrodynamical conditions and available surface area and thus are assigned medium functional values. Mangroves appear to have a low functional value with limited nitrogen fixing on prop roots (Hogarth, 1999).

3.3. Primary production

3.3.1. Physical and biotic controls of primary production and key photosynthesising taxa

Photosynthesis is a fundamentally important process in reef systems, as it uses light energy to create organic material. Measurements of gas fluxes, such as the production of oxygen, can be used to estimate the rate of photosynthesis, which can be converted into primary productivity and expressed as mass of organic matter per unit area per unit time (e.g., Hatcher, 1988). As is discussed, patterns of primary productivity vary significantly across reef habitat and zones depending on the components of their communities. In addition to variations caused by benthic communities, there are overarching spatial controls on primary productivity, the most obvious of which is light availability (reviewed by Larkum, 1983; Hatcher, 1990). Gross primary productivity decreases with increasing depth on a forereef as light and photosynthetic area decrease. However, the relationship between productivity and changing depth is complicated by photoadaption, grazing, self-shading, topographical complexity, stability of the reef surface and disturbance regimens (de Ruyter van Steveninck and Breeman, 1981; Barnes and Devereux, 1984; Hatcher, 1997b).

Along with investigating the effects of light, the apparent paradox of relatively low nutrient levels in tropical waters and high primary productivity has led to considerable research. While scarcity of nutrients has great potential for limiting photosynthesis, the link between nutrient concentrations and primary productivity is highly complex. A series of case studies of anthropogenic input of additional nutrients has provided variable results and detailed predictions are difficult (see, for example, Connor and Adey, 1977; Lapointe and O'Connell, 1989; Larned, 1998; Hughes *et al.*, 1999). Furthermore, few of these data are habitat specific and further interpretation is outside the scope of this review. In addition to physical controls, spatial variation in grazing pressure is an important controlling factor of primary productivity (see Section 3.4). However, linking grazing pressure to primary productivity is complicated by feedbacks caused by the evolution of defence mechanisms and intraspecific and interspecific feeding selectivity, which have significant effects on the algal community structure present in a given area (Hatcher, 1988).

Calculating community primary productivity for a particular habitat from organism productivity is complex because of methodological difficulties such as calculating surface area in rugose environments, differing spatial and temporal scales of measurement and the inclusion or exclusion of heterotrophic respiration (Hatcher, 1988). However, because of the lack of community-scale data on primary productivity, we provide a brief overview of the primary productivity rates of major benthic taxa that can be used to calculate values for whole habitats (e.g., Wanders, 1976b; Rogers and Salesky, 1981). Much of the research on primary productivity has focused on the coral–algal symbiosis to the detriment of work on algae, seagrass and phytoplankton (Hatcher, 1988). Despite a bias towards coral research, it is clear that algal communities are a major source of reef primary production (e.g., Lewis, 1977) and there is a pattern between the functional groups. Generally there is a negative relationship between resources dedicated to herbivore resistance and those dedicated to primary productivity. Therefore, highly grazed sheet and filamentous algae are generally more productive than fleshy and coarse branched species, which have some protection from grazing, which are in turn more productive than lightly grazed, but heavily protected, calcareous and coralline species (Littler *et al.*, 1983b; Littler and Littler, 1984; Morrissey, 1985). For example, net photosynthetic rates in Belize were 6.28 mg C g organic dry weight^{-1} h^{-1} for sheet algae, 5.48 for coarsely branched species and 0.16 for crustose species (Littler *et al.*, 1987). Rates for turf algae were relatively low (1.67 mg C g organic dry weight^{-1} h^{-1}), possibly because of the compact configuration and particulate matter content of the species studied. On a shallow reef in Bonaire, rates were 61.44 μg O_2 cm^{-2} h^{-1} for crustose corallines and 72.87 μg O_2 cm^{-2} h^{-1} for sparse turfs (van Rooij *et al.*, 1998). A more dramatic difference between functional forms was demonstrated in Curaçao where annual productivity rates were 350 g gross of organic C m^{-2} for crustose Corallinaceae (0.02 mg O_2 cm^{-2} h^{-1}) and 710 g C m^{-2} (0.05 mg O_2 cm^{-2} h^{-1}) for algal turfs (Vooren, 1981).

Filamentous (turf) algae are a particularly important component of the epilithic algal community because they exploit the high surface area that the complex topography of a reef provides. Indeed, Adey and Steneck (1985) suggest that shallow reef productivity corresponds with the distribution and abundance of turf algae. Constant grazing keeps turf algae in an exponential growth phase and turfs have a higher surface to volume ratio than macroalgae (Littler and Littler, 1984; Hatcher, 1997b). In shallow water, high primary productivities by turf algae are maintained despite extremely high light intensities and exposure to ultraviolet (UV) because they have a high saturating light intensity and there is an apparent lack of photoinhibition (Vooren, 1981; Carpenter, 1985a). Adey and Goertemiller (1987) refer to algal turfs as "master producers" and use harvesting techniques to give production rates up to 14 g (dry) m^{-2} d^{-1}, which decline with increasing depth. Rogers and Salesky (1981) give net productivity rates of 0.23–0.93 g O_2 m^{-2} h^{-1} (gross productivities of 0.76–0.89 g O_2 m^{-2} h^{-1} for a limited number of samples) for algal turf communities in St. Croix and compare these to values of 0.30–0.64 g O_2 m^{-2} h^{-1} on a Curaçao reef crest (Wanders, 1976b).

Macroalgae, such as *Acanthophora*, *Halimeda*, *Padina*, *Penicillus* and *Sargassum* are also important primary producers (e.g., Hillis-Colinvaux, 1980; Rogers and Salesky, 1981; Hatcher, 1988). High densities of herbivores limit macroalgal growth, but algae are particularly abundant when grazing pressure is reduced, such as in deeper water or following *Diadema* urchin mass mortality (Hatcher, 1997b). Adey *et al.* (1977) discuss bank barrier reefs in Martinique where corals have been replaced on the reef crests by dense stands of fleshy algae, particularly *Sargassum*, forming a "fleshy algal pavement." Macroalgal reef crests are highly productive, demonstrated by the primary productivity on Martinique being twice that of the back reef at St. Croix because macroalgal standing crop was 20–30 times higher than the filamentous algae in St. Croix, which more than counteracted for filamentous algae being 10–20 times more productive per unit weight. Adey *et al.* (1977) documented similar formations on Grenada and St. Lucia and suggested that these reefs are characterised by high turbidity and lack large-scale porosity, meaning that they do not have large populations of grazing *Diadema* and parrotfishes. Rogers and Salesky (1981) give net productivity rates of 1.16–8.98 g O_2 m^{-2} h^{-1} (gross productivity of 2 g O_2 m^{-2} h^{-1} for one sample) for macroscopic algal communities in St. Croix. The gross productivity of *Sargassum platycarpum* and two species of *Dictyota* were recorded as 6.0–15.6 g O_2 m^{-2} d^{-1} (net productivities 3.1–10.3 g O_2 m^{-2} d^{-1}) on a Curaçao reef crest (Wanders, 1976a).

The coral–algal symbiosis has high rates of primary productivity because, for example, zooxanthellae densities and coral growth forms are able to change with decreasing light intensities (reviewed by Hatcher, 1988;

Muller-Parker and D'Elia, 1997) and research has facilitated the production of detailed energy budgets for particular species (Edmunds and Spencer Davies, 1986). As for many algal studies, research on the primary productivity of corals has been predominantly in shallow water and Rogers and Salesky (1981) give net productivity rates of 0.15–0.54 g O_2 m^{-2} h^{-1} (gross productivity of 0.52–0.76 g O_2 m^{-2} h^{-1} for three samples) for *A. palmata* in St. Croix and show how these values are similar to previous data in the Caribbean. Production rates for six species of coral ranged from 33.06–782.51 kcal m^{-2} yr^{-1} in Barbados (Lewis, 1981). Coral productivity can vary intraspecifically between habitats and *A. palmata* net primary productivity was highest in a shallow forereef (0.5–1.0 m, 0.44 g O_2 m^{-2} h^{-1}), intermediate in a back reef (0.36 g O_2 m^{-2} h^{-1}) and lowest in the deep forereef (8–10 m, 0.28 g O_2 m^{-2} h^{-1}) where there was less light (Gladfelter and Monahan, 1977). Such intraspecific, and indeed interspecific, changes have been linked to zooxanthellae types within corals; Diekmann *et al.* (2002) showed that *Montastraea annularis* and *Acropora cervicornis* had strong habitat-related correlations between zooxanthellae type and depth. In contrast, there was no correlation between *Madracis* zooxanthellae and depth, so this species has a generalist zooxanthellae–coral association, which is equally successful over a range of habitats.

3.3.2. *Community primary productivity*

The importance of organic production on reefs has led to a large number of studies using a variety of techniques and addressing a range of research topics. These studies of primary productivity have allowed a succession of authors to propose standard empirical values for coral reef zones. For example, Kinsey (1983) suggested that shallow unperturbed Pacific reef systems have four or five "modes" of metabolic performance, particularly "coral/algal," "algal pavement" and "sand/rubble" with community gross photosynthesis rates of 20, 5 and 1 g C m^{-2} d^{-1}, respectively (see also Kinsey, 1985, for more examples). The concept of modes of metabolic performance was extended by Hatcher (1988, 1990), who presented a figure summarising, from the available literature, primary productivity for entire reefs plus six reef zones and seven major benthic taxa contributing to reef productivity. Although the work of Kinsey (1985) and Hatcher (1988, 1990), summarising productivity rates across standardised habitats, epitomises the approach taken by this chapter, most of the empirical studies they cited were from the Indo-Pacific and their extrapolation to Caribbean reefs is difficult and are not used here to assign functional values. Indeed, there are further difficulties comparing Caribbean primary productivity rates before and after the mass mortality of *Diadema antillarum* (discussed in more detail in Section 3.4).

Data from St. Croix clearly show the decrease in net productivity of algal turf communities over the course of a few months (37% per unit area from 0.68 to 0.43 g O_2 m^{-2} d^{-1}) because of the decrease in grazing and ammonium from *Diadema* excretion (Carpenter, 1988; Williams and Carpenter, 1988).

Although absolute values of primary productivity are difficult to transfer between regions because of differences in community composition, the general trends are likely to be universal because of the overarching control of photosynthesis by light and its attenuation with increasing depth and they are supported by some Caribbean empirical data. Perhaps clearest of these trends is the high productivity of back reefs because of the large surface area, high light intensities and the steady flux of nutrients (reviewed by Hatcher, 1997b). In St. Croix, three back reefs (depth <0.9 m) and three shallow forereefs (<6.3 m) differed significantly in their mean gross primary production (62.0 g O_2 m^{-2} d^{-1} vs 15.7) and net primary production (36.5 g O_2 m^{-2} d^{-1} vs 8.9) (Adey and Steneck, 1985). Adey and Steneck (1985) also showed that algal turfs were the major producers in each zone and attributed differences in productivity to lower surface areas, less water movement and higher coral cover in the forereef sites. Data from St. Croix also highlighted intersite differences in back reef productivity linked to geological age; turf algae was most abundant on a reef with intermediate age because of the high surface area provided by dead colonies of the rugose coral *A. palmata* in comparison to younger sites with either abundant living *A. palmata* or older sites with limited surface area. The values for the back reef were higher than the rates (27 g O_2 m^{-2} d^{-1}) for a shallow *A. palmata*–dominated (45% cover) reef crest (Rogers and Salesky, 1981). For a different shallow water habitat (algal ridges) in St. Croix, Connor and Adey (1977) provided similarly high productivity rates (gross production 64.8–121.5 g O_2 m^{-2} d^{-1}). Elsewhere in the Caribbean, equivalent gross production rates were reported for both a shallow *A. palmata* reef and a *Sargassum*-dominated plateau (41.4 and 28.0 g O_2 m^{-2} d^{-1}, respectively) in Curaçao (Wanders, 1976a,b). In a rare study on a shallow (3–4 m) reef dominated by *Montastraea* rather than *A. palmata*, Rogers (1979) obtained gross productivity rates in Puerto Rico of 5.4 g O_2 m^{-2} d^{-1} and contrasted the results with the higher rates (20–44 g O_2 m^{-2} d^{-1}) reported by Odum (1959), also in Puerto Rico, which were in shallower areas with lower coral cover (more algae).

Studies of primary productivity on forereefs are remarkably rare in the Caribbean, and indeed elsewhere (Hatcher, 1988), because of sampling difficulties using traditional flow respirometry. The new "Submersible Habitat for Analysing Reef Quality" (SHARQ) (Yates and Halley, 2003) may provide an important tool for measuring a range of community metabolism parameters from a range of habitats. Currently, SHARQ has only been used in the Caribbean (Florida) on patch reefs, dense and sparse seagrass and sand. Patch reef data indicated that gross production is 5.4 g O_2 m^{-2} d^{-1} and sand production was 1.8 g O_2 m^{-2} d^{-1} (Yates and Halley, 2003). The latter value supports previous research that has shown that carbonate sands have limited topographical complexity and a depauperate benthic community but have productive microalgae in their top layer (Dahl, 1973; Kinsey, 1985; Hatcher, 1988) and can occupy vast areas, so their contribution to the primary productivity of whole systems may be important.

Seagrass beds frequently contribute large portions of the primary production of coastal ecosystems (e.g., Thayer *et al.*, 1984; Fourqurean *et al.*, 1992) and *Thalassia testudinum* has long been recognised as one of the most productive of all plants (e.g., Odum, 1956; Westlake, 1963). The high productivity of seagrasses is supplemented by a range of other taxa in seagrass beds, particularly epiphytic algae, benthic microalgae and macroalgae and phytoplankton (e.g., Bach, 1979). Seagrass habitats are routinely described in terms of the density or biomass of plants and there are clear data showing that leaf productivity of *T. testudinum* is closely and positively correlated to leaf standing crop and the relationship is consistent over a range of sediment types and water depths (Zieman *et al.*, 1989). In addition to leaf production, a high proportion of the productivity of whole *T. testudinum* plants is accounted for by the rhizomes (e.g., 35% in a subtropical lagoon; Kaldy and Dunton, 2000). There is some evidence that the two most abundant Caribbean seagrasses (*T. testudinum* and *Syringodium filiforme*) have similar specific productivity (Barber and Behrens, 1985). Normally productivity of seagrass decreases with depth as light is attenuated (e.g., Kaldy and Dunton, 2000), but in south Florida, Fourqurean *et al.* (2001) reported the opposite relationship. The increasing productivity with depth was attributed to buffering against temperature extremes and the turbidity of nearshore shallow waters. Van Tussenbroek (1995) showed that *Thalassia testudinum* in a lagoon was more productive than in a back reef environment, probably because of nutrient availability. Seagrass productivity also exhibits a strong seasonal signal (e.g., Fourqurean *et al.*, 2001).

In addition to the range of factors that cause intrahabitat variations in productivity, methodological differences in calculating the productivity of seagrass limit comparisons to reef habitats. Many studies, because of complex problems using gas-exchange methods with vascular hydrophytes (Zieman, 1975), measure *Thalassia testudinum* using a variety of leaf-marking techniques with results usually expressed as g (dry weight) m^{-2} d^{-1} for "aboveground" productivity. Areal productivity varies significantly across the Caribbean, as shown by CARICOMP (1997b) who provides values for 14 sites ranging from 0.8 (Bahamas) to 7.5 g m^{-2} d^{-1} (Mexico). A series of studies across a variety of spatial and temporal scales and across gradients of depth and water conditions in Florida give values ranging from 0.3 to 4.0 (Zieman, 1975; Bach, 1979; Zieman *et al.*, 1989; Tomasko and Lapointe, 1991; Fourqurean *et al.*, 2001) with comparable data available from Belize (0.5–1.3 g m^{-2} d^{-1}) (Tomasko and Lapointe, 1991) and Mexico (0.88–1.46 g m^{-2} d^{-1}) (van Tussenbroek, 1995). Yates and Halley (2003) convert the data of Fourqurean *et al.* (2001) to provide a range of net primary productivity values of 0.05–3.52 g O_2 m^{-2} d^{-1}. Perhaps the best data comparable to values presented for coral habitats are from use of the SHARQ in Florida, which generated gross productivity values for dense and sparse seagrass beds (2.9 and 3.2 g O_2 m^{-2} d^{-1}, respectively) (Yates and Halley, 2003). Using smaller benthic chambers, higher values of 3.82–4.96 g C m^{-2} d^{-1} were recorded in the Bahamas along with a net primary productivity rate for epiphytes of 5.22 g C kg^{-1} d^{-1} (Koch and Madden, 2001).

Comparing mangrove primary production with reef habitats is particularly difficult because of methodological difficulties of measuring rates for mangroves themselves along with the algal and seagrass production on the sea floor and prop roots that maximise productivity in mangal systems (Hogarth, 1999). The metabolism of mangrove trees displays considerable variation at both local and regional scales, primarily because of environmental control (by tides, climate and seawater composition) (Gattuso *et al.*, 1998). CARICOMP (1997c) provide litterfall data for seven sites across the Caribbean with values ranging from ~0.5 to 9.5 g m^{-2} d^{-1} with significant seasonal variation. Lugo and Snedaker (1974) reviewed published studies from Florida and Puerto Rico using carbon dioxide–exchange techniques, which give gross primary productivity rates of 5.3–13.9 g C m^{-2} d^{-1} and give some evidence that rates of photosynthesis and respiration vary between species and zones of mangrove forests. For example, an area of red mangrove (*Rhizophora mangle*) leaf has a higher net primary productivity than an equivalent area of black mangrove (*Avicennia germinans*) leaf in the adjacent zone and individuals displaced from their normal zone had a lower productivity than individuals characteristic of that zone. One of the few studies considering prop-root algae gives a net primary productivity rate of 8.54 g C kg^{-1} d^{-1} (Koch and Madden, 2001).

Yates and Halley (2003) provide gross production-to-respiration ratios (P:R) of 0.80, 0.90, 1.08 and 0.85 for patch reefs, sand areas, sparse seagrass beds and dense seagrass beds, respectively. P:R ratios are important because they indicate whether a reef, zone or benthic component is autotrophic (P:R $>$ 1) or heterotrophic (P:R $<$ 1). As expected from the limited number of productivity studies in the Caribbean, there are few P:R values available in the literature. Koch and Madden (2001) recorded P:R values of 1.6 and 1.7 for mangroves and seagrass beds, respectively. Lewis (1977) reviews previous studies to give P:R values of 0.8–1.4 for *Thalassia* beds in Florida and Puerto Rico. Rogers (1979) gives a P:R of 0.7 for a shallow *Montastraea* reef and data in Adey and Steneck (1985) allow calculation of values of 0.98 and 1.01 for their forereef and back reef sites, respectively. Shallow reefs in

Puerto Rico are reported as having a P:R of 1.1 (Odum *et al.*, 1959). The available data correspond to values in reviews dominated by Indo-Pacific studies (Hatcher, 1988), which give P:R values ranging from 0.5–5.5 (forereef), 1.0–4.0 (reef crest), 0.7–3.2 (back reef) and 0.7–1.4 (patch reef) and indicate ratios typically >1 in high energy zones, especially those with algal turf (organic sources), and <1 in lower energy zones (organic sinks). The spatial variation of autotrophic and heterotrophic zones is an interaction of factors such as light, water movement aiding nutrient uptake and grazing. Hatcher (1997b) states that in shallower habitats, gross productivity is high enough to offset respiration so that P:R is >1 and organic matter is exported downstream by wave pumping, by gravity down the slope to deeper water, laterally by advection or by feeding of pelagic consumers. Therefore, reef structure (e.g., proportion of shallow habitats) is a major determinant of net production. Furthermore, there is some evidence that the P:R of 1, with a variation of only ±0.1, proposed for a "standard" Pacific reef flat and a ratio for a whole reef ecosystem very close to 1 (Kinsey, 1983, 1985), may also be true in the Caribbean.

3.3.3. Habitat functional values (Figure 1)

High functional values are assigned to habitats with rates of gross primary productivity >15 g O_2 m^{-2} d^{-1} (back reefs and reef crests). Medium functional values are given to habitats with rates of gross primary productivity between 5 and 15 g O_2 m^{-2} d^{-1} (shallow *Montastraea* reefs and patch reefs). The abundance of productive brown macroalgae in relatively shallow water but, with low rugosity and grazing pressure, indicates that gorgonian-dominated forereefs are also likely to fall in the 5–15 g O_2 m^{-2} d^{-1} range (medium functional value). Similarly, there are no data for deeper *Montastraea* reefs or escarpments, so they are assigned low functional values (i.e., <5 g O_2 m^{-2} d^{-1}) because of the attenuation of light with increasing depth. Sand has a low functional value (1.8 g O_2 m^{-2} d^{-1}), although this rate is likely to be an overestimate of the sand habitat in Figure 1, as it was generated in shallow water (Yates and Halley, 2003). Yates and Halley (2003) also provide data for seagrass beds, which indicates that they may have a low functional value (2.9–3.2 g O_2 m^{-2} d^{-1}), but because of the limited data, problems with gas-exchange techniques, evidence of higher rates elsewhere (Koch and Madden, 2001) and the known seasonal variations, we assign a medium functional value. Comparable rates of gross primary productivity for mangrove stands are not available, but the combination of mangrove trees along with the algal and seagrass production on the sea floor and prop roots indicates that rates would be at least 5–15 g O_2 m^{-2} d^{-1} (medium functional value).

3.4. Secondary production

3.4.1. Overall patterns of herbivore densities and their effects

Herbivory, the grazing of primary producers, is a vital process in trophic energy flow on a coral reef (e.g., Lubchenco and Gaines, 1981). Inevitably, secondary productivity is inextricably linked to primary productivity because high levels of primary productivity are necessary to support an abundant herbivore community. Conversely, high grazing pressure is an important causal agent of the zonation of primary producers (Ogden, 1976; Hay, 1981a; Hay *et al.*, 1983; Littler *et al.*, 1983a, 1987; Hay, 1985). Section 3.3 has reviewed the observed patterns of primary productivity across a seascape, and this section aims to document one of the key factors that determine these patterns. Initially, we discuss the overarching pattern of density of herbivores across a reef ecosystem then provide details of the distributions of the four most important taxa of the Caribbean macroherbivore community: Scaridae, Acanthuridae, Pomacentridae and *D. antillarum* (e.g., Ogden, 1976). Herbivore density is used as a proxy for secondary production because calculations of production also require parameters such as production/biomass and consumption/biomass ratios, which are scarce for reef ecosystem fishes (van Rooij *et al.*, 1998) and variations between habitat types are unclear. Microherbivores (e.g., amphipods), though important grazers in reef communities (Carpenter, 1997), are not included in this chapter because their habitat preferences are not well studied. Larger herbivores (e.g., turtles and manatee) have an important influence in seagrass beds on the plants, other associated grazers and fauna and chemical and decompositional processes occurring within a meadow (Ogden *et al.*, 1983; Thayer *et al.*, 1984). However, they are omitted here because of the lack of data and the effects of overharvesting, which has reduced their ecological role in reef ecosystems (e.g., Jackson, 1997). Grazing by herbivores is an important component in reef bioerosion, but this is treated separately in Section 3.8.

Variation in the density of herbivores across tropical seascapes and the patterns has been linked to a few key factors such as topography, proximity to nearby shelter, predator abundance, density of territorial competitors and local availability of food resources (Lewis and Wainwright, 1985). For fishes, grazing is mainly inversely related to tidal exposure and wave action and positively correlated with the availability of shelter from predators (Hixon, 1997). Therefore, the density of herbivorous fishes is highest on shallow, rugose sections of the reef and lowest in areas that are deep, topographically simple or where water movement interferes with feeding (Hay, 1981b). Densities of *Diadema* are also higher in shallower reef areas and *Diadema* generally accentuates patterns of fish grazing (decreasing with increasing depth with the exception of very shallow turbulent water). Not surprisingly, such a strong trend has been supported by herbivory assays and a *Thalassia* bioassay showed that feeding, predominantly by fishes, in shallow (1–10 m) zones was significantly higher than deep (30–40 m) reefs or very shallow flats (Hay and Goertemiller, 1983). A similar assay showed *Thalassia* loss on a reef flat and sand plain to be very low relative to that of a shallow reef slope and that across the reef slope, herbivory decreased linearly with depth and was highest in the most topographically complex habitats (Hay *et al.*, 1983). Therefore, grazing was highest in an *Acropora* and ledge habitat, lowest on a sandy slope and intermediate in a *Porites*, massive coral and gorgonian-dominated habitat. Lewis and Wainwright (1985) and Littler *et al.* (1987) showed that the order of herbivory, from lowest to highest rates, was seagrass bed (too shallow for fishes, limited shelter), lower forereef, outer ridge (both too deep for many herbivores), upper forereef and then the rubble and carbonate pavement of the back reef (shallow with plenty of shelter and fast algal growth rates).

The relative importance of fish grazing compared to urchin grazing on the distribution of algae is equivocal. Hay *et al.* (1983) showed that herbivorous fishes accounted for 97% of grazing during the day and 90% of the total, while urchins accounted for only 9% of the total. In contrast, Foster (1987) used caging experiments to show that the effect of fishes on grazing of fleshy algal turfs on shallow moderately exposed reef flat habitats was limited compared to *Diadema*. Hay (1984) suggested that studies stressing the importance of urchins were usually on overfished reefs and fishes are the most abundant grazers on "natural" reefs (see also Horn, 1989). The balance between grazing by fishes and *Diadema* and the ecology of Caribbean reefs were fundamentally altered in the early 1980s by the mass mortality of the urchin because of a waterborne pathogen (e.g., Lessios, 1988). The mass mortality of *Diadema* and its effects on benthic communities are discussed in more detail in the subsequent section dedicated to *Diadema*, but it is appropriate to highlight here the interactive effect on fish communities. The loss of *Diadema* on many reefs increased populations and led to the spatial redistributions of fishes because of previous exploitative competition, but the changes rarely maintained grazing pressure at premortality levels, especially in areas with high fishing pressure. For example, in St. Croix fish grazing intensity increased by 380% 1 wk after the mass mortality of *Diadema* (Carpenter, 1985b). In the longer term Carpenter (1990a) showed that fishes were three times more abundant in the back reef and shallow (2 m) forereef, two times more abundant on the middepth (5 m) forereef and four times more abundant on the deep (10 m) reef. The additional fishes were mainly juvenile parrotfishes except in the shallow forereef where they were generally surgeonfishes. Overall, however, grazing intensity only increased in three of the four zones (not in the shallow forereef). The degree of change in grazing intensity was dependent on initial conditions, the change of fish populations and which fish taxa were affected (e.g., surgeonfishes appear to respond differently to changes in algal abundance). Further data specifically for surgeonfishes showed that *Acanthurus chirurgus* and *A. coeruleus* increased their population sizes, but *A. bahianus* did not (Robertson, 1991), possibly because it is much less reliant than the other two species on habitats (i.e., those on the reef) that had been most affected by *Diadema*. As fishes are less systematic grazers than urchins, increases in fish abundance could not compensate for the loss of *Diadema* and algal cover increased in cover and biomass in St. Croix (Carpenter, 1990a). Similarly, after *Diadema* mass mortality, Morrison (1988) showed on an area of shallow reef that despite increases in fish grazing, abundances of erect and filamentous algae increased and abundances of corallines decreased, but *Diadema* mortality had little effect on the deeper reef. *Diadema* having a major role on shallow reefs but only a minor role relative to fishes in deeper communities is particularly important and is discussed in more detail in subsequent sections.

3.4.2. Scaridae distributions

Parrotfishes are extremely important herbivores on coral reefs and commonly predominate in slightly deeper areas (>5 m) than surgeonfishes (e.g., Lewis and Wainwright, 1985). Most adult parrotfishes decrease in density with increasing depth (van Rooij *et al.*, 1996a) and significantly influence algal cover in different habitats because of differential grazing pressures (Lewis, 1985; Lewis and Wainwright, 1985; Horn, 1989). Species that crop or scrape algae from corals can also alter coral distributions. The effect of parrotfish grazing on coral distributions was demonstrated by Littler *et al.* (1989) who showed that zonal patterns of *Porites astreoides* and *Porites porites* forma *furcata* in a back reef were strongly associated with parrotfish feeding intensity. Like all herbivores, parrotfish distributions are reliant on factors such as proximity to nearby shelter, food resources and biological interactions. Habitat rugosity is, therefore, a key variable determining parrotfish densities because it affects the number of available shelters and type of food resources available. By extension, topography has an important effect on social behaviour because parrotfish behaviour can be adaptive with changing density (see van Rooij *et al.*, 1996b for an example). Parrotfish distributions can generally be grouped by feeding modes as species feeding by "sucking" are most abundant over sand in back reefs and lagoons, while "croppers" and "scrapers" are more abundant in shallow reef areas (Horn, 1989). However, there has been extensive research to document more specific interspecific habitat preferences of the Caribbean Scaridae. Because there are a relatively large number of species of parrotfishes in the Caribbean, the habitat preferences of perhaps the most studied species (*Sparisoma viride*) is described in detail here and data for other species are summarised elsewhere (Table 3). *Sparisoma viride* is also one of the most abundant herbivores in reef ecosystems, accounting for 22–31% of total herbivore biomass in Bonaire (Bruggemann *et al.*, 1996; van Rooij *et al.*, 1998), where its biology has been studied in detail (Bruggemann *et al.*, 1994a,b,c; van Rooij *et al.*, 1995a,b, 1996a,b,c; van Rooij and Videler, 1996, 1997).

Tolimieri *et al.* (1998) studied recruitment rates to forereefs in the Virgin Islands and reported rates of ~0–4 recruits 60 m^{-2} and further showed that rates were higher in the back reef (~3.5–8 recruits 60 m^{-2}) compared to the reef crest (~0.5–2.0 recruits 60 m^{-2}) or reef base (~0.5–1.0 recruits 60 m^{-2}) (Tolimieri, 1998b). *Sp. viride* juveniles commonly use a variety of nursery areas, particularly shallow reefal zones such as seagrass beds, the back reef, patch reefs, reef crest and *Acropora cervicornis* and "dropoff" zones from 4 to 12 m (Hanley, 1984; van Rooij *et al.*, 1996a; Overholtzer and Motta, 1999; Nagelkerken *et al.*, 2000c). Nagelkerken *et al.* (2000c) stated that seagrass beds were the most important biotope for juvenile *Sp. viride* in Bonaire (density 26.1 fish 1000 m^{-2}) and the reef from 3 to 5 m was also important. However, *Sp. viride* was absent from seagrass beds in Panama, Curaçao, St. Croix and south Florida (Weinstein and Heck, 1979; Thayer *et al.*, 1987; Nagelkerken *et al.*, 2000a; Mateo and Tobias, 2004) and rare in the Bahamas (Newman and Gruber, 2002). *Sparisoma viride* is rarely seen in mangrove stands: a density of 1.4 fish 1000 m^{-2} in Bonaire (Nagelkerken *et al.*, 2000c), 0.7 fish 100 m^{-2} in Curaçao (Nagelkerken and van der Velde, 2002), no individuals seen in south Florida (Thayer *et al.*, 1987), only one individual in mangroves in Biscayne Bay (Serafy *et al.*, 2003) and one fish in mangroves among a total of >65,000 fish in the Bahamas (Newman and Gruber, 2002).

Van Rooij *et al.* (1996a) surveyed five reef habitats in Bonaire, and densities of juvenile *Sp. viride*, interpolated from their graphs, were ~40, 125, 400, 380 and 150 fish ha^{-1} for the shore zone, *A. palmata* zone, *A. cervicornis* zone, drop off and upper reef slope, respectively. However, juvenile densities varied significantly around the island, particularly in shallow water with maxima of ~3,500, 2,100 and 1,500 fish ha^{-1} for the shore zone, *A. palmata* zone and *A. cervicornis* zone, respectively at one site because of intrahabitat variations in benthic communities (van Rooij *et al.*, 1996b). Similarly, lower values were recorded at another site (~60 and 25 fish ha^{-1} for the *A. palmata* zone and upper reef slope, respectively). A density of ~25 juvenile fish ha^{-1} was given for a gorgonian-dominated zone. In Mexico, the density of *Sp. viride* juveniles on a series of forereefs (12 m) depth was 1.7 fish 100 m^{-2} (González-Salas *et al.*, 2003). Within nursery areas there are intrahabitat patterns of preferred microhabitats as shown by Tolimieri (1998a) in a shallow (from 3 to 6 m to emergent) back reef, containing patch reefs, in the U.S. Virgin Islands. Tolimieri (1998a) showed that recruitment rates were higher to colonies of live and dead *P. porites* compared to *M. annularis*, but there was no evidence of microhabitat choice at settlement (i.e., caused by differential mortality or movement or both). Furthermore, recruits settled in higher numbers on patch reefs with conspecifics, persistence was greater at higher recruit densities and the presence of damselfishes had no effect on settlement but did reduce recruitment. The data led Tolimieri (1998a) to conclude that both presettlement and postsettlement processes can alter recruitment patterns of *Sp. viride* from initial settlement patterns. Tolimieri (1998b) showed that within a site, recruitment was correlated with the percentage cover of *P. porites* and at a larger scale, the cover of *P. porites* at 10 sites on three islands explained 66–81% of the variation in recruits in 3 of 4 yr. Contemporary adult abundance was correlated with mean recruitment at the scale of sites and islands, so microhabitat characters that affect recruitment may influence adult abundance at large spatial scales (Tolimieri, 1998b).

Intermediate or midphase *Sp. viride* are commonly seen in shallow back reefs and reef crests (Hanley, 1984). In Bonaire, sexually inactive male intermediate or midphase *Sp. viride* were restricted to shallow areas because terminal phase adults held territories deeper than 3 m where food resources were greater (van Rooij *et al.*, 1996c). Within their reefal habitat, adult *Sp. viride* have specific food preferences that influence the quality of a territory (Bruggemann *et al.*, 1994a). In contrast to intermediate phase fish, territorial terminal phase adults increase in physical condition with increasing depth because in deeper areas they have a lower reproductive effort, reduced territory defence and an increased availability of high yield grazing patches (van Rooij *et al.*, 1995a). In addition to forereefs, terminal phase adults can also be found in a range of shallow habitats including reef crests (Hanley, 1984) and in Bermuda prefer agitated water near exposed reefs and shorelines (Gygi, 1975). A survey across the Belize Barrier Reef gave densities of 3, 11, 7, 2 and 3 intermediate and terminal phase fish 400 m^{-2} for back reef, high relief spur and groove, low relief spur and groove, the inner reef slope and outer ridge, respectively (Lewis and Wainwright, 1985). Further data for a mixed community back reef in Belize showed densities of *Sp. viride* varied from 2.8 to 9.7 fish 400 m^{-2} during a 12-mo period, which contrasted with their absence at three macroalgal-dominated sites (Lewis, 1986). Van Rooij *et al.* (1996a) surveyed five habitats in Bonaire and densities of adult *Sp. viride*, interpolated from their graphs, were ~600, ~250, ~200, ~125 and ~50 fish ha^{-1} for the shore zone, *A. palmata* zone, *A. cervicornis* zone, drop off and upper reef slope, respectively, which were similar to those found at two other sites (van Rooij *et al.*, 1996b). Also in Bonaire, mean densities on four forereef sites (0–3, 3–5, 10–15 and 20–25)

Table 3 Habitat preferences of selected Caribbean Scaridae[a]

Species	Juveniles	Adults
All species	Use nursery areas, particularly lagoonal seagrass beds, patch reefs, back-reef areas and *Acropora cervicornis* zones (4–6 m) before moving to deeper parts of the reef (e.g., van Rooij *et al*., 1996a; Nagelkerken *et al*., 2000c); *Scarus* spp. are relatively dominant in *Acropora palmata* zones from 2 to 4 m (van Rooij *et al*., 1996a)	
Scarus guacamaia	Has a functional dependency on mangroves (Mumby *et al*., 2004a)	Prefers reefs (Gygi, 1975; Nagelkerken and van der Velde, 2002)
Scarus iserti	Use the back reef, and to a lesser extent patch reefs (Adams and Ebersole, 2002) and seagrass beds and mangroves (Nagelkerken and van der Velde, 2002)	Use the back reef, and to a lesser extent patch reefs (Adams and Ebersole, 2002); includes patch-reef halos in its foraging (Overholtzer and Motta, 1999); associates with forereef *Porites* rubble and live colonies (Tolimieri, 1998c); strongly correlated with substrate rugosity (Mumby and Wabnitz, 2002); may aggregate in foraging groups generally in 1–3 m of water over a bottom of coral rubble, sandy sediment and scattered coral heads (Ogden and Buckman, 1973); migrates diurnally from shallow feeding areas to deeper nocturnal resting areas (Ogden and Buckman, 1973)
Scarus vetula	Found on shallow (2 m) reef habitats (Nagelkerken and van der Velde, 2002)	Associates with forereef *Porites* and *Acropora* rubble (Tolimieri, 1998c); preferred sleeping areas are near reef slopes with dense coral cover, particularly *Acropora cervicornis* (Dubin and Baker, 1982)

Sparisoma aurofrenatum	Use the back reef and patch reefs (Adams and Ebersole, 2002) and forereefs (5–15 m) (Nagelkerken and van der Velde, 2002)	Use the back reef, and to a lesser extent patch reefs (Adams and Ebersole, 2002); includes areas of *Thalassia* in foraging (Overholtzer and Motta, 1999); associates with forereef *Porites* rubble (Tolimieri, 1998c); more abundant in deeper habitats (Lewis and Wainwright, 1985)
Sparisoma chrysopterum	Favours mangroves (Nagelkerken and van der Velde, 2002)	Found on patch reefs (McAfee and Morgan, 1996); more abundant in shallower habitats (Lewis and Wainwright, 1985; Nagelkerken and van der Velde, 2002).
Sparisoma radians	Almost exclusively associated with dense stands of seagrass and macroalgae (Ogden, 1976; Lobel and Ogden, 1981)	
Sparisoma rubripinne	Favours shallow (2 m) forereefs (Nagelkerken and van der Velde, 2002)	Associates with forereef *Porites* rubble (Tolimieri, 1998c); uses seagrass and reef crests (McAfee and Morgan, 1996) and shallow forereefs (Nagelkerken and van der Velde, 2002)

were 11.1, 34.6, 11.4 and 6.3 fish 1000 m^{-2} (Nagelkerken *et al.*, 2000c). On the adjacent island of Curaçao, mean densities at four forereef sites (2, 5, 10 and 15) were 2.7, 2.3, 2.6 and 1.9 fish 100 m^{-2} (Nagelkerken and van der Velde, 2002). Mean densities for back reef/reef crest, shallow (2 m), mid-depth (5 m) and deep (10 m) forereef sites in St. Croix before and after the mass mortality of *Diadema* were 18.9, 37.8, 41.9 and 23.2 fish 310 m^{-2} (Carpenter, 1990a). Densities on a series of reef crest and forereef sites (8–12 m) in the Bahamas were 4.7 and 1.6 fish 100 m^{-2}, respectively (Kramer *et al.*, 2003), 12.8 on reef crests and 9.4 on forereef sites in St. Vincent (Deschamps *et al.*, 2003), 1.3 fish 100 m^{-2} on forereef sites in Cuba (Claro and Ramos, 2003) and 1.1–2.7 fish 100 m^{-2} on forereef sites in the Windward Netherlands Antilles (Klomp and Kooistra, 2003). The mean density of *Sp. viride* in four deep (15–20 m) forereef sites in southeastern Hispaniola was 0.14 fish 40 m^{-2} (Schmitt *et al.*, 2002). Terminal phase adults avoid carbonate platforms in gorgonian zones and sandy bottoms and seagrass beds with limited shelter (Gygi, 1975; Hanley, 1984; Bruggemann *et al.*, 1994b). Data from Belize found densities of ~4.5 200 m^{-2} for *Sp. viride* on a topographically complex *Montastraea* reef compared to ~0.5 200 m^{-2} for a gorgonian-dominated terrace (Mumby and Wabnitz, 2002). On a pavement with dense gorgonians in Bonaire, a density of ~175 fish ha^{-1} was reported (van Rooij *et al.*, 1996b). Densities of 13 fish 500 m^{-2} were recorded along the edge between a deep reef slope (~15–20 m) and algal plain (Barlow, 1975). On the sides of sheltered patch reefs in Panama, mean *Sp. viride* densities were ~5–10 fish 60 m^{-2} compared to ~0 60 m^{-2} on surrounding seagrass beds (McAfee and Morgan, 1996). Similarly, densities were shown to be low in *Thalassia* beds and a sand channel in Belize (densities of all Scarids 0.5 and 0.0 400 m^{-2}) (Lewis and Wainwright, 1985). On a coral–algal patch reef in Bermuda, densities were 0.96 fish 100 m^{-2} (Gygi, 1975), 6.4 fish 100 m^{-2} on patch reefs in St. Croix (Mateo and Tobias, 2004) and 2.8 fish 100 m^{-2} for a patch reef in Costa Rica (Fonseca and Gamboa, 2003). Adults were absent below a depth of 22 m in Bonaire (van Rooij *et al.*, 1998).

*3.4.3. Habitat functional values (*Sparisoma viride*; Figure 1)*

Forereef sand channels (all Scarids absent; Lewis and Wainwright, 1985) appear to have no functional value. Assigning functional values for other habitats is confused by wide ranges in densities caused by biogeographical and intrahabitat substrate variations and data presented for various life phases, but we define low functional values where densities are generally <1 fish 100 m^{-2} (mangroves, seagrass beds and escarpments). Functional values are medium where values are generally 1–2 fish 100 m^{-2} (gorgonian-dominated pavements and deep *Montastraea* reefs) and high where densities are generally >2 fish 100 m^{-2} (patch reefs, back reefs, reef crests and shallow *Montastraea* reefs). Documented ranges (Figure 1) are for juveniles and adults only and do not include recruits, but it appears that back reefs are particularly important for *Sp. viride* recruitment (Tolimieri, 1998b).

3.4.4. Acanthuridae distributions

There are three species of surgeonfish in the Caribbean (*Acanthurus bahianus*, *A. chirurgus* and *A. coeruleus*), which occur as individuals or large highly aggregated mixed-species schools (Reinthal and Lewis, 1986; Lawson *et al.*, 1999). Surgeonfishes are generally more common in shallower habitats (<5 m) than parrotfishes, but a similar combination of factors including topography, proximity to nearby shelter, predator abundance, density of territorial competitors and local availability of food resources dictates interspecific abundances and distributions (Bardach, 1958; Foster, 1985; Lewis and Wainwright, 1985). For example, Robertson (1991) showed that ~50% of adult *A. bahianus* on a patch reef were found feeding in sand and seagrass, while *A. coeruleus* rarely left the reefs and only ~15% of *A. chirurgus* were seen away from the reef. Predation is a particularly important factor structuring populations, and *A. chirurgus* and *A. bahianus* settlement in Panama was low at the edge of patch reefs, intermediate in the grazed halo and highest in dense seagrass because of predation rates (Sweatman and Robertson, 1994). Risk (1998) showed that the settlement of *A. bahianus* was increased in the presence of conspecifics and decreased in the presence of *Stegastes leucostictus*. Such interactions with conspecifics and other species may play an important role in ontogenetic habitat shifts (postsettlement persistence).

Like many fish species, juvenile surgeonfishes use shallow nursery areas before an ontogenetic shift into slightly deeper water (van Rooij *et al.*, 1996a; Nagelkerken *et al.*, 2000c). While such ontogenetic shifts are relatively easy on continuous areas of reef, adults of all three species relocate between isolated patch reefs and substantially alter the size and composition of populations so that postsettlement mortality or relocation overrides the effects of settlement patterns (Robertson, 1988). In a study in Bonaire, Nagelkerken *et al.* (2000c) showed that seagrass beds were most important for *A. chirurgus*, shallow reef areas were used by *A. bahianus* and *A. coeruleus* used a variety of biotopes including mangrove roots, seagrass beds and four depth zones from 0 to 20 m on the reef. On Curaçao, *A. chirurgus* mean densities in mangroves and seagrass beds were 0.7 and 0.6 fish 100 m^{-2}, while the other two species were absent (Nagelkerken and van der Velde, 2002). A single fish was seen in 60 m^2 of mangrove in Florida (Serafy *et al.*, 2003). The presence of surgeonfishes in mangroves and seagrass beds has also been shown in Florida, the Bahamas and Panama (Weinstein and Heck, 1979; Thayer *et al.*, 1987; Newman and Gruber, 2002). In Barbados, Lawson *et al.* (1999) showed that the density of small and large juvenile *A. bahianus* was highest in the back reef and declined in the reef crest and was lowest in a spur-and-groove habitat. Newly settled *A. coeruleus* were only found on the reef crest and in the spur-and-groove zone, but larger juveniles were more common in the back reef. On isolated patch reefs in Panama, Robertson (1988) documented that the settlement habitat of *A. bahianus* and *A. chirurgus* was the reef–seagrass interface (<3 m) with scattered corals and patches of bare rock. The settlement habitat for *A. coeruleus* was the outer shallow periphery of patch reefs (10 m wide, <2 m deep) plus areas in the emergent centres that consisted of rock substrate with sparse corals. Adams and Ebersole (2002) showed the importance of lagoonal patch reefs and rubble areas, as opposed to other lagoon habitats (seagrass, algal plain and sand), as nurseries for *Acanthurus* spp. in St. Croix but stated that these areas were used in preference to the back reef. In Barbados, Sponaugle and Cowen (1996) showed that the settlement pattern of *A. bahianus* was modified by postsettlement processes (e.g., habitat selection) of juveniles and this was more important than larval supply. There was some evidence that the postsettlement processes were linked to a preference for shallow depths, lower abundances of algal turf, less rock cover and lower rugosity and hence juveniles were usually found on shallow sand-rubble regions (Sponaugle and Cowen, 1996).

The density of all acanthurid species are grouped in many studies or can be calculated from reported values for each species. For example, across the Belize Barrier Reef, acanthurid density was 0.4, 50.5, 42.2, 31.5, 2.8, 0 and 2.0 fish 400 m^{-2} in a *Thalassia* bed, back reef, high relief spur and groove zone, low relief spur and groove zone, inner reef slope, sand channel and outer ridge, respectively (Lewis and Wainwright, 1985). In a back reef/reef crest site and three forereef sites (depths of 2, 5 and 10 m) in St. Croix, densities were 35.4, 349.3, 97.8 and 24.6 fish 310 m^{-2} (Carpenter, 1990a). Nagelkerken *et al.* (2000c) give densities in Bonaire as 13.6, 3.6, 102.4, 41.2, 13.9 and 9.7 fish 1000 m^{-2} in a seagrass bed, mangroves and four reef habitats (0–3, 3–5, 10–15 and 20–25), respectively. On the adjacent island of Curaçao, mean densities at four forereef sites (2, 5, 10 and 15) were 22.1, 6.7, 6.3 and 2.4 fish 100 m^{-2} (Nagelkerken and van der Velde, 2002). In a study of back reef habitats in Belize, adult density was 12.8 fish 100 m^{-2} in a mixed community compared to 0–2.4 fish 100 m^{-2} for macroalgal-dominated sites (Lewis, 1986). Juvenile densities at the same sites were 5.2 fish 100 m^{-2} (mixed community) and 1–12.1 fish 100 m^{-2} (macroalgal dominated). Also in Belize, a forereef at 12 m had a density of acanthurids of 0.9–1.6 25 m^{-2} (Williams *et al.*, 2001) and the density in a high relief spur-and-groove zone was 637.9 fish ha^{-1} (Reinthal and Lewis, 1986). The mean density of acanthurids in four deep (15–20 m) forereef sites in southeastern Hispaniola was 1.78 fish 40 m^{-2} (Schmitt *et al.*, 2002). Densities on patch reefs in St. Croix were ∼7 fish 60 m^{-2} and ∼3 fish 150 m^{-2} on a shallow *A. palmata*/*Millepora* reef in St. Thomas (Hay and Taylor, 1985). Lawson *et al.* (1999) did not survey *A. chirurgus* in Barbados, but densities for *A. bahianus* and *A. coeruleus* combined were 23.6, 4.9 and 1.6 fish 50 m^{-2} in back reef, reef crest and spur-and-groove habitats, respectively. Similarly, *A. chirurgus* was not surveyed in a shore zone, *A. palmata* zone, *A. cervicornis* zone, dropoff and upper reef slope in Bonaire, but densities for the other two species combined were ∼9,750, ∼1,000, ∼250, ∼1,000 and ∼50 fish ha^{-1}, respectively (van Rooij *et al.*, 1996a). Densities of *A. bahianus* and *A. chirurgus* on patch reefs and seagrass beds in St. Croix were 65.3 and 0.3 fish 100 m^{-2}, respectively (Mateo and Tobias, 2004). The mass mortality of *Diadema* affected surgeonfish populations, and in Panama, densities of *A. coeruleus* and *A. chirurgus* increased by 160–250%, but no changes were seen for *A. bahianus* (Robertson, 1991). Densities were also clearly affected by marine reserves in Barbados (Rakitin and Kramer, 1996) but not the Netherlands Antilles or Belize (Polunin and Roberts, 1993).

AGRRA surveys, conducted across the Caribbean from 1997 to 2000 (Kramer, 2003), counted acanthurids as an indicator of herbivory and represent an extensive database of densities on reef crests and shallow (generally 8–15 m) forereefs. All the following studies used the AGRRA protocol, but only fish counts collected using belt transects in specific habitats are included to ensure comparability with other studies. In Andros (Bahamas), densities varied from 9.9 to 12.7 on the reef crest and 4.0–4.7 fish 100 m^{-2} on the forereef (Kramer *et al.*, 2003). In Costa Rica, densities were 2.5 on a carbonate bank, 20.0 on a patch reef, 25.0 in a spur-and-groove zone and 3.2 fish 100 m^{-2} on a forereef platform (Fonseca and Gamboa, 2003). On forereef spurs in Cuba densities were 2.2–4.5 fish 100 m^{-2} (Claro and Ramos, 2003), 3.9–5.7 fish 100 m^{-2} on forereefs in Mexico (Núñez-Lara *et al.*, 2003), 11.1 fish 100 m^{-2} on fringing reefs in Curaçao (Bruckner and Bruckner, 2003) and 19.3 fish 100 m^{-2} in the Windward Netherlands Antilles (Klomp and Kooistra, 2003). In St. Vincent, densities were 12.0 on reef crests and 2.0 on the forereef sites (Deschamps *et al.*, 2003) and in the Turks and Caicos were 15.0 on patch reefs and 5.2–5.4 fish 100 m^{-2} on fringing reefs (Hoshino *et al.*, 2003). In reef crest sites in Venezuela, the mean density was 29.7 fish 100 m^{-2} and 11.0 fish 100 m^{-2} on fringing reefs (Posada *et al.*, 2003). The density on a series of fringing reefs in the Virgin Islands was 18.2 fish 100 m^{-2} (Nemeth *et al.*, 2003). In Abaco (Bahamas), densities were 27.8 and 51.4 fish 100 m^{-2} in a back reef and reef crest, respectively, and 7.7 and 8.6 fish 100 m^{-2} on fringing reefs in Belize and Bonaire, respectively (Kramer and Bischof, 2003).

3.4.5. Habitat functional values (Figure 1)

Forereef sand channels appear to have no functional value for surgeonfishes (Lewis and Wainwright, 1985). We define low functional values as densities generally <2, medium functional value as 2–10 and high functional value as >10 fish 100 m^{-2}. Therefore, we assign low functional values to mangroves, seagrass beds, deep *Montastraea* reefs and escarpments, medium functional value to shallow *Montastraea* reefs and high functional values to patch reefs, back reefs and reef crests. There are few data for gorgonian-dominated forereefs, but because of the lack of topographical complexity, we assign this habitat a low functional value.

3.4.6. Pomacentridae distributions

Nonplanktivorous damselfishes are a conspicuous component of the benthic reef fish community and defend small contiguous territories against intruding fishes (e.g., Randall, 1967; Itzkowitz, 1977b; Hay, 1981b). Territorial defence is so strong that surgeonfish and parrotfish density may be inversely related to damselfish density (Lewis and Wainwright, 1985). Damselfishes have a vital role within the ecology of a reef because of their abundance and territoriality. Importantly within the context of this review, damselfishes have specific habitat preferences so that their effects have significant spatial variation across a seascape. The effects of damselfishes are caused by the distinct biotic patches within damselfish territories having functional differences to benthic communities outside territories (Hay, 1985). Horn (1989) reviews the research on damselfishes and shows that fishes affect (1) coral recruitment, growth and bioerosion; (2) local microfaunal abundance; (3) nitrogen fixation by cyanobacteria and (4) algal abundance and local diversity. Algal mats within territories appear to inhibit settlement of corals by encouraging filamentous algae (e.g., Lobel, 1980). Conversely, there are data from the Great Barrier Reef showing coral recruits can be increased compared to nonterritory areas (e.g., Sammarco and Carleton, 1981), but it is not clear whether this represents a regional difference or reflects subtle variations between species or habitats. External bioerosion in damselfish territories generally decreases because there is less grazing and predation by fishes (Sammarco *et al.*, 1986), but internal bioerosion is unchanged (Sammarco *et al.*, 1987) or significantly increased (Risk and Sammarco, 1982). Damselfishes can significantly affect algal communities because many studies show biomass, and potentially productivity, is higher inside their territories (reviewed by Horn, 1989). The effects of damselfishes on algal biomass and diversity were investigated in a study by Brawley and Adey (1977) in Jamaica where outside damselfish territories on the Jamaican lower reef terrace (22 m) areas were heavily grazed, and there were only small quantities of noncrustose algae. In comparison, in the damselfish territories, there were many algal turf species covering an *A. cervicornis* framework and *Lobophora*. It was concluded that only calcified encrusting algae would be on the terrace if damselfishes were absent and that damselfishes significantly influence the dynamics of some reefs by increasing the abundance of turf algae and hence reef productivity. Effects were even more profound on the reef flat (0–2.5 m) because reef flat damselfish territories were contiguous, and therefore, the algal community across the whole zone had been altered (Brawley and Adey, 1977). Increases in algal diversity inside *Stegastes planifrons* territories (compared to outside) were also demonstrated on a back reef in Puerto Rico (Hinds and Ballantine, 1987). In contrast, other data show that damselfish species may increase the density of vegetation but not the species composition (de Ruyter van Steveninck, 1984). The effect of damselfishes on algal diversity is such that damselfishes are sometimes labelled *keystone species* of shallow reef areas (Hixon and Brostoff, 1983). Since there are a relatively large number of species of damselfishes in the Caribbean, the habitat preferences of perhaps the most studied species (*S. planifrons*) is described in detail here and patterns for other species are summarised elsewhere (Table 4).

Segastes planifrons is either absent from mangrove, lagoonal sand and seagrass habitats (Weinstein and Heck, 1979; Thayer *et al.*, 1987; Adams and Ebersole, 2002; Newman and Gruber, 2002; Serafy *et al.*, 2003) or in very low densities (0.1 and 0.01 fish 100 m^{-2} in mangroves and seagrass, respectively, in Curaçao; Nagelkerken *et al.*, 2000a) and prefers to recruit to coral heads (Booth and Beretta, 1994). For example, *S. planifrons* recruited exclusively to living coral on patch reefs in Panama at a rate of ~1.5 m^{-2} (Gutiérrez, 1998) and at two fringing reef sites (depths of 4.5–10 m and 12.7–13.3 m) in the U.S. Virgin Islands was 1.72 recruits 25 m^{-2} and 0.83 25 m^{-2}, respectively (Booth and Beretta, 1994). The relationship between *S. planifrons* and coral substrata has also been investigated by Tolimieri (1995) in the U.S. Virgin Islands, where densities of settlers on patch reefs ranged from 0 to ~8 m^{-2}. At a scale of 0.25 m^2, patch reefs consisting of *M. annularis* had higher numbers of settlers, caused by a microhabitat choice during settlement, but these small-scale recruitment patterns did not scale up to explain large-scale variations between sites. Recruitment rates on forereefs (6–10 m) throughout the Virgin Islands were from 0 to ~1.75 fish 30 m^{-2} (Tolimieri *et al.*, 1998). Itzkowitz (1977a) also indicated that juvenile *S. planifrons* were particularly associated with *Montastraea* corals.

An ontogenetic habitat shift of *S. planifrons* has been highlighted by Ebersole (1985) who showed that juvenile fish inhabited back reef areas of

Table 4 Habitat preferences of selected Caribbean Pomacentridae

Species	Juveniles	Adults
Microspathodon chrysurus	Rare on back reefs and commonly found on shallow forereefs in association with live and dead *Acropora* and *Millepora* (Itzkowitz, 1977a; Williams, 1991; Tolimieri, 1998c)	
Stegastes diencaeus	May firstly be attracted to the presence of conspecifics and secondly adopt a position adjacent to a live coral or *Acropora* rubble in preference to sand (Foster, 1985; Robertson, 1996; Tolimieri, 1998c); favours shallow (2–15 m) forereefs (Nagelkerken and van der Velde, 2002)	
Stegastes dorsopunicans	In back reefs, which have a lower biomass of turf algae than required by adults (Foster, 1985); settlers predominate on reef crests with a rocky substratum (Gutiérrez, 1998); favour shallow (2 m) forereefs (Nagelkerken and van der Velde, 2002)	Generally found in *Acropora palmata*/*Acropora* rubble habitats with a high biomass of preferred algal turf (Foster, 1985; Tolimieri, 1998c).
Stegastes leucostictus	Settles preferentially in shallow water (1–2 m depth) and almost exclusively in calm back reef areas (Shulman, 1984; Ebersole, 1985; McGehee, 1995; Robertson, 1996); areas of *A. palmata* are avoided (Ebersole, 1985)	Territories are in areas of living (all types) and dead corals (particularly *Porites* rubble) of $\sim$1 m^2 (Ebersole, 1985; Wellington, 1992; Tolimieri, 1998c) or more generally "small rubble and sand" or "low-profile rubble" (Itzkowitz, 1977a; Williams, 1991); may favour mangrove habitats (Nagelkerken and van der Velde, 2002)
Stegastes partitus	Recruit to back reefs but settle at similar densities on both the back reef and forereef in coral-rubble habitats, particularly *Montastraea annularis* and *Porites* rubble (Sponaugle and Cowen, 1996; Nemeth, 1997; Tolimieri, 1998c)	Adults are more abundant on the forereef (Nemeth, 1997), particularly between 5 and 15 m (Nagelkerken and van der Velde, 2002); differential mortality rates, which are higher in back reefs compared to forereefs, can explain apparent preferences for forereefs (e.g., McGehee, 1995)
Stegastes variabilis	Found in water deeper than 10 m because of habitat selection at settlement (Wellington, 1992; Robertson, 1996); possibly because of the lower levels of competition in deeper water, has no clear microhabitat associations, although it requires areas of living and dead corals and can have large territories up to 14 m^2 (Wellington, 1992; McGehee, 1995)	

sand with scattered corals in a narrow depth band (1.5–3.7 m), but adults were found on the main reef and other areas dominated by acroporids. The ontogenetic habitat shift means that adult *S. planifrons* are common on shallow forereef areas (e.g., McGehee, 1995; Gutiérrez, 1998) but are only found on branching or creviced coral heads, such as *Porites* and *Montastraea*, with relatively complex internal structure (Ebersole, 1985) and *Acropora* rubble (Tolimieri, 1998c). In a comparison between back reefs and shallow forereefs in Puerto Rico, *S. planifrons* was more abundant in the forereef (0.47 vs 0.05 individuals m^{-2}; McGehee, 1994). Lirman (1994) has documented a link between *S. planifrons* and *Agaricia tenuifolia* in Honduras and shown that adult fish prefer living foliose heads on the main reef, whereas juveniles favour dead foliose colonies in the lagoon (back reef). Lirman (1994) indicated that juveniles seem to settle onto adult territories until they are too large and then move to the lagoon before shifting back out onto the reef. *S. planifrons* actively defend their territories against conspecifics so ontogenetic shifts reduce competition for space between adults and juveniles. Densities of recruits were also correlated with the density of conspecific adults in the U.S. Virgin Islands (Booth and Beretta, 1994).

Acropora and *Porites* rubble are important microhabitats in back reefs (Tolimieri, 1998c) along with pure stands of *A. palmata* and *Agaricia agaricites* (Robertson *et al.*, 1981; Ebersole, 1985) and *Millepora* (Williams, 1991). In Jamaican back reefs, densities of *S. planifrons* were negatively correlated with patch size of *A. cervicornis*, indicating intraspecific territorial spacing on larger patches (Williams, 1978). The link between *S. planifrons* abundances and *A. cervicornis* patches can be further complicated by the pattern of patches. In Jamaica Itzkowitz (1977b) showed that colonies <1 m^2 had to be within 6 m of a larger colony to be inhabited. Densities in *A. cervicornis* patches in Jamaican back reefs were 0–2.0 fish m^{-2} (Itzkowitz, 1977b) and ~1.5–3.75 fish m^{-3} (Williams, 1978). There is evidence that female *S. planifrons* in particular favour *M. annularis* heads for territory sites (Williams, 1978). In Panama, *S. planifrons* has a "refuge" habitat (virtually only species found and mainly adults) of *Agaricia* at 1.5–10 m on the sides of patch reefs with densities across whole patch reefs of 0.1–1.5 m^{-2} (Robertson, 1996) but can reach 2.89 m^{-2} on patch reefs dominated by *Agaricia* (Robertson *et al.*, 1981). One of the few studies of the density of *S. planifrons* in a range of habitats was undertaken in Bonaire (van Rooij *et al.*, 1996a) and densities in a shore zone, *A. palmata* zone, *A. cervicornis* zone, dropoff and upper reef slopes were ~0, ~0, ~2,000, ~3,500 and ~1,000 fish ha^{-1}, respectively. On the adjacent island of Curaçao, mean densities at four forereef sites (2, 5, 10 and 15) were 1.0, 12.2, 26.0 and 28.8 fish 100 m^{-2} (Nagelkerken and van der Velde, 2002). The mean density of *S. planifrons* in four deep (15–20 m) forereef sites in southeastern Hispaniola was 1.3 fish 40 m^{-2} (Schmitt *et al.*, 2002).

*3.4.7. Habitat functional values (*Stegastes planifrons*; Figure 1)*

S. planifrons clearly favours habitats with corals and is either absent or at very low densities of ≤ 0.1 fish 100 m^{-2} in seagrass beds and mangroves, so these habitats have no functional value. Sand beds are also assigned no functional value because of the lack of coral cover, although data are absent. A single survey of an *A. palmata* reef crest indicated *S. planifrons* was absent (van Rooij *et al.*, 1996a), but because of the presence of coral heads in this habitat, it is likely to support individuals elsewhere and is assigned a low functional value. Patch reef and back reef habitats are obviously important sites for recruits and juveniles (e.g., Tolimieri, 1995) and with densities often >50 fish 100 m^{-2} (high functional values). Forereef *Montastraea* habitats are a preferred habitat of adult *S. planifrons*, with densities commonly 1–50 fish 100 m^{-2} (medium functional values). Data are scarce for gorgonian-dominated habitats and escarpments, but the low coral cover and low primary productivity in these habitats, respectively, indicate that their functional values are probably low.

3.4.8. Diadema antillarum *distribution*

Diadema antillarum inhabits a range of habitats, particularly rock, coral reef, mangrove roots, seagrass beds and sand (Randall *et al.*, 1964). *Diadema* has intermediate abundances in very shallow water because excessive wave action affects grazing rates (Foster, 1987) but intertidal densities can be high (Bauer, 1980). On forereefs, densities are highest from 2 to 10 m (~15 m^{-2} in heavily fished reefs in Jamaica) and then decrease with increasing depth, and *Diadema* is effectively absent from <20–25 m (e.g., Ogden and Lobel, 1978; Liddell and Ohlhorst, 1986; Morrison, 1988; Jackson, 1991). *Diadema* densities are also correlated with habitat structural complexity and cover of algal-covered, dead coral substratum (Weil *et al.*, 1984). Density patterns may also vary temporally; in Panama, *Diadema* abundance declined or disappeared from reef flats during seasons of repeated subaerial exposures, but recolonised the habitat during periods of higher water levels (Cubit *et al.*, 1986). Within shallow areas, *Diadema* is strongly correlated with changes in structural heterogeneity (Lewis and Wainwright, 1985) but is found across coral reefs along with sandy areas and *Thalassia* beds (Lessios, 1991). Structural heterogeneity is also important for juvenile *Diadema* as individuals recruit into small crevices in the reef, but this process is further dependent on low algal biomass (Bak, 1985).

Reflecting these general trends, an extensive study throughout the West Indian Marine Province found densities of 2.4–25.8 m^{-2} for different types of reef crests (excepting one anomalous site in Tobago with a density of

0.04 m^{-2} and ≥ 7.8 when *A. palmata* was common), 0.5–4.5 m^{-2} for gorgonian-dominated habitats, 9.8 m^{-2} for shallow (<7 m) *Montastraea* reefs and 0.1–1.7 for deep (>10 m) *Montastraea* reefs (Bauer, 1980). In Venezuela, mean densities were 2.74 m^{-2} in the inner reef flat (back reef), 3.10 m^{-2} on the outer reef flat (reef crest), 5.6 m^{-2} on the reef front and 0.67 m^{-2} on the deep forereef (Weil *et al.*, 1984). Across the Belize Barrier Reef, densities were 0.13 m^{-2} in the back reef, 4.31 m^{-2} in a high relief spur and groove zone, 0.05 m^{-2} in a low relief spur and groove zone, 0.14 m^{-2} on the inner reef slope and 0.69 m^{-2} on the outer ridge (Lewis and Wainwright, 1985). In a back reef/reef crest site and three forereef sites (depths of 2, 5 and 10 m) in St. Croix, densities were 6.4, 13.4, 9.0 and 5.8 m^{-2} (Carpenter, 1990a). Hughes *et al.* (1987) reviewed a series of Jamaican studies to give densities of 3.9 m^{-2} for a back reef site, 8.1–11.7 for shallow (<10 m) forereefs and 3.5–12.2 m^{-2} for deep (>10 m) forereefs and 0.7 m^{-2} for a site at 20 m. High densities of 33.5–72.8 m^{-2} have been recorded for Jamaican patch reefs (Sammarco, 1982). Further data for Jamaica gave densities of 3.1–3.4, 8.1–9.1 and 13.6–18.0 individuals m^{-2} for the back reef, shallow forereef (3 m) and deeper forereef (10 m), respectively (Steneck and Dethier, 1994), and *Diadema* densities of 5.8–15.8 m^{-2} were recorded on a Jamaican reef crest (Morrison, 1988). Bak *et al.* (1984) give densities on the deep (9–36) reef slope in Curaçao as 0.26–0.73 m^{-2}, which contrasted with values of $\sim$12 m^{-2} for an *A. palmata* and shallow forereef zones (Bak and van Eys, 1975). Densities on patch reefs in St. Croix were 6.7–12.0 m^{-2} (Ogden *et al.*, 1973; Hay and Taylor, 1985). *Diadema* are absent from sand channels on the forereef (Lewis and Wainwright, 1985) and densities in seagrass beds vary from 1.2–2.8 m^{-2} in the Florida Keys (Randall *et al.*, 1964; Bauer, 1976, 1980) to being absent in Belize (Lewis and Wainwright, 1985).

The abundance of *Diadema* in shallow water exacerbates the influence of herbivory by parrotfishes, surgeonfishes and damselfishes on benthic communities, adding to the significant differential effects of herbivores across the seascape. There is extensive research on the effect of *Diadema* on algal communities, but much of the work is small scale (e.g., on patch reefs) and often on overfished areas (Hay, 1984). For example, *Diadema* grazed $\sim$20% of the monthly net benthic primary production of a fringing coral reef in Barbados (Hawkins and Lewis, 1982). *Diadema* has a strong preference for algal turf, and in enclosure experiments, algal species richness and algal community primary production were maximised at intermediate *Diadema* densities (Carpenter, 1981). In addition to the effects on reefs, *Diadema* grazing is a major factor in establishing sandy "halos" around patch reefs (Ogden *et al.*, 1973). Although *Diadema* has a strong preference for algal turf, the seasonal reduction of this food source can result in the use of alternatives, particularly live coral (Carpenter, 1981). *Diadema* has a further effect on coral community structure in shallow water because of the interaction between algae and coral recruits (Sammarco, 1980).

Much of the work on the ecology of *Diadema* is on relatively natural reefs, but as previously mentioned, the abundance of *Diadema* was dramatically reduced in the early 1980s by a mass mortality caused by a waterborne pathogen (for a review of the spread of the disease, see Lessios *et al.*, 1984). There is also evidence of another smaller mortality event in 1990/91 in the Florida Keys (Forcucci, 1994), leading to densities no greater than 0.05 m^{-2} (Chiappone *et al.*, 2002a). Densities elsewhere were also <1 m^{-2}, even in shallow water (Bak *et al.*, 1984; Hunte *et al.*, 1986; Liddell and Ohlhorst, 1986; Carpenter, 1988; Levitan, 1988; Moses and Bonem, 2001). Since the premortality distribution of *Diadema* varied significantly across Caribbean reefs, it was inevitable that mass mortality should have differential effects across habitats with the most significant effects in the upper 10 m. Carpenter (1990b) studied the patterns of effects across different zones, namely the back reef, reef crest, shallow (<2 m), middepth (<5 m) and deep (10 m) forereefs. Prior to mortality, *Diadema* densities were highest in the shallow forereef and decreased with depth, so at 10 m, densities were the same as the back reef and reef crest. Mass mortality reduced densities over all zones by 95–99%. *Diadema* mortality had the effect of increasing algal biomass by 319, 439, 305 and 22% in back reef, shallow forereef, middepth forereef and deep forereef, respectively (i.e., the effect was less dramatic in deeper water). Algal productivity per unit area initially decreased by 37% in the back reef, then increased with increasing biomass. At 2 m, productivity decreased initially but, unlike the back reef, did not subsequently increase. There were no significant changes in productivity at 5 and 10 m. Productivity per unit biomass also decreased at all sites except 10 m and was clearly correlated with the previous densities of *Diadema*. Although the shallow zones were more productive than premortality values, the additional algal biomass was not available to herbivores. The increased, but unavailable, algal biomass led to an increase of algal detritus in the back reef and lagoon as algae died and were dislodged, leading to a fundamental change in the functioning of these communities (Carpenter, 1990b). In Jamaica, the mean effect of *Diadema* mortality on benthic coral communities was an algal abundance increase of 95% and a coral cover decrease by up to 60% of original levels (Hughes *et al.*, 1987). Hughes *et al.* (1987) showed that reduction of coral cover was especially apparent in shallow water, in part because deeper corals are more resistant to overgrowth.

The potential recovery of *Diadema* to reestablish the spatial variations in densities that were apparent premortality remains enigmatic. Following mass mortality, there has been only limited recovery of *Diadema* populations, despite the apparently vacant niche. Low recovery rates could be caused by low fertilisation success, lack of suitable substrates for recruitment, postsettlement mortality and interspecific competition (summarised by Chiappone *et al.*, 2002b). However, a study by Edmunds and Carpenter (2001) on the north coast of Jamaica found evidence of a recovery of *Diadema* on shallow forereefs (densities ~5 m^{-2}). The increased densities of *Diadema* have reduced macroalgal cover and increased the density of juvenile corals. Whether such a recovery of *Diadema*, and the potential to increase coral cover, will occur in other parts of the Caribbean is an important issue for future research.

*3.4.9. Habitat functional values (*Diadema antillarum*; Figure 10)*

Diadema appear to be absent from forereef sand channels (Lewis and Wainwright, 1985) and escarpments (e.g., Morrison, 1988), so these habitats appear to have no functional value. Although *Diadema* are recorded as occurring among mangrove roots (Randall *et al.*, 1964), there are no quantitative data on their density and this habitat is assigned a putative low functional value. There is significant intrahabitat variation in natural densities in the remaining habitats, but we assign a low functional value to habitats where densities are generally <1 m^{-2} (deep *Montastraea* reef), medium function value to habitats where densities are generally 1–5 m^{-2} (seagrass beds, back reefs and gorgonian-dominated forereefs) and high functional value to habitats where densities are generally >5 m^{-2} (patch reefs, reef crests and shallow *Montastraea* reefs). The effect of the mass mortality was to reduce densities of *Diadema* to <1 m^{-2}, so we present a second set of functional values for post-1983 habitats where each is reduced to a low functional value, although higher values have been recorded in certain areas (Edmunds and Carpenter, 2001).

3.5. Tertiary production

Tertiary producers in a coral reef ecosystem encompass a wide range of taxa, but for the purposes of this chapter, our discussion is limited to the dominant group, fishes. As for secondary production, we use tertiary producer densities as a proxy for tertiary production; the differences between habitat types of key variables to convert biomass to production are unclear. Since there is a high diversity of predators, this section provides an overview of the densities of tertiary producers in different habitat types and, with the exception of specific examples, does not include the habitat preferences of all individual species, as was possible for secondary producers. Furthermore, although the interactions between densities of primary and secondary producers have been well studied, the effects of varying densities of tertiary producers on secondary producers are less clear. Although tertiary consumers also feed on one another (e.g., Hobson, 1991), *tertiary producers* is used here as a generic term for species not feeding on primary producers.

3.5.1. Planktivores

The diverse assemblage of planktivores present on reefs can be classified as "tertiary producers" because most feed on zooplankton (reviewed by Hobson, 1991), which are most abundant along reef edges adjacent to deep water (Hobson and Chess, 1978, 1986). Caribbean diurnal planktivores, such as *Chromis cyanea* and *Clepticus parrae*, were most abundant in deeper zones (terraces and deep lagoonal patch reefs) in the San Andres Providencia archipelago where there is a high availability of prey (Mejia and Garzon-Ferreira, 2000). Similarly, Alevizon *et al.* (1985) reported dramatically higher abundances of both *C. cyanea* and *Chromis multilineata* in two forereef habitats compared to the reef crest and back reef patch reefs in the Bahamas. In Curaçao, mean densities of *C. cyanea* were 0.1, 4.8, 76.5 and 65.3 fish 100 m^{-2} on four forereef sites (2, 5, 10 and 15 m, respectively) (Nagelkerken and van der Velde, 2002). At the same sites, densities of *C. multilineata* were 3.6, 13.4, 48.5 and 14.0 fish 100 m^{-2} and densities of *C. parrae* were 0.6, 0.1, 3.9 and 10.8 fish 100 m^{-2}. The mean densities of *C. cyanea*, *C. multilineata* and *C. parrae* in four deep (15–20 m) forereef sites in southeastern Hispaniola were 36.4, 16.7 and 2.2 fish 40 m^{-2}, respectively (Schmitt *et al.*, 2002). *Chromis* spp. and *C. parrae* were found on patch reefs and in back reefs but comprised <3% of the individuals in these habitats (Adams and Ebersole, 2002). *Chromis* spp. and *C. parrae* are not found in mangroves and seagrass beds (Weinstein and Heck, 1979; Thayer *et al.*, 1987; Nagelkerken and van der Velde, 2002; Newman and Gruber, 2002; Serafy *et al.*, 2003).

Smaller individuals of planktivorous species are often more widely distributed because of the high predation pressure on deeper reefs, and if shelter is limited at the reef edge, even the larger individuals found in this habitat may have migrated from other areas to feed (Hobson, 1991). In Mexico, the mean densities of juvenile *C. cyanea* and *C. parrae* on a series of forereefs (12 m) depth were 26.1 and 17.5 fish 100 m^{-2}, respectively (González-Salas *et al.*, 2003). Available shelter at the reef edge is dependent on the type of benthic community and rugose: coral-rich habitats provide better shelter than habitats with low coral cover. For example, *C. cyanea* is typically found in aggregations (<100) centred on a prominent coral (de Boer, 1978). In addition to shelter requirements, on the Great Barrier Reef large, stationary aggregations of planktivores have been documented where water movement brings abundant food to the reef edge (Thresher, 1983), and this seems likely to be true in the Caribbean. Therefore, densities of planktivores along a reef edge will be patchy because of both variations of water movement and changes of benthic community.

3.5.2. Habitat functional values (Figure 1)

There are few habitat-specific data for densities of planktivores, but it is clear that the highest densities (>90 fish 100 m^{-2}) are found in deeper *Montastraea* reefs and presumably, although data are particularly scarce, escarpment habitats (high functional values). Densities on shallower *Montastraea* reefs are generally lower (18.3–128.9 fish 100 m^{-2}), and this habitat is assigned a medium functional value. All the other reef habitats (patch reefs, back reefs, reef crests and gorgonian-dominated forereefs) have some shelter and will be inhabited by planktivores, but food availability is limited by the distance to deepwater (low functional values). Mangroves, seagrass beds and sand have no functional value.

3.5.3. Invertivores

Fish predation on benthic invertebrates is reviewed by Jones *et al.* (1991), and there appears to be considerable spatial variation in both the densities and the effects of invertivores, but data are limited despite between 27 and 56% of some fish communities being benthic invertebrate predators. The potential effects of invertivores on invertebrate populations was highlighted by Keller (1983) in Jamaica where fish predators influence the population dynamics of the urchins *Tripneustes ventricosus* and *Lytechinus variegatus* in seagrass beds. Corallivorous fishes represent a discrete group of benthic invertivores that are worthy of special mention as they might be expected to vary spatially between habitats in accordance with coral cover. Despite efforts to link butterflyfish (Chaetodontidae) abundances with coral cover (e.g., Findley and Findley, 2001), there are few obligate corallivores in the Caribbean and this link is less clear than might be expected. However, Chaetodontidae species do tend to be most abundant on shallow forereefs, where coral cover is highest (e.g., Findley and Findley, 2001).

Major families of invertivores on reefs include Labridae, Holocentridae and Balistidae, but we focus on the habitat preferences of the Haemulidae (grunts) because they are arguably the best studied and have some fisheries importance. Grunts make ontogenetic migrations between habitats because of changes of diet and habitat requirements for reproduction, and Appeldoorn *et al.* (1997) showed a general inshore to offshore ontogenetic migration for *Haemulon plumieri* in Puerto Rico and the Bahamas. Small juvenile *H. plumieri* were among *Thalassia* and small coral colonies then migrated to patches of *A. cervicornis* in seagrass beds and sheltered reef edges near *Thalassia*. Subadults preferred reefs, high relief back reefs or areas with moderate surge and sand with gorgonians. Adult *H. plumieri* were usually solitary either on forereefs or, if inshore, on a reef–sand interface.

Grunts use a range of nursery habitats but show interspecific variations in habitat preferences (Nagelkerken *et al.*, 2000c). Seagrass beds are important for juvenile *Haemulon flavolineatum* and *H. sciurus* and shallow reefs for *H. chrysargyreum*. Shulman and Ogden (1987) showed that 95% of *H. flavolineatum* settled onto sand and in seagrass beds and then migrated to nearby reefs and the remaining 5% settled directly onto reef structures. Some grunts may use lagoon patch reefs and rubble areas as nurseries in preference to the back reef and other lagoon habitats (Nagelkerken *et al.*, 2000c; Adams and Ebersole, 2002). If lagoonal habitats such as seagrass beds are scarce, higher densities of grunts settle directly onto reefs (Tupper and Juanes, 1999). Lindeman *et al.* (1998) provides a detailed discussion of grunt settlement patterns within Biscayne Bay, Florida. Mangroves are also important nursery habitats for grunts (Thayer *et al.*, 1987; Newman and Gruber, 2002). The role of mangroves for grunts was clearly demonstrated in Belize by Mumby *et al.* (2004a) who showed that in reef systems (e.g., atolls) where mangroves were present, Haemulidae biomasses on patch reefs, shallow forereefs and *Montastraea* reefs increased by 478%, 240% and 40%, respectively, compared to systems where mangrove was absent. Habitat preferences of adult grunts are less well studied than those of the juveniles, but Gaut and Munro (1983) provide an excellent summary table of the characteristic habitats of 14 species of Haemulidae. Although adult grunts have preferred diurnal habitats, they also undertake nocturnal migrations to lagoonal feeding areas, particularly seagrass beds (Ogden and Zieman, 1977). This functional link between habitats is discussed in more detail in Section 4.1.

To assign habitat functional values for invertivores, we review published densities of *H. flavolineatum* as a representative species of the Haemulidae. In Curaçao, juvenile densities were 82.7–99.8 and 15.1–32.1 fish 100 m^{-2} in mangroves and seagrass beds, respectively, with significant decreases in density at night (Nagelkerken *et al.*, 2000a,b; Cocheret de la Morinière *et al.*, 2002; Nagelkerken and van der Velde, 2002). The decreased densities in the seagrass at night (1.4 fish 100 m^{-2}) reflected juveniles, which are susceptible to predation, seeking shelter and censuses only counting larger nocturnally migrating individuals (Nagelkerken *et al.*, 2000b). Densities of 0–21 fish 500 m^{-2} were given for surveys in seagrass beds at night in St. Croix (Ogden and Zieman, 1977). On the adjacent island of Bonaire, densities in mangroves and seagrass beds were 59.9 and 115.3 fish 1000 m^{-2}, with seagrass cited as the most important biotope for juveniles (Nagelkerken *et al.*, 2000c).

Where mangroves were scarce (St. Croix), juvenile *H. flavolineatum* recruited to seagrass beds and back reefs and peak densities in back reefs were 1.1–1.3 fish m^{-2} (Shulman and Ogden, 1987). In St. Croix, densities on seagrass beds and patch reefs were 0.5 and 51.0 fish 100 m^{-2}, respectively (Mateo and Tobias, 2004) and 4.5 fish 100 m^{-2} for a patch reef in Costa Rica (Fonseca and Gamboa, 2003). Densities on a series of reef crest sites in the Bahamas were 21.0 fish 100 m^{-2}, respectively (Kramer *et al.*, 2003). Densities on the forereef in Curaçao were 0.5, 4.0, 2.7 and 2.2 fish 100 m^{-2} at 2, 5, 10 and 15 m, respectively (Nagelkerken and van der Velde, 2002). Densities on the forereef in Bonaire were 52.4, 37.4, 12.4 and 2.9 fish 1000 m^{-2} at 0–3, 3–5, 10–15 and 20–25 m, respectively (Nagelkerken *et al.*, 2000c). The mean density of *H. flavolineatum* in four deep (15–20 m) forereef sites in southeastern Hispaniola was 0.71 fish 40 m^{-2} (Schmitt *et al.*, 2002) and 5.5 fish 100 m^{-2} on shallower (8–12 m) forereef sites in Cuba (Claro and Ramos, 2003). Densities of *H. flavolineatum* (>15 cm) were 0.13–0.4 (back reef) and 2.92–5.8 (crest spurs) fish 240 m^{-2} and 9.7–23.17 fish (>5 cm) 400 m^{-2} on shallow fringing reefs in Barbados with no significant difference inside and outside a marine reserve (Rakitin and Kramer, 1996; Chapman and Kramer, 1999). There was also no significant difference in abundances inside and outside a reserve in Belize, but abundance, mean length and biomass of *H. flavolineatum* were higher inside a reserve in Saba (Polunin and Roberts, 1993).

*3.5.4. Habitat functional values (*Haemulon flavolineatum*; Figure 1)*

Mangroves, seagrass beds, patch reefs, back reefs and reef crests appear key habitats for *H. flavolineatum*, particularly as nursery habitats, with densities generally >5 fish 100 m^{-2} and are assigned high functional values. Seagrass beds are also important nocturnal feeding areas for adult grunts (Ogden and Zieman, 1977). Densities on forereefs (shallow and deep *Montastraea* reefs) are generally 1–5 fish 100 m^{-2} and are assigned medium functional values. Escarpments are assigned a low functional value as densities appear to be <1 fish 100 m^{-2}. There are few data for gorgonian-dominated forereefs, but the low topographical complexity indicates that this habitat may have a low functional value. Sand channels, with no structural relief, are likely to have no functional value.

3.5.5. Piscivores

Piscivores are a diverse group that can comprise up to 53% of the species in an area (Hixon, 1991). There are few available data suggesting overall patterns of piscivore densities across a reef profile and there has been little systematic work demonstrating predation rates across mangrove, lagoon and reef habitats. Even across the reef itself, such empirical data are scarce compared to the information available on herbivory and its consequent effects on algal zonation. However, the habitat preferences of individual species are well studied, and we initially present a detailed discussion of the habitat requirements of the commercially important *Epinephelus striatus* (Nassau grouper). The review of *E. striatus* is followed by a more general discussion of the habitat preferences of other serranids and lutjanids. The detail provided for *E. striatus* reflects (1) the amount of empirical data available in the literature and (2) the research interest in constructing spatially-explicit population models to aid conservation of remaining stocks of this species.

A significant proportion of the work on *E. striatus* juveniles and their ontogenetic shifts has been conducted in the central Bahamas and further research is needed to refine the characteristics of key habitats and assess variations in habitat preferences across the Caribbean region. Eggleston (1995) showed that recently settled fish resided, generally solitarily, within coral clumps (especially *Porites* spp.), which are covered by macroalgae (especially *Laurencia*) in off-reef tidal creek systems and lagoons (mean density 0.37–2.12 fish m^{-2} with a maximum of 8 m^{-2}) and absent in seagrass. *Laurencia* cover was, therefore, positively correlated with postsettlement grouper density, but algal displacement volume, numbers of holes, ledges and sponges were not significant determinant factors. Densities of juvenile *E. striatus* in macroalgal-dominated tidal creeks are an order of magnitude higher than any other habitat (Eggleston, 1995; Dahlgren and Eggleston, 2001), but other substrata (e.g., seagrass or corals without macroalgae) are utilised, particularly in areas that lack expansive macroalgal meadows. Hence, Colin *et al.* (1997) record recently settled *E. striatus* on artificial substrates (cement blocks and conch shells), natural reefs and rubble mounds protected by the sand tilefish (*Malacanthus plumieri*).

Larger juveniles tend to reside outside or adjacent to algal-covered coral clumps and, like smaller juveniles, are mostly solitary (88%), and densities were 0–0.06 m^{-2} (Eggleston, 1995). The ontogenetic shift from algal clumps seems to occur when the advantages of the higher growth rates, which are possible outside *Laurencia* clumps, outweigh the need to avoid predators (Dahlgren and Eggleston, 2000, 2001). Predation rates increase with decreasing size, so small juveniles must remain within the algal-covered coral clumps. When *E. striatus* juveniles are large enough (typically 120–150 mm), they tend to exhibit an ontogenetic habitat shift from patches of macroalgae and *Porites* spp. to patch reef habitats (Eggleston, 1995). On patch reefs, *E. striatus* (like all serranids) exhibit high site fidelity to territories (e.g., Eggleston *et al.*, 1997). Territories within a patch reef environment may span several patches and groupers have been observed moving freely from reef to reef but exhibit homing tendencies to their territory (Bardach, 1958; Beets and Hixon, 1994). There is also evidence on artificial and natural patch reefs (~0.04 fish m^{-2}) in the U.S. Virgin Islands that larger individuals were found on reefs with larger shelter holes (Beets and Hixon, 1994).

It has long been recognised that groupers move into deeper water as they mature and adult *E. striatus* are widely dispersed on coral rich forereefs (e.g., Bardach, 1958). Adults are highly sedentary living among the benthic community in holes, caves and crevices (Eggleston, 1995; Chiappone *et al.*, 2000). Although groupers are seen in a variety of habitats in the 1–300 m depth range (Chiappone *et al.*, 2000), dependence on specific habitat characteristics appears relatively strong. Habitat dependence occurs because groupers commonly feed by ambushing prey and are more dependent on hard substrate habitat with suitable shelter than other predators such as lutjanids (Parrish, 1987; Sluka *et al.*, 2001). Therefore, existing research has more commonly linked *E. striatus* densities to high or moderate topographical relief (Sluka and Sullivan, 1996; Sluka *et al.*, 1996b, 1997). In the heavily fished Florida Keys, mean densities were 0.045 fish 100 m^{-2} on patch reefs, 0.04 100 m^{-2} in a high-relief spur-and-groove zone, 0.01–0.02 100 m^{-2} in a low-relief spur-and-groove zone and 0.04 100 m^{-2} in a deep (20–30 m) forereef slope (Sluka *et al.*, 1998, 2001). Densities in the Bahamas were ~0.2–0.4, ~0.1–0.25 and ~0.1–0.35 fish 100 m^{-2} on channel reefs, windward hard-bottoms and fringing reefs, with higher densities inside a marine reserve (Sluka *et al.*, 1996a). Sluka *et al.* (1997) also clearly showed the effect of the same marine reserve on *E. striatus* with a biomass inside a park of 574 g 100 m^{-2} compared to 118–156 g 100 m^{-2} outside.

Reproductively active *E. striatus* have specific habitat requirements for transient mass spawning events, but they are poorly understood. Mass spawning sites have commonly been seen near continental shelf breaks or the edges of insular shelves (Colin *et al.*, 1997; Domeier and Colin, 1997). Further work is required to refine the location of specific spawning sites based on requirements such as available migration routes and oceanographic currents that transport larvae to optimal settlement conditions (e.g., Colin *et al.*, 1997). Fish have been documented to migrate at least 220 km (Bolden, 2000), so the functional value of particular spawning sites must be very high. The mean number of *E. striatus* at an aggregation site in Little Cayman was 400–5200 individuals (Whaylen *et al.*, 2004).

E. striatus shows a pattern typical of many larger serranids of an ontogenetic shift from lagoonal nursery grounds to deeper forereef areas as adults. Density patterns are different for the smaller groupers, *Epinephelus cruentatus*, *E. fulvus*, *E. guttatus* and *E. adscensionis*. *E. cruentatus* prefers channel reefs (Sluka *et al.*, 1996b), particularly areas with high relief. High coral cover provides high topographical relief, and *E. cruentatus* densities are correlated with coral cover, especially that of *M. annularis* and *Agaricia*. *E. cruentatus* juveniles are found at all depths but have a highly variable distribution (Luckhurst and Luckhurst, 1977; Nagelkerken, 1977; Sluka *et al.*, 1994). *E. fulvus* prefers patch reefs surrounded by sandy shoals and seagrass beds (Sluka *et al.*, 1994) and low-relief windward hard-bottom sites (Sluka *et al.*, 1996b). *E. guttatus* also favours windward hard-bottom sites. In the Leeward and Windward Islands, *E. fulvus* and *E. guttatus* are very abundant on sandy bottoms with isolated coral patches (Nagelkerken, 1981). *E. adscensionis* was most abundant on fringing reefs in the Bahamas compared to channel reefs or windward hard-bottom areas (Sluka *et al.*, 1996b).

Adult lutjanids generally have a weaker habitat dependence than serranids because they lead less sedentary lives and are less reliant on an ambush strategy, which requires specific habitat characteristics (Parrish, 1987). Like serranids, juvenile snappers have specific lagoonal nursery habitat requirements. Nursery habitats are generally in shallower water than adults, and readers are referred to Lindeman *et al.* (1998) for a detailed analysis of the habitat preferences of newly settled lutjanids. Almost all adult and juvenile snappers associate strongly with either a hard-bottom area or a habitat with some structural relief such as tidal creeks and mangroves (Parrish, 1987; Thayer *et al.*, 1987; Newman and Gruber, 2002). Indeed, the absence of mangroves as a nursery habitat reduces the biomass of adult snapper seen on adjoining reefs (Mumby *et al.*, 2004a). Specifically, *Lutjanus analis* are frequently associated with seagrass beds near inlets and patch reefs (Mueller *et al.*, 1994). *L. apodus* juveniles are found among mangrove prop-roots, tide pools and shallow lagoonal areas; small adults are common in *A. palmata* areas and larger individuals are found in both mangrove and coral reef habitats (Rooker, 1995; Nagelkerken *et al.*, 2000c). Juveniles of *Lutjanus mahogoni* and *L. griseus* are found in seagrass beds in bays, mangroves or in shallow water along the shore; larger individuals are commonly near stands of *A. palmata* and escarpments while adults are found in deeper zones (Nagelkerken *et al.*, 2000c; Nagelkerken and van der Velde, 2002). However, newly settled stages of *L. griseus* are not found on hard-bottom communities (Lindeman *et al.*, 1998). Lirman (1999) showed that in Florida and the U.S. Virgin Islands, areas of *Acropora palmata* had higher abundance of snappers than areas without this coral, which provides high topographical relief. In contrast to many other snappers, *Ocyurus chrysurus* is perhaps least constrained in its feeding environment, as it forages freely throughout much of the water column for plankton and small fishes (Parrish, 1987). Juvenile *O. chrysurus* (<8 cm) are particularly common and relatively sedentary in seagrass beds in bays and stony, sandy areas close to shore (Watson *et al.*, 2002) and mangroves (Nagelkerken and van der Velde, 2002). Adults are mainly in more rugose areas closer to escarpments (Watson *et al.*, 2002).

*3.5.6. Habitat functional values (*Epinephelus striatus*; Figure 1)*

Assigning functional values based on the density of *E. striatus* is complicated by the effects of fishing and marine reserves and the lack of systematic density assessments across seascapes. However, macroalgal tidal creek systems appear to be the most important settlement areas for *E. striatus* with densities up to 212 fish 100 m^{-2} (Eggleston, 1995) and are assigned a high functional value for mangroves. Though less important than tidal creeks in the Bahamas, seagrass beds also function as settlement areas, particularly in areas without *Laurencia* clumps in tidal creeks, and are given a medium functional value. Patch reefs are an important habitat during ontogenetic migration (Eggleston, 1995), although densities vary significantly and are assessed as having a high functional value. Densities on forereef habitats vary from 0.1 to 0.35 fish 100 m^{-2} and are assigned a medium functional value (gorgonian-dominated forereefs and shallow and deep *Montastraea* habitats). A single published density for an escarpment was <0.1 fish 100 m^{-2}, but this habitat is often important for mass spawning (Domeier and Colin, 1997) and thus is assigned a medium functional value. Few studies discuss the use of back reefs and reef crests, but the offshore ontogenetic migration indicates that individuals may use these habitats and they are given putative low functional values. Sand channels, with no structural relief, are likely to have no functional value.

3.6. Densities of *Panulirus argus* and *Strombus gigas*

Panulirus argus (Caribbean spiny lobster) and *Strombus gigas* (queen conch) are two of the most important fishery species in the Caribbean (Birkeland, 1997; Cochrane and Chakalall, 2001). The high commercial demand for the two species and the need to conserve remaining stocks have led to considerable research interest in mapping their distributions and constructing population dynamics models, so we include a detailed review of their habitat preferences. *P. argus* feeds mainly on benthic autotrophs, gastropods and bivalves, and *S. gigas* feeds on detritus, benthic autotrophs and polychaetes (Opitz, 1996), so they are discussed here separately from secondary and tertiary producers.

3.6.1. Panulirus argus

Panulirus argus larvae have a well-documented series of pelagic stages (Butler *et al.*, 2001). As soon as *P. argus* larvae move inshore to settle, they begin a complex spatial interaction with the seascape. Firstly, planktonic larvae must avoid predation, which is highest over coral reefs but lower near shore (Acosta and Butler, 1999). Subsequent predation on benthic settlers is also higher on the reef than in vegetated habitats in a lagoon and bay. To minimise predation, postlarval *P. argus* exhibit several behavioural traits, such as migration during the darkest lunar phase, use of surface waters to move across the reef and settlement in vegetated habitat (Acosta and Butler, 1999). Settlement preferences have also been seen in the Bahamas where surveys showed that there were mainly juveniles and preadults on seagrass beds with no individuals on unvegetated areas (Smith and van Nierop, 1986). Further work in the Bahamas demonstrated that some nursery habitats always had higher settlement than others because of wind-induced along-shore transport (Eggleston *et al.*, 1998b). In addition to along-shore transport, other biological and physical factors such as postlarval patchiness and coastal upwelling were important. Further, there was a general decline in settlement rates from more seaward nursery sites to more inshore sites. The seaward-inshore decrease in settlement rates was caused by the dilution of larvae, as incoming water mixed with water on the banks, and the ever decreasing abundance of larvae still available to settle (Eggleston *et al.*, 1998b). Large-scale patterns between sites >50 km apart were also affected by regional variation in hydrodynamic transport.

Panulirus argus phyllosome larvae are released from eggs hatched on the seaward fringes of coral reefs before preferentially settling in nursery habitats (Stockhausen *et al.*, 2000). Hence, the hydrodynamic link between adult populations and benthic settlers is very important. Lipcius *et al.* (1997) suggested that postlarval supply is probably decoupled from adult abundance by physical transport and that adult abundance is likely to be decoupled from postlarval supply by the effects of varying habitat quality upon survival (mean density of adults at four sites, encompassing a range of habitats was 0–150 ha^{-1}). Lipcius *et al.* (1997) then showed that in the Bahamas, the decoupling can generate sinks and sources of postlarvae. Hence, one site was a sink because adult abundance was the lowest even though it had the highest postlarval supply, but little nursery habitat compared to three other sites (sources), which had higher adult abundances despite lower postlarval supply.

Within vegetated nursery areas, postlarval *P. argus* appear to seek clumps of algae as a settlement habitat and as a residence for early benthic phase juveniles. In the Florida Keys, and potentially many other parts of the Caribbean, the favoured alga tends to be patches of the highly branched *Laurencia*, which provide refuge and an abundant, diverse prey fauna (Marx and Herrnkind, 1985; Herrnkind and Butler, 1986). In contrast, within an unproductive Mexican lagoon with low-standing crop of *Laurencia*, density and distribution of early benthic phase juveniles (146–263 ha^{-1}) were related to patches of *Lobophora* (Briones-Fourzán and Lozano-Álvarez, 2001).

Seagrass biomass does not significantly influence juvenile survival (Lipcius *et al.*, 1998; Briones-Fourzán and Lozano-Álvarez, 2001). The role of algal patches in reducing predation has facilitated the development of a habitat-survival function (HSF) for algal-stage juveniles (Lipcius *et al.*, 1998). An HSF model's survival changes with habitat structure and encompasses all characteristics of the habitat within three elements: the absolute abundance of elements, relative abundance of elements and the scale of area or volume used to measure elements (McCoy and Bell, 1991), which in this case is plant biomass. The HSF for *P. argus* was hyperbolic for algal biomass and even modest increases in habitat structure significantly enhanced *P. argus* survival, especially at low-to-moderate levels of habitat structure, which should theoretically be avoided by juveniles (Lipcius *et al.*, 1998). The HSF is supported by empirical data, and Butler *et al.* (1997) concluded that recruitment in Florida was tightly linked to a nursery habitat that is heterogeneous and ephemeral, and predictions of adult populations need to be coupled with information on the spatial and temporal changes in nursery habitat structure.

After algal-stage juvenile *P. argus* outgrow their algal refugia, they dwell in small crevices provided by sponges, gorgonians, coralline algae, seagrass, patch reef and rock-rubble habitats (Lipcius *et al.*, 1998; Acosta and Robertson, 2003). The mean densities of juveniles on patch reefs inside and outside a marine reserve in Belize were 55.9 and 32.1 ha^{-1}, respectively (Acosta and Robertson, 2003). The change to a "postalgal" juvenile occurs when individuals attain a partial size refuge from predation (typically 16–25 mm carapace length) and are able to forage relatively safely at night (Smith and Herrnkind, 1992). The shift from algal dwelling to crevice sheltering could potentially be a bottleneck for *P. argus* populations (Childress and Herrnkind, 1994). At two sites in the Florida Keys, densities of mainly postalgal juveniles were found to be generally highest in channels (0.0247–0.0642 m^{-2}), followed by hard-bottom habitats (~0.04 m^{-2}) and patch reefs (~0.01–0.09 m^{-2}), but they were rarely in seagrass (0.001 m^{-2}) and never in mangrove prop-roots, and densities in all habitats were reduced by a 2-d fishing miniseason (Eggleston and Dahlgren, 2001). The mean densities of juveniles in shallow Florida hard-bottom habitats were ~454 ha^{-1} (Forcucci *et al.*, 1994), 278 ha^{-1} (Marx and Herrnkind, 1985) and 0–18 400 m^{-2} (Childress and Herrnkind, 1997). Eggleston and Dahlgren (2001) showed that postalgal juvenile density was related to the density and volume of large sponges in channel habitats because they provided abundant refugia and a possible corridor for migrating juveniles. The relationship with sponges in channels was dramatically demonstrated when cyanobacterial blooms caused sponge mortalities in ~20% of the Florida Keys' nursery (Butler *et al.*, 1995; Herrnkind *et al.*, 1997). The reduction in available sponge microhabitats led to *P. argus* using alternative shelters, such as coral heads and solution holes. Overall, there was a relatively low effect on *P. argus* densities because of continued production in a larger unaffected nursery region and a fortuitously high postlarval supply. It was suggested that the latter was unlikely to remain until the sponges had recovered.

Many regions of the Caribbean have seagrass and patch reef areas, instead of the extensive hard-bottom areas with large sponges and solution holes present in Florida. Acosta and Butler (1997) suggest that mangroves may play a larger role in the life history of *P. argus* because of the areal coverage of seagrass beds in these regions. Their work in Belize showed that juveniles to subadults sheltered among mangrove prop roots, in undercut peat banks and under corals near islands. Although juvenile and subadult *P. argus* preferred large stony corals, the use of mangrove roots and peat banks increased when coral density was low. Furthermore, population sizes were higher near mangrove islands surrounded by shallow seagrass beds compared to those isolated by deeper water. Similarly, further research demonstrated that *P. argus* was more abundant, with a higher proportion of juveniles, in mangrove islands or large coral patch reefs surrounded by seagrass compared to areas surrounded by sand and rubble (Acosta, 1999). The work of Acosta and Butler (1997) and Acosta (1999) clearly show that vegetated areas may function as movement corridors for juveniles.

Subadults move to dens provided by patch reefs, boulders and undercut limestone ledges and seagrass banks (Lipcius *et al.*, 1998; Stockhausen *et al.*, 2000). Adults may migrate seaward to a depth of ~100 m but are found in a range of sheltered habitats including reefs, rocky bottoms, rock or coral outcrops, undercuts along seagrass blowouts and sponge and gorgonian aggregations associated with reefs (Kanciruk, 1980; Smith and van Nierop, 1986; Cox *et al.*, 1997; Stockhausen *et al.*, 2000; Eggleston and Dahlgren, 2001). Mean densities of adult lobsters in marine reserve in Belize was 45.7–91.2 ha^{-1} on a patch reef, 38.3 ha^{-1} on a reef wall and 15.2 ha^{-1} on the forereef at 5–7 m (Acosta and Robertson, 2003). *P. argus* forages opportunistically throughout its home range, feeding in rocky areas, grass and algal flats and favours areas with a diversity of habitat types (Lipcius *et al.*, 1997; Acosta and Robertson, 2003). In Florida, adult *P. argus* were seen at night emerging from dens on a spur-and-groove forereef to forage on the reef flat in sand (10.6 ha^{-1}), *Thalassia* beds (18.1–38.6 ha^{-1} but only 5.4 ha^{-1} for *Syringodium*) and rubble (54.3 ha^{-1}) habitats (Cox *et al.*, 1997). Foraging *P. argus* adults were most common in an extensive rubble ridge because this habitat had abundant and accessible prey. Fishing pressure disrupts natural distribution patterns, and Acosta and Robertson (2003) showed that, outside marine reserves (where mean densities across three habitats were 8.2 ha^{-1} compared to 32.1 ha^{-1} inside the reserve), adult *P. argus* were predominantly on the deep lightly fished reef wall. Similarly, on offshore reefs in the Florida Keys, densities were significantly reduced, from initial values of

$\sim$0.003–0.02 m^{-2}, after a 2-d fishing miniseason (Eggleston and Dahlgren, 2001). Densities of *P. argus* across four habitats (reef, gorgonian-dominated pavements, *Thalassia* beds and barren sediments) in the Bahamas were 1.8, 2.9, 1.65 and 0 individuals 3,000 m^{-2} (Smith and van Nierop, 1986).

The presence of appropriate diurnal dens is particularly important for explaining interhabitat and intrahabitat variations of subadult and adult *P. argus* densities. Den availability is linked to habitat topography, which might be expected to be highest in *Montastraea* reef habitats, but few data are available, especially for adults. Dens provide protection from predators, but the relationship is complex and variations are caused by a suite of factors, particularly predation risk and aggregation with conspecifics. The relationship between the presence of dens, predators and conspecifics was examined by Eggleston and Lipcius (1992). These authors demonstrated that when conspecific density was low and predation risk was low, *P. argus* used shelters whose dimensions scaled to their own size (i.e., they were the best "fit"). In contrast when conspecific density was high and predator density was low, large shelters with the highest potential for gregariousness were used. When conspecific and predator density was high, there was gregarious habitation in smaller shelters. Finally, when conspecific density was low and predation risk was high, smaller shelters were used by individuals. Similarly, Eggleston *et al.* (1997) showed that predator pressure and the size of shelters jointly explained the observed distribution and abundance of *P. argus* on patch reefs. Predator avoidance may also explain, at least in part, the single file chains or "queues" of adults autumnally migrating from shallow to deep water (Herrnkind and Cummings, 1964; Kanciruk and Herrnkind, 1978). Marx and Herrnkind (1985) suggest that aggregation may also depend on the local distribution of food. The change of density during aggregation in a hard-bottom (6–8 m depth) "pathway" site prior to migration in Bimini was from 2–10 lobsters ha^{-1} to hundreds in the available crevices (Kanciruk and Herrnkind, 1978).

*3.6.2. Habitat functional values (*Panulirus argus*; Figure 1)*

Laurencia in seagrass beds and mangrove channels is commonly a preferred settlement habitat for *P. argus* (juvenile densities 10–642 ha^{-1}), so these habitats are assigned a high functional value. Seagrass banks may also be used by subadults and as a foraging habitat for adults with densities of 5.5–38.6 ha^{-1}. Similarly, mangroves may be important to subadults in some areas (Acosta and Butler, 1997). Shallow hard-bottom areas are important for juveniles in some areas (particularly Florida), but this habitat is not represented in our schematic profile (Figure 1). Patch reefs are used by postalgal animals (10–263 individuals ha^{-1}) and adults (5.5–38.6 individuals ha^{-1}) and are given a high functional value. Adults appear to use a range of hard-bottom habitats (2–15.2 individuals ha^{-1}; there are few data from deeper *Montastraea* reefs), so each is assigned a medium functional value. In an unfished population, mean density of *P. argus* was higher on the escarpment than the forereef (38.6 ha^{-1}; Acosta and Robertson, 2003) and is assigned a high functional value. Sand may have a low functional value as a foraging habitat (Cox *et al.*, 1997). Few studies give densities for reef crests and back reefs, but the offshore ontogenetic migration indicates that individuals may use these habitats and they are putatively given low functional values.

3.6.3. Strombus gigas

Strombus gigas juveniles use nursery habitats that range from shallow sand and coral-rubble reef flats to moderate-density seagrass (Randall, 1964; Davis and Stoner, 1994; Stoner *et al.*, 1996b). After ~1 yr, infaunal *S. gigas* emerge from the sediment and feed epibenthically on algae and detritus (Randall, 1964). *S. gigas* nurseries contain important metamorphosis cues for the planktotrophic larvae and laboratory work has shown that the alga *Batophora oerstedii* induces the highest proportion of metamorphosis (Davis and Stoner, 1994). Davis and Stoner (1994) found other cues to be sediment, *Thalassia* blades and detritus, but there was a low response to *Laurencia*. Similarly, in the Bahamas, *Batophora oerstedii* was the dominant alga in nurseries and its abundance provided the best index of habitat quality (Hanisak, 1992). Highest growth rates occurred when *S. gigas* was feeding on *Batophora*, which indicates why nurseries more frequently contain this alga compared to *Laurencia* and seagrass detritus, although epiphytes are the actual metamorphic cue rather than the macrophytes themselves (Davis and Stoner, 1994).

Metamorphic cues appear to vary across the Caribbean region. In the Turks and Caicos Islands, *Laurencia* was among the most effective metamorphosis inducers of farmed larvae, along with the *Thalassia* epiphyte *Foslielalla* sp. and *Batophora* (Boettcher and Targett, 1996). Laboratory work found no metamorphic response to seagrass, but high rates of metamorphosis on a substratum of complex physical and biotic structures such as the calcareous red algae *Neogoniolithon*, *Dasycladus* and the matrix of algae and sediment attached to rock (Stoner *et al.*, 1996b). In the Florida Keys, *S. gigas* is commonly found on hard-bottoms because seagrass is long, dense and silty and inhibits juvenile movement (Stoner *et al.*, 1996b). Therefore, the presence of epiphytes and appropriate macroalgae is more important in the Florida Keys. Irrespective of the exact metamorphic cue, it is important that juvenile *S. gigas* find a nursery area of high algal productivity to ensure good growth and survival (Stoner, 1989). Indeed *S. gigas* densities in nursery habitats may be limited by food abundance (Stoner, 1989). Davis and Stoner (1994) showed that metamorphosis was higher for *Thalassia* test detritus from nursery grounds than for test detritus from outside nursery areas because it varies in composition and quality. Stoner *et al.* (1996b) suggest that detritus from nursery areas has a unique bacterial and algal film that leads to higher growth rates of *S. gigas* and that nursery areas have high algal recruitment.

Medium-density seagrass beds are commonly preferred habitats for juvenile *Strombus gigas* because there is a lower predation risk than sandy areas or sparse seagrass areas (Ray and Stoner, 1995). Mortality rates are also higher in dense seagrass than medium-density seagrass because high seagrass biomass can hamper locomotion and there are often more predators (Ray and Stoner, 1994). Ray and Stoner (1995) concluded that postsettlement mortality is high in all habitats and that predation is the most important mechanism influencing *S. gigas* distribution. *S. gigas* also aggregate to reduce predation pressure and groups of ~100,000 juveniles have been seen (Iversen *et al.*, 1986; Stoner and Ray, 1993; Ray and Stoner, 1994; Stoner and Lally, 1994; Ray-Culp *et al.*, 1999). *S. gigas* may also reduce predation pressure by behavioural patterns such as concentrating in shallow waters (<1 m) and burying (Iversen *et al.*, 1986). Densities of juvenile conch in seagrass beds in the Bahamas were 0–2.0 individuals m^{-2} (Stoner, 1989; Ray and Stoner, 1994, 1995; Stoner *et al.*, 1995, 1996a) but can aggregate at densities of 2.5–295 m^{-2} (Stoner and Lally, 1994). Within a marine reserve in the Turks and Caicos Islands, algal plains were an important habitat for juvenile *S. gigas* (483 ha^{-1}) and densities were greater than seagrass beds (179 ha^{-1}), sand plain (232 ha^{-1}) and gorgonian/sponge plain (21 ha^{-1}) (Béné and Tewfik, 2003). Densities outside the reserve were not significantly lower (331, 497, 85 and 24 ha^{-1}, respectively).

On the Great Bahama Bank, most of the juveniles were found in aggregations in seagrass beds at a water depth between 1.5 and 4.0 m, which constituted only 1.5% of the available area (Stoner *et al.*, 1996a). Such research has important consequences for management because only specific parts of seagrass beds are important nursery areas (Stoner *et al.*, 1995). Only the most persistent aggregations could be predicted on the basis of preferred seagrass biomass, but important nurseries were always located in tidal channels, which supplied clear, oligotrophic water (Stoner *et al.*, 1996a). Nurseries in tidal channels are subject to flushing with oceanic water on every tide, and although this could cause preferable temperatures, a more likely hypothesis was the role of indirect effects such as larval transport and recruitment or the effects on benthic productivity. Therefore, the boundaries of *S. gigas* nursery habitats are set by precise combinations of physical and biological factors, but the exact locations of aggregations shift from year to year (Stoner *et al.*, 1996a). In a review of *S. gigas* nursery habitats, Stoner (2003) further stresses the need to combine traditional habitat definitions with the "dynamic features and ecological processes that provide a functional space for subject species."

Adult *S. gigas* tend to prefer deeper water compared to juveniles and are found to at least 70 m, but rarely >30 m. Adults ontogenetically migrate from nursery habitats to denser seagrass areas, tidal channels and gorgonian-rich plains and can also be found on gravel and coral rubble (Randall, 1964; Appeldoorn and Rolke, 1996; Stoner *et al.*, 1996a). *S. gigas* may also migrate seasonally. In the Turks and Caicos Islands, individuals preferred a *Syringodium* bed parallel to the shore during the summer then shifted offshore, beyond the seagrass beds, to sparse algae and sand habitats during the winter (Hesse, 1979). Densities of juvenile and adult conch in the Turks and Caicos Islands, measured using transect across a series of habitats, was 9.48 100 m^{-2}. Habitat-specific data inside a marine reserve in the Turks and Caicos Islands gave densities of 833, 410, 78 and 3 adults ha^{-1} for algal plains, seagrass beds, sand plain and gorgonian/sponge plain, respectively (Béné and Tewfik, 2003). Fishing significantly reduced densities outside the reserve (86, 24, 28 and 7 ha^{-1}, respectively). In back reefs (1–10 m) in the Florida Keys, adult densities were 13.4–111 ha^{-1} and conch favoured this habitat over adjacent seagrass beds (Glazer and Kidney, 2004). In a survey in a range of habitats from the back reef to shore across Belize, densities of *S. gigas* were 0–45.2 ha^{-1} (hard-bottom habitats), 8.7–46.1 ha^{-1} (seagrass), 8.1–13.3 ha^{-1} (sand) and 11.7–15.8 ha^{-1} (patch reefs) (Appeldoorn and Rolke, 1996).

Although density is thought to generally decrease with increasing depth, deep populations could be sustaining shallow highly exploited fisheries (Stoner and Sandt, 1992). The unfished population described by Stoner and Sandt (1992) occurred at 18 m in the Bahamas, had a relatively constant density and included few juveniles. Density was highest on sandy areas in July as a result of immigration from surrounding winter hard-ground feeding areas and subsequent emigration. The sandy areas may be best for egg laying because sand sticks to the eggs and acts as camouflage and a physical deterrent (Randall, 1964). A preference for a sand habitat by reproducing *S. gigas* adults has also been documented in back reefs in the Florida Keys (Glazer and Kidney, 2004). The close proximity of feeding and reproductive habitats may be an important characteristic of an optimal spawning site in deeper water (Stoner and Sandt, 1992). Mean densities, over 4 yr, for the various habitats were 0.77, 3.62, 3.05 and 0.06 individuals 100 m^{-2} for the reef front, rubble field, mounds and sand transects, respectively (Stoner and Sandt, 1992). Stoner and Ray-Culp (2000) have shown that per capita rates of population growth become negative at low population densities ("Allee effect") in *S. gigas* populations when adults cannot find reproductive mates. Mating in a bare-sand habitat (depth of 10–20 m) in the Bahamas never occurred when density was <56 animals ha^{-1} and spawning never occurred at <48 animals ha^{-1} (range of densities 2–2,793 ha^{-1}, with highest densities inside a marine park).

*3.6.4. Habitat functional values (*Strombus gigas*; Figure 1)*

Assigning functional values to habitats for *S. gigas* densities is complicated by the effects of ontogenetic shifts, marine reserves, juvenile aggregations and the limited number of biotopes studied. However, seagrass beds are a key habitat for both juvenile and adult *S. gigas*, with densities of 0–20,000 ha^{-1} and juvenile aggregations of up to 295 individuals m^{-2} (high functional value). Algal plains are also important for juveniles and adults (Béné and Tewfik, 2003), but this habitat is not represented in our schematic profile (Figure 1). Densities of 0–50 animals (generally adults) ha^{-1} have been documented for patch reefs, back reefs and gorgonian plains, and these habitats are assigned medium functional values. Densities for sand plains vary widely (2–310 ha^{-1}), but they are important sites for reproduction with aggregations up to 2,793 individuals ha^{-1} and so are assigned a high functional value (Stoner and Ray-Culp, 2000). Mangal systems contain some seagrass and sand beds in creeks, so they are assigned a low functional value. Reef crests have received limited attention in the literature, but the turbulence at reef crests limits the presence of coral-rubble and sand, so this habitat might be expected to have a low functional value. *Montastraea* reefs are not explicitly considered in the literature but do tend to contain small areas of sand and coral rubble, so it is assigned a low functional value. *S. gigas* adults are rarely found >30 m, so escarpments appear to have no functional value.

3.7. Calcification and reef growth

In tropical marine ecosystems, biological calcium carbonate production (calcification) is the metabolic process with the largest "end product" and is dominated by contributions from corals, coralline red algae and calcareous green algae (Smith, 1983). Community calcification rates are used to assign functional values to habitats (Figure 1), but because of the limited amount of data, we first briefly review the calcification rates of individual taxa, which can be used to calculate community rates based on their areal cover (Chave *et al.*, 1972; Hubbard *et al.*, 1990). We also review patterns of interior framework building, but functional values are not assigned because of the lack of quantitative data.

3.7.1. Calcification rates of individual taxa

There are a range of calcifying taxa in tropical marine ecosystems including calcareous algae, foraminifera, molluscs, echinoderms and bryozoans, but scleractinians have received the most research attention. Coral calcification and growth rates are not strictly synonymous because the former measures an increase in mass while the latter is generally based on linear extension. Conversion of growth rates to mass of $CaCO_3$ must be adjusted for density and shape of the organism (Stearn *et al.*, 1977; Hubbard *et al.*, 1990 provide example calculations). However, calcification and growth are grouped together here, as the difference is relatively minor in the context of assessing the spatial pattern of coral calcification across a reef. Overall, depth, light, turbidity and sedimentation rate are the major controls of coral growth and calcification rates, although the slope of the substratum and rates of heterotrophy may also be important (Gladfelter and Monahan, 1977; Foster, 1980; Hubbard and Scaturo, 1985; Tomascik and Sander, 1985). Depth is a particularly important variable because it represents the combined effects of light, water movement and sometimes temperature and salinity (Buddemeier and Kinzie, 1976). The effects of light (depth in combination with turbidity) are important because a coral's metabolism relies on photosynthetic zooxanthellae (e.g., Muller-Parker and D'Elia, 1997), although the mechanistic link between zooxanthellae and photosynthetically enhanced calcification is still unclear and growth rates also vary with coral morphology (Fagerstrom, 1987; Jackson, 1991). The relationship between depth and growth rate is rarely linear, and generally within the upper 10–15 m of a reef, growth is dependent on the species present and other local environmental factors, such as sedimentation. Below 10–15 m, growth rate generally declines dramatically with increasing depth (Buddemeier and Kinzie, 1976). There may be a smaller effect of photoinhibition in very shallow water, so the highest growth rates are often a short distance below the surface (Huston, 1985b).

Many forereef habitats are dominated by the major reef-builder *M. annularis* and the correlation between growth rate and depth has been well documented for this species. For example, in Curaçao, growth was found to be light saturated to a depth of 15 m (8–16 mm yr^{-1}), then decreased rapidly (2–3 mm yr^{-1} at a depth of 30 m) (Bosscher and Meesters, 1993). In St. Croix, Hubbard and Scaturo (1985) showed that *M. annularis* growth rates could be grouped into those <12 m (0.7–0.9 cm yr^{-1}) and those >18–20 m (0.2 cm yr^{-1}). Hubbard and Scaturo (1985) suggested that the change represented a "light compensation depth"; at all depths shallower than 12 m, maximum growth rates can be sustained and are suboptimal below ~18 m. However, patterns of growth rates with changing light intensities are not consistent between species. Huston (1985b) demonstrated that like *M. annularis*, growth rates decreased with depth (from 1 to 30 m) for *Porites astreoides*, *Colpophyllia natans* and *Siderastrea siderea*, but rates for *Montastraea cavernosa* were highest in the middle of its depth range and did not change with depth for *A. agaricites*. Growth rates for *Diploria labyrinthiformis*, *Colpophyllia natans*, *Montastraea cavernosa*, *P. astreoides*, *S. siderea* and *Stephanocoenia* were 0.15–0.45 cm yr^{-1} in St. Croix (Hubbard and Scaturo, 1985). Also in St. Croix, rates of 3.0–3.5 mm yr^{-1} (*P. astreoides*), 71 mm yr^{-1} (*A. cervicornis*), 59–82 mm yr^{-1} (*A. prolifera*) and 47–99 mm yr^{-1} (*A. palmata*) were reported by Gladfelter *et al.* (1978). Hubbard *et al.* (1990) use growth rates and coral cover data to give gross carbonate production rates by corals in a reef system in St. Croix as being 0–5.78 kg m^{-2} yr^{-1} (mean for entire shelf was 1.13 kg m^{-2} yr^{-1}). Coral $CaCO_3$ production for individual habitats in St. Croix were 0.9, 2.3, 3.8, 0.6 and 0.8 kg m^{-2} yr^{-1} for hardground, shallow reef, coral gardens, sand flat and slope and deep reef, respectively (Sadd, 1984).

Calcifying algae can be divided into three groups (coccolithophores, aragonite depositing and calcite depositing) based on the location, organisation and nature of their deposits (Borowitzka, 1983). Coccolithophores are predominantly midoceanic species, so their contribution to reefal budgets is low. There is great interspecific and intraspecific variation in calcification rates, linked to environmental and physiological conditions during measurement and the techniques used, but calcification rates for the aragonite-depositing green and brown algae are generally higher than those for calcite-depositing coralline reds (Borowitzka, 1983). Crustose (lithothamnioid) coralline algae also have a functional role different from that of green and brown algae. Crustose coralline algae have long been recognised to have an important role in consolidating reef frameworks (Howe, 1912), whereas calcifying species of green and brown algae tend to generate sediment (Hillis-Colinvaux, 1980), a proportion of which is then bound into the reef structure. Red coralline algal biomass is generally highest in the turbulent shallows and lowest at 40 m because of patterns of grazing pressure (e.g., Liddell and Ohlhorst, 1987; Steneck, 1997) but are found on solid substrata intertidally and subtidally to 268 m (Littler and Littler, 1984). Although coralline algae grow more vigorously in the shallows, weight accretion is greater in deeper reef areas because there is a reduced grazing pressure (Bak, 1976). Calcification rates of coralline algae are difficult to measure because of the confounding effects of herbivory, but in St. Croix rates of growth were estimated at ~0.03 mm yr^{-1} leading to gross carbonate production rates of 0.02 kg m^{-2} yr^{-1} (Hubbard *et al.*, 1990). Rates were higher (growth 0.9–2.3 mm yr^{-1}) in a further study in St. Croix (Adey and Vassar, 1975) and in Barbados where growth rate was 2 mm yr^{-1}, with a potential calcification rate (if cover was 100%) of 0.167–2.378 kg m^{-2} yr^{-1} and actual productivity (using percentage cover data from the reef) of 0.025–0.95 kg m^{-2} yr^{-1} (Stearn *et al.*, 1977).

Calcifying green and brown algae are most common in habitats with light grazing pressure, a pattern that has been significantly altered by overfishing, the mass mortality of *Diadema* and anthropogenic nutrient inputs. The increase of macroalgal biomass on Caribbean reefs has affected the distribution of calcareous plants and they are now found in almost every habitat type. Before the increase of macroalgae, Hillis-Colinvaux (1980) provided a detailed description of *Halimeda* abundances across a Jamaican reef and showed percentage cover to be linked to the availability of hard substrates free of other biota and grazing pressure. In addition, Hillis-Colinvaux (1980) and Littler and Littler (1984) showed that the ability to produce attachment sites allows dense patches of calcifying Chlorophyta, such as *Halimeda*, to grow on protected shallow areas with soft bottoms, often in association with seagrass, and on deeper reef slopes. Calcifying Phaeophyta, such as *Padina*, are common on the reef flat but also subtidally to moderate depths (Littler and Littler, 1984). Rates of calcification for calcareous macroalgae can reach ~2,400 g $CaCO_3$ m^{-2} yr^{-1} in the Bahamas and Panama (Freile *et al.*, 1995; Freile and Hillis, 1997).

3.7.2. Community calcification rates

Community calcification rates are highest in shallow (<10 m) areas because calcification and primary productivity are generally positively correlated (Smith and Buddemeier, 1992; Gattuso *et al.*, 1999). Within shallow zones, calcification is affected by community composition but is highest for areas of continuous coral, lower for algal pavement and lowest for sand and rubble (Done *et al.*, 1996; Gattuso *et al.*, 1998). However, calcification in a given habitat decreases with an increasing percentage cover of fleshy algae. From a literature review, Smith and Kinsey (1976) proposed two common calcification rates for shallow reef communities; 4 kg $CaCO_3$ m^{-2} yr^{-1} for seaward areas and 0.8 kg $CaCO_3$ m^{-2} yr^{-1} for protected areas because of variations in water motion. They suggested that the "standard" rates are insensitive to coral versus coralline algal dominance. Smith (1983) suggested that 90–95% of coral reef areas calcifies at the lower rate and 5–10% calcifies at the higher rate and extended the concept by introducing a higher rate of 10 kg $CaCO_3$ m^{-2} yr^{-1} (see also Smith, 1981; Kinsey, 1985). Smith (1983) indicated that 1–2% of reef areas may calcify at the highest rate, while 4–8% and 90–95% calcify at the 4 and 0.8 kg $CaCO_3$ m^{-2} yr^{-1} rates, respectively. Such figures are "net calcification," measured by decreases in alkalinity, and measure net precipitation minus dissolution, and these hydrochemical methods are restricted to very shallow areas (Vecsei, 2001). Much of the data summarised by Smith and Kinsey (1976) were from Pacific reefs but were proposed as appropriate global standards, although extrapolation to the

Caribbean is equivocal and there will be considerable spatiotemporal variation and dependence on environmental conditions. Kinsey (1981) reflects on the comparison between Pacific and Atlantic growth rates and states that differences are more of a function of discrimination of zones for study (finer in the Atlantic) than any fundamental difference in the communities' calcification rates, but functional values in this review are assigned using only Caribbean data. Kinsey (1981) also assessed calcification rates in Jamaica and gives values of 3.5–3.8 kg $CaCO_3$ m^{-2} yr^{-1} for the back reef and 6.1–8.0 kg $CaCO_3$ m^{-2} yr^{-1} on an *Acropora palmata*–dominated reef crest.

Further data from Caribbean reefs are available but are often calculated by "biological estimate" (or "gross production" or "census-based") techniques. Biological estimates are generated by combining calcified standing crop of each component in a benthic community and its growth or turnover, but this is tedious unless an area is dominated by a few organisms (Chave *et al.*, 1972; Smith, 1983). The methodological difference from the "net calcification" values provided by Smith and Kinsey (1976) is important because the biological estimate approach gives higher values of calcification rates. Chave *et al.* (1972) generated data, using hypothetical community assemblages, for shallow sand flats (0.4 kg $CaCO_3$ m^{-2} yr^{-1}), coral mounds on sand (10 kg), algal ridges (9 kg) and complete coral coverage on outer slopes (60 kg). Using actual data on community composition, Stearn *et al.* (1977) provide a value of 15 kg $CaCO_3$ planimetric m^{-2} yr^{-1} (9 kg $CaCO_3$ m^{-2} of reef surface yr^{-1}) on a fringing reef (<10 m) in Barbados (calculated from production of corals and red coralline algae). The rates for a Jamaican forereef terrace (0–20 m) and for a forereef slope (20–60 m) were, respectively, 4.6 kg $CaCO_3$ m^{-2} yr^{-1} and 0.6 kg $CaCO_3$ m^{-2} yr^{-1} (Land, 1979). In St. Croix, calcification rates for five habitats were 1.2, 3.1, 5.0, 0.85 and 1.0 $CaCO_3$ kg $CaCO_3$ m^{-2} yr^{-1} for hardground, shallow reef (depth of 5–8 m), coral gardens, sand flat and slope (6–20 m) and deep reef (20–32 m), respectively (Sadd, 1984). Incorporating more detail on spatial variability and geological history, a reef-wide average (from the beach to a depth of 40 m) for the same site was calculated as 1.21 kg $CaCO_3$ m^{-2} yr^{-1} but up to 5.78 kg $CaCO_3$ m^{-2} yr^{-1} at some survey sites (Hubbard *et al.*, 1990). A rate of ~3.1 kg $CaCO_3$ m^{-2} yr^{-1} was calculated for a forereef (5–10 m) in Curaçao (Bak *et al.*, 1984).

Vecsei (2001) modified the biological estimate approach to deduce regional assessments of forereef carbonate production using averaged coral cover, coral extension and density data. Values for very shallow forereefs with a dense ramose coral (*Acropora*) framework in the Caribbean (mainly for the period 1960–1990) were ~10 kg $CaCO_3$ m^{-2} yr^{-1}. In contrast, shallow biodetrital (low proportion of framework and high rubble and sediment content) forereefs such as in St. Croix produce only ~1.5 kg

$CaCO_3$ m^{-2} yr^{-1}. Furthermore, Vecsei (2001) showed that production rates decrease exponentially with depth. For framework reefs (e.g., Jamaica, Bonaire and Curaçao) values for all community types were 10.1–17.3 kg $CaCO_3$ m^{-2} yr^{-1} at 0–10 m, 4.5–8.1 kg at 10–20 m and 0.8–3.0 kg at 30–40 m. On biodetrital reefs, production drops from 1.5 kg $CaCO_3$ m^{-2} yr^{-1} at 0–20 m to 0.1–0.8 kg at 20–40 m. Vecsei (2004) advanced the concept of regional assessments and gave values, for both framework and biodetrital reefs with explicit treatment of algal production, of 1.6–10.3 (0–10 m), 1.9–4.7 (10–20 m), 0.8–1.0 (20–30 m) and 0.3 kg $CaCO_3$ m^{-2} yr^{-1} (30–40 m), and these values are used in preference to the 2001 data when considering functional values.

Data for calcification rates in soft-sediment habitats are limited, but carbonate shelves have received some attention. Data for the Great Bahama Bank, using equilibrium thermodynamics, showed how rates were 4–5 kg $CaCO_3$ m^{-2} yr^{-1} on the bank margins and ~0 kg $CaCO_3$ m^{-2} yr^{-1} in the shallowest, innermost areas (Demicco and Hardie, 2002). The new "Submersible Habitat for Analysing Reef Quality" (SHARQ), developed by Yates and Halley (2003), is an excellent tool for assessing community calcification (and dissolution) rates in a range of habitats but calculates net rates using hydrochemical methods, which are difficult to compare with the gross rates for reef habitats. Mean net daily calcification in Florida was highest on patch reefs (1.14 g $CaCO_3$ m^{-2}) and lowest in dense seagrass beds (0.25 g $CaCO_3$ m^{-2}). Calcification rates in sparse seagrass beds and on a single sandy area were approximately equivalent (0.44 and 0.41 g $CaCO_3$ m^{-2}, respectively).

3.7.3. Habitat functional values (Figure 1)

Community calcification rates appear highest in reef crests and shallow *Montastraea* reefs, with values generally >5 kg $CaCO_3$ m^{-2} yr^{-1} (high functional values). However, the abundance of *Acropora* has been reduced by white band disease (see Section 5.3) and consequently calcification rates, and the functional value, of reef crests may be lower than values in the published literature. Rates for back reefs and deep *Montastraea* reefs are generally 1–5 kg $CaCO_3$ m^{-2} yr^{-1} and are assigned medium functional values. A single value of 0.4 kg $CaCO_3$ m^{-2} yr^{-1} is available for patch reefs (Yates and Halley, 2003) but was measured using hydrochemical techniques, and we assume gross production rates would be higher (potentially 1–5 kg $CaCO_3$ m^{-2} yr^{-1}) and it is assigned a medium functional value. Rates in sand and escarpment habitats are generally <1 kg $CaCO_3$ m^{-2} yr^{-1} and they are given low functional values. There are few data for gorgonian-dominated habitats, but the abundance of octocorals and fleshy algae and low coral cover indicates that they have a low functional value. Similarly, mangroves and seagrass beds are given a low functional value because of the presence of calcified algae and occasional colonies of *Manicina* and *Porites*. The only published (net) calcification rate for seagrass beds (0.09–0.16 kg $CaCO_3$ m^{-2} yr^{-1}) is consistent with this assessment (Yates and Halley, 2003). Carbonate shelves are also important sites for calcification (Demicco and Hardie, 2002) but are not represented in our schematic profile (Figure 1).

3.7.4. Reef interior framework building

Calcification is a key process of reef growth and is a component of construction, which Fagerstrom (1987) lists as one of five interacting processes of reef development along with binding, sediment deposition and transportation and destruction. The five processes produce a recently dead semiconsolidated reef mass, which is then converted into lithified reef limestone by diagenesis. All of the processes described by Fagerstrom (1987) vary between reef habitats, but the focus in this section is on construction and binding because the spatial variation in sediment transport and deposition and destruction (bioerosion) are reviewed in the next section (Section 3.8). Reef construction in a habitat is not solely dependent on calcification rates because reef development is influenced by the type of framework in a given area, which in turn depends on the net balance of light, wave, sediment and exposure stresses (Chappell, 1980). In addition to calcification rates, reef growth is also affected by antecedent topography, sea-level changes and subsidence, which are likely to be complex and variable across a continental shelf (Davies, 1983; Hubbard, 1997). Davies (1983) also lists turbidity, temperature and water chemistry as affecting Holocene reef growth, but the link between all these variables and reef framework construction at the scale of habitats is poorly understood.

Coring work (e.g., Hubbard, 1997) showed that, at least on certain reefs, the correlation between coral communities and the interior frameworks of reefs is less than previously thought. The majority of cores in some habitats show out-of-place coral debris mixed with loose sediment and other carbonate debris. The abundance of out-of-place coral debris in the interior framework of a habitat is particularly apparent on biodetrital reefs such as those studied by Hubbard *et al.* (1986) in St. Croix. Biodetrital reef frameworks consist mainly of coral rubble tossed onto the shelf by hurricanes. Within a reef, there is evidence of variation in the general pattern of framework retention. Deeper slower accreting reefs may have higher proportions of retention, though still <35%, of "original" corals, than shallower areas (Hubbard, 1997). Furthermore, more exposed reefs have higher proportions of framework retention than sheltered ones, possibly because they have more robust coral growth.

In Jamaica, Perry (1999) examined framework preservation in back reef, forereef, forereef terrace and deep forereef habitats. Back reefs had limited framework development and extensive framework alteration because of grazing and boring (<5% of *in situ* framework preservation and 95% sediment and rubble). Deeper (30 m) forereefs also had limited framework preservation (~20%) because of high rates of bioerosion, particularly by sponges, and slower calcification rates and increased skeletal densities. On shallower forereefs and terraces (<12 m), ~50% of the relatively abundant and fast-growing corals had been preserved *in situ*. Massive and lobate corals, such as *Montastraea annularis*, are particularly likely to be preserved *in situ*, despite their susceptibility to macroboring (Perry, 1998a). Furthermore, rubble from the many corals broken by storms was rapidly encrusted and cemented within shallower zones (Perry, 1999). Rasser and Riegl (2002) reported that rubble cementation was highest in intertidal and supratidal zones, back reefs, reef-flats and shallow forereef rubble accumulations. Diagenetic cementation is primarily correlated with rapid seawater pumping through the framework leading to precipitation of magnesium calcite and aragonite crystals. The process of cementation is often seen to be particularly important in shallow water sites. Coralline algae, and other organisms, can rigidly bind rubble but appear less important than diagenetic cementation and may be restricted to specific zones, such as shallow forereef environments where coralline algae are abundant. Overall, rubble binding into interior reef frameworks was demonstrated to vary significantly between habitat types. Rubble binding was highest on forereefs with low sloping angles because rubble can accumulate and there are high rates of diagenetic cementation and frequent coralline algal binding. In deeper sites and framework cavities, microbially driven cementation is also important (Camoin *et al.*, 1999).

The work of Rasser and Riegl (2002) supports the suggestions of Macintyre (1997) that the importance of coralline algae cover in the buildup of modern reefs is less than previously thought. Sponges may play a role in reef framework consolidation (Goreau and Goreau, 1973) and their abundance varies between habitats. Goreau and Goreau (1973) suggested that in Jamaica, *Millepora* and lithothamnoid algae were important cementers in the exposed surf zone and reef flat, but this was mainly achieved by coralline red algae and the foraminiferan *Gypsina* in the forereef. Within taxa, there is further interspecific variation in the pattern of diagenesis. Constantz (1985) showed the species most susceptible to diagenesis are those with the narrowest (e.g., *Acropora*) and most loosely arranged (e.g., *Porites* and *Agaricia*) aragonite fibres. *Montastraea* and *Diploria* are less susceptible, so habitats dominated by *Acropora* may exhibit faster rates of diagenetic cementation than those characterised by *Montastraea*.

3.8. Bioerosion and sediment transport

Calcified organisms and structures on a reef are broken down in part by bioerosion to produce a proportion of the carbonate sediments that fill interstitial framework spaces during reef accretion. Three key processes determining the composition of the internal fabric of a reef are the type and intensity of bioerosion and net rate of sediment transport and settlement (Fagerstrom, 1987; Hubbard, 1997). In St. Croix, Hubbard *et al.* (1990) showed that nearly 55% of the carbonate production on a reef was reduced to sediment by bioerosion each year, and Bruggemann *et al.* (1996) stated that variation in bioerosion rates is as important as calcium carbonate production in shaping the physical and biological features of a reef. However, with increasing degradation of reef communities by anthropogenic impacts, some habitats may be dominated by bioerosion (Done *et al.*, 1996; Glynn, 1997), potentially weakening corals, reducing topographical complexity and assisting asexual fragmentation. This section focuses on carbonate sediment production by bioerosion and the spatial patterns of sediment settlement and movement across a reef seascape. Functional values are presented only for bioerosion because of the lack of habitat-specific quantitative data for the latter. Physical damage also creates carbonate sediment but is a function of wave energy, and these patterns are discussed in Sections 3.1 and 5.1. Mechanical erosion may be negligible other than during heavy storms (Scoffin *et al.*, 1980).

3.8.1. Major bioeroding taxa

There are few habitat-specific data on rates of community bioerosion (incorporating all taxa for a particular habitat), so we provide a brief review of the major bioeroding taxa, as densities and erosion rates can be combined to estimate total $CaCO_3$ destruction (e.g., Scoffin *et al.*, 1980). Many taxa are bioeroders (Risk and MacGeachy, 1978; Glynn, 1997), although research on the spatial distributions and rates and controls of erosion of some taxa is limited. Perry (1998a) provides one of the few comprehensive assessments across a Caribbean reef of invertebrate macroboring communities and the amount of reef framework they remove. Perry (1998a) showed that sponges were the dominant macroborers on forereef sites, whereas sipunculans and polychaetes were only important at back reef, lagoon and shallow forereef sites in Jamaica. Bivalves were important within back reef and lagoon patch reef habitats. Overall, macroboring was highest in the back reef and deep (>20 m) forereef habitats.

Boring siliceous sponges are frequently cited as a significant component of bioerosion (e.g., Scoffin *et al.*, 1980; Perry, 1998a). In Bermuda, Gygi (1975) showed that boring by *Cliona* may have had up to 100 times greater effect than grazing by the parrotfish *Sp. viride*. Indeed, Davies (1983) and Wilkinson (1983) suggest that sponges may be the primary eroders in some reef environments, and their proportional contribution has presumably increased since the mass mortality of *Diadema*. The rate of bioerosion by sponges was 24.9×10^6 g yr^{-1} (although this also includes minor contributions by bivalves, barnacles and worms) for a fringing reef in Barbados (Scoffin *et al.*, 1980), which is converted to 180 g $CaCO_3$ m^{-2} yr^{-1} by Glynn (1997). Further data for sponge bioerosion rates include 256 g^{-3} kg $CaCO_3$ m^{-2} yr^{-1} in Bermuda (Rützler, 1975) and 0.19–3.29 kg $CaCO_3$ m^{-2} yr^{-1} in St. Croix with a correlation to carbonate production (Moore and Shedd, 1977).

The percentage cover of boring sponges varies spatially and in Jamaica ranges between 0 and 32% of the benthos. Sponge cover is negatively correlated with depth, possibly because of the lack of turbulence-induced mechanical damage to hard substrata (Liddell and Ohlhorst, 1987). Bioerosion rates vary, depending on skeletal density, with dense species (e.g., *M. annularis*) more bored, and the percentage of dead skeletal surface available for recruitment by borers (Highsmith *et al.*, 1983). The density of borers may also be promoted by grazers providing suitable substrata, which is a key factor affecting bioerosion by sponges (reviewed by Wilkinson, 1983). Substratum availability, combined with nutrient availability, mechanical stimuli, high light intensity and strong currents in shallow areas (Rützler, 1975), leads to a positive correlation between high rates of coral growth and sponge bioerosion. However, the effects of sponge bioerosion may be more obvious in deeper water because of the lower calcification rates of coral (Wilkinson, 1983; Fagerstrom, 1987). Furthermore, sponge bioerosion may be reduced in areas with very high water velocities. In a comparison of shallow habitats, Holmes (2000) found that *Cliona* abundance in the rubble component of the back reef supported significantly fewer invasions than that of the reef crest and forereef zones of Barbados' fringing reefs. In Barbados, the back reef zone is a zone of heavy wave action (Lewis, 1960) and the scour and high sedimentation possibly lead to an inhospitable environment for sponges, which require considerable amounts of energy to clear blocked canals (Reiswig, 1971).

In addition to boring species, a major component of bioerosion in most habitats is grazing by herbivorous fishes and sea urchins (Bruggemann *et al.*, 1996). Consequently, bioerosion varies significantly across a reef because the density of herbivores decreases with increasing depth. For example, the rate of bioerosion by herbivorous fishes is highest in the shallows and decreases with depth (Ogden, 1977; Bruggemann *et al.*, 1996). Since the patterns of density of key bioeroders, namely parrotfishes and the urchin *D. antillarum*, are documented in detail elsewhere (Section 3.4), they are not repeated here. Generally, the erosion of calcium carbonate and reworking of sand by *Diadema* during grazing on algae and corals is much higher than that attributable to fishes (reviewed by Bak, 1994) and even since its mass mortality, *Diadema* is still a significant source of bioerosion on shallow Jamaican forereefs (Perry, 1999). Before *Diadema* mortality, Hunter (1977) calculated that *Diadema* produced 9.7 kg carbonate m^{-2} yr^{-1} and was probably the major sediment producer in Barbados. Comparative figures for fishes and boring sponges were 0.1–0.2 kg m^{-2} yr^{-1} and 0.5–1 kg m^{-2} yr^{-1}, respectively. Also in Barbados, Scoffin *et al.* (1980) calculated rates of 0.4×10^6 g $CaCO^3$ yr^{-1} for *Sparisoma viride* and 97.5×10^6 g yr^{-1} for *Diadema*, with the latter converted to 5.3 kg $CaCO_3$ m^{-2} yr^{-1} by Glynn (1997). In St. Croix, Ogden (1977) showed that *Diadema* generated 4.6 kg m^{-2} yr^{-1} and *Echinometra lucunter* produced 3.9 kg m^{-2} yr^{-1} compared to 0.49 kg m^{-2} yr^{-1} for the parrotfish *Scarus iserti* in Panama. Hubbard *et al.* (1990) showed that bioerosion in St. Croix was primarily by sea urchins (0.17 kg m^{-2} yr^{-1}). The high rates of bioerosion by urchins are in part because *Diadema*'s grazing rate is much higher than that of parrotfishes (Scoffin *et al.*, 1980).

Herbivorous fishes, particularly parrotfishes, may be less significant bioeroders than *Diadema*, although postmortality data are scarce, but they are wider ranging and a geologically significant agent in the transformation of reefs into sediment (Gygi, 1975; Ogden, 1977). For example, parrotfishes have been estimated to reach a summer maximum of >150,000 bites m^{-2} d^{-1} in the Caribbean (Carpenter, 1986); this is mainly from dead coral areas since living corals are rarely grazed (Scoffin *et al.*, 1980; Bruggemann *et al.*, 1996; Hixon, 1997). On Jamaican forereefs, grazing rates of all fish species were 800 bites m^{-2} h^{-1} (6–8 m, dominated by *Scarus iserti*) and 121 bites m^{-2} h^{-1} (16–18 m, dominated by *Sparisoma atomarium*), which increased at the shallower site after *Diadema* mortality (Morrison, 1988). Bioerosion rates of parrotfishes, using a range of techniques, have been estimated at 7.62, 2.40, 1.43 and 0.69 kg m^{-2} yr^{-1} (*Scarus vetula* and *Sparisoma viride* only) on a shallow reef, gorgonian zone, dropoff and reef slope in Bonaire (Bruggemann *et al.*, 1996), 0.02 kg m^{-2} yr^{-1} in St. Croix (Hubbard *et al.*, 1990), 0.11 kg m^{-2} yr^{-1} in Bermuda (Bardach, 1961), 40–168 g m^{-2} yr^{-1} in Barbados (Frydl and Stearn, 1978) and 174 kg ha^{-1} per summer month in Bermuda (Gygi, 1975). Grazing also alters the microtopography of the coral substratum and may determine the success of settlement of internal bioeroders (Sammarco *et al.*, 1986) because any condition that causes coral tissue mortality increases the probability of invasion by borers (Glynn, 1997). Damselfishes further influence external bioerosion by reducing grazing pressure (Section 3.4.4) and may influence internal bioerosion by affecting the population dynamics of the boring cryptofaunal community (Sammarco *et al.*, 1986).

Microborers (e.g., cyanobacteria, chlorophytes, rhodophytes and fungi) are a further important component of the bioeroding community and there are well-established interhabitat distribution patterns, although actual habitat-specific rates of bioerosion are scarce. Generally the abundances of microborers are linked to light intensities as many are photosynthetic. In Belize, May *et al.* (1982) documented two endolithic microorganisms assemblages in mounted carbonate fragments along a reef transect; the upper photic zone ($<$12 m) was dominated by cyanophytes and chlorophytes and the lower photic zone was characterised by rhodophytes. There was some evidence that the unidentified subsurface microborers in the shallow lagoon were fungi and bacteria. There were no subsurface microborers in the forereef sand zone, indicating that endoliths require organic nutrient sources such as are available in lagoonal seagrass beds. Perry (1998b) also showed that in Jamaican sediments, two distinct microboring communities were associated with the transition from upper to lower photic zone. In water shallower than 18 m, the sediments were dominated by cyanobacteria and chlorophytes, but deeper than 18 m, rhodophytes and fungi were most abundant. In more turbid water with greater rates of light attenuation, the community shift may occur at 5–10 m (Perry and Macdonald, 2002). The highest infestation of carbonate grains by microborers was in low-energy back reef habitats (Perry, 1998b). Vogel *et al.* (2000) measured microbial bioerosion rates at a shallow leeward site in the Bahamas as being up to 520 g m^{-2} yr^{-1}. The bioerosion rate declined with depth and was only 1–2 g m^{-2} yr^{-1} at 275 m.

3.8.2. *Community bioerosion rates*

Estimates of community bioerosion rates are scarce, with most research focusing on specific taxa or characterising bioeroding community composition. The gross $CaCO_3$ destruction for a shallow ($<$10 m) fringing reef in Barbados was estimated as 123×10^6 g yr^{-1} (Scoffin *et al.*, 1980), and bioerosion across a fringing reef in St. Croix, from the beach to a depth of 40 m, was calculated as 0.65 kg $CaCO_3$ m^{-2} yr^{-1} (Hubbard *et al.*, 1990). Furthermore, *Diadema* mortality affected both coral cover and bioerosion, and Bak *et al.* (1984) concluded that postmortality carbonate dynamics had been significantly altered in Curaçao. Before mass mortality, there was a slight negative carbonate budget (production of ~3.1 kg $CaCO_3$ m^{-2} yr^{-1} $<$ bioerosion ~3.3 kg $CaCO_3$ m^{-2} yr^{-1}) on shallow forereefs (5–10 m), but changes in *Diadema* abundance and the consequent reduction of bioerosion (to ~0.4 kg $CaCO_3$ m^{-2} yr^{-1}) meant there could be a net carbonate accumulation.

3.8.3. *Habitat functional values (Figure 1)*

Habitat-specific community bioerosion rates are limited to shallow fringing reefs and appear to range from ~0.4 to 3.3 kg $CaCO_3$ m^{-2} yr^{-1}, although higher rates have been published for individual taxa alone (e.g., Hunter, 1977). Therefore, functional values are assigned here using the densities of *Diadema* and parrotfishes (Section 3.4) and known distributions of boring sponges. Densities of *Diadema* have been reduced significantly by mass mortality in the 1980s (Lessios, 1988; and Section 3.4.5, earlier in this chapter), but there are few quantitative data on changes to bioerosion rates or compensatory changes by other taxa so the putative functional values assigned here refer to reefs with premortality densities of urchins. Mangroves, seagrass beds and sand areas clearly do not have a carbonate structure and so have no functional value for bioerosion. Although there is significant variation, rates of bioerosion by *Diadema* have generally been reported as higher than those of fishes (0.17–9.7 vs 0.02–7.62 kg $CaCO_3$ m^{-2} yr^{-1}, respectively). Patch reefs, reef crests and shallow *Montastraea* reefs had the highest densities of *Diadema*, high or medium densities of *Sp. viride* and the highest percentage cover of boring sponges (e.g., Liddell and Ohlhorst, 1987) and so are assigned high functional values. Back reefs had medium densities of *Diadema* but have high densities of *Sp. viride* and the highest bioerosion by invertebrates (Perry, 1998a) and so are also assigned a high functional value. Gorgonian-dominated forereef habitats and deep *Montastraea* reefs have low or medium densities of *Diadema* and *Sparisoma viride* and medium or high percentage cover of boring sponges and are given medium functional values. *Diadema*, *Sp. viride* and boring sponges either have low densities or are absent on escarpments, and this habitat is assigned a low functional value.

3.8.4. Sediment transport

The reef crest and lagoon-reef flats are the main sources of local sediment production within a reef (Fagerstrom, 1987). Reef crests are characterised by a high density of rapidly growing corals and bioeroders and the lagoon-reef flats support abundant calcified algae with fast turnover rates. However, reef sediments are moved between habitats by (1) wind-driven shallow water waves and currents that move from the open ocean to the reef flat and lagoon; (2) tide-driven currents moving across the reef in both directions; and (3) gravity-driven movements to, for example, shallow depressions and deep reef slopes. Sediment transport processes are supplemented by biologically induced transport, but this is less important than physical processes (Sadd, 1984). However, burrowing and bioturbation by the infauna of flat and lagoon communities can be important in resuspending sediments in areas where currents are too weak to resuspend them but are strong enough to move them (Fagerstrom, 1987). An understanding of sediment transport is vital for understanding reef growth; at some sites sediment can constitute ~40% of a reef's interior, which is more than that of recognisable corals

(Hubbard *et al.*, 1990). Sediment, particularly on reefs, can be constantly reworked. Scoffin *et al.* (1980) showed that 17% of the weight of coral skeletal carbonates was incorporated back into a Barbados reef and may later be reworked by bioerosion.

As discussed in Section 3.1, the reef crest plays a vital role in energy dissipation and, along with being a significant source of sediment, is a critical demarcation between the two main directions of sediment transport. Sediment moves from the reef crest to the reef flat or by gravity from the crest down the seaward slope. Wave-driven currents continuously flow onshore over reef crests and have the greatest velocity at low tide when wave breaking is at its most intense. Reef crest currents provide a mechanism for moving water and sediment from the forereef shelf into back reef lagoon (Suhayda and Roberts, 1977). Similarly, Lugo-Fernández *et al.* (1994) highlighted that reef-produced sediment (i.e., mainly from shallow areas) was transported primarily into back reef lagoons. Turbulence causes grain size to be largest at the reef crest and decrease with decreasing turbulence towards the deeper forereef (Gischler, 1994). Although the reef crest is a zone of high calcification rates, the topography and turbulence make it effectively "self-cleaning" with little or no accumulation of fine calcareous sediments, which are transported to the lagoon and deep reef slope (Goreau and Goreau, 1973). Gischler (1994) showed that on Belizean atolls, back reefs and lagoons had more fine-grained sediment than forereefs (more fragments of coral, coralline algae and *Halimeda*). Molluscs, and consequently mollusc fragments, are more abundant in back reefs than forereef habitats.

Seaward of the reef crest, some calcareous detritus is exported from shallower zones into deeper water under the impetus of currents induced by gravity waves. Gravity-induced movement generally increases with increasing slope angle and is influenced by reef topography. For example, the grooves of spur-and-groove formations act as sediment "chutes" (Goreau and Goreau, 1973). In Jamaica, movement caused by gravity results in a sand-covered slope starting at 30–35 m with sand from shallower zones and sedimentary fans with apices at forereef canyons (Goreau and Goreau, 1973). On the Belizean atolls, the constant transport of sediment over the brow of the reef and down the reef walls has led to a distinct increase in coarse *Halimeda* fragments in sediments on the ledges of the wall and finer sediment in deeper areas (Gischler, 1994).

Except during storms, gravity-induced sediment movement down forereef slopes is relatively limited (Sadd, 1984). During winter storms, a significant seaward movement of sediment occurs because of wave-generated oscillatory currents (Scoffin *et al.*, 1980; Sadd, 1984; Macintyre *et al.*, 1987). Sand channels are important "corridors" of sediment transport during both storm and nonstorm conditions (e.g., Hubbard *et al.*, 1990). Movement of sediments during storms has been studied in detail on a narrow (300-m) shelf in a semiprotected bay in St. Croix. Sadd (1984) showed that sediment accumulates on the shelf for most of the year and then is moved seaward during winter storms across a sandy forereef terrace and through sand-filled channels at the shelf edge. Sediments are not transported under nonstorm conditions because an algal mat binds the upper layer of grains in sediment-rich habitats. Currents generated during winter storms exceed a critical energy threshold that destroys the algal mat and facilitates sediment movement. Storm events are vital because calculations indicate that sediment transport processes occurring under nonstorm conditions could not remove all the sediment produced by reef organisms. Hurricanes and storms stop the reef from "drowning" in its own sediment (Sadd, 1984). Macintyre *et al.* (1987) suggest that the differential transport by high bottom-water velocities during storm periods affects the size distribution of sediments in Belize. Finer sediments are further away from the reef crest and this is an important factor leading to the zonation of five back reef zones. Lugo-Fernández *et al.* (1994) showed that changes to the amount of exposed sediment and the size of seagrass beds in Puerto Rico were a product of sediment transport by hurricane-generated waves. Hubbard (1992) assessed the importance of a hurricane for moving sediments and showed that at least 2 million kg of sand were removed from a reef in St. Croix during the event. Sediment transport rates were 11 orders of magnitude higher during the hurricane than those during calm conditions.

Sediment deposition is a function of the dissipation of wave energy by baffling and then trapping and stabilisation (Fagerstrom, 1987). For example, habitats such as spurs and grooves or seagrass can act as a baffle leading to sediment deposition (Fagerstrom, 1987), and at a smaller scale, turf algae trap sediment (e.g., Birkeland, 1977). Patterns of sediment deposition on some reef flats cause a concentric zonal arrangement of grain size linked to turbulence, and similar sediment zonations are present across whole reef complexes (Fagerstrom, 1987). Similarly, in the Caymans, Suhayda and Roberts (1977) showed that the sediment distribution in a lagoon reflected current patterns and wave characteristics at the shore. Scoffin *et al.* (1980) showed that compositional variations in sediment across a fringing reef in Barbados were highly irregular and did not reflect the ecological zonation of the reef. Gischler (1994) showed on Belizean atolls that no reef zones could be distinguished from their sediments alone.

3.9. Habitat recovery

Hatcher (1997a) lists maintenance of biodiversity as a major ecosystem process of coral reefs. Measures of this process occur at a range of spatial and temporal scales and include ecosystem speciation and extinction, community succession and response and recovery from disturbance and interorganism competition. Detailed long-term studies of Caribbean habitat recovery are surprisingly scarce, at least partly because of the stochastic nature of disturbances and the lack of funding for long-term monitoring. There is even less information on spatial variation in recovery rates of different habitat types under different disturbance regimens. Setting recovery in the context of specific disturbance regimens is important because each type of disturbance has different effects. For example, temperature, sedimentation, pollutants and predation cause organism mortality, but reef structure and topography are not altered significantly. Storms, blasting and dredging cause both mortality and dramatic changes of reef topography (Smith, 1988). Furthermore, it is clear that recovery rates from disturbances are far from predictable because of factors such as synergistic effects of different disturbance types (Pearson, 1981; Hughes and Connell, 1999). In St. Croix, the competitive ability of *Acropora palmata* had been reduced by white band disease; thus, *Diploria strigosa* was more abundant than normal. The shift in community structure led to more destruction (loss of coral cover) on a shallow forereef during a hurricane because *Acropora palmata* is better adapted to recovery from hurricanes by the reestablishment of living fragments (Bythell *et al.*, 1993). Pearson (1981) reviewed early work on reef recovery, but few data were available. More recent monitoring programmes have provided some empirical insights into habitat recovery. Dustan and Halas (1987) reported increasing coral cover in a shallow (0–7 m) reef zone in Florida and decreases in deeper forereefs (10–22 m). The changes in Florida were caused by *Agaricia agaricites*, *Helioseris cucullata*, *Favia fragum* and *P. porites* colonising the shallows, possibly because of physical damage to the dominant *Acropora palmata*.

Data on reef recovery have been generated by monitoring reef communities following hurricanes. Available data show how the suite of spatial factors affecting reef damage and fragment survival contribute to widely variable rates of reef recovery. Recovery at small scales can be relatively rapid because of coral growth and regeneration (Steneck, 1994). Indeed *A. palmata* is adapted to life in high-energy environments with fast growth rates and its main form of propagation being by colony fragmentation, which enables it to rapidly repopulate areas disturbed by intense physical disturbances (Highsmith *et al.*, 1980; Highsmith, 1982). However, massive, encrusting and foliaceous corals may become more abundant on reefs frequently exposed to higher wave energies than *A. cervicornis* can withstand because, if there is almost total mortality, the latter has slow rates of sexual recruitment (Woodley *et al.*, 1981). Furthermore, simultaneous hurricane and bleaching events can reduce coral recruit densities to ~20% of predisturbance levels (Mumby, 1999a). Variations in the reduction of recruit densities may have been caused by protective microhabitats or the proximity of habitats to reef cuts, which may aid the dissipation of storm surge.

Given the time frames necessary for studying reef recovery, modelling approaches represent an attractive method to assess the putative effects of different disturbance regimens. Simulations by Hughes and Tanner (2000) based on data from Jamaican reefs provided an example of how species-specific data can be used in modelling reef recovery. Hughes and Tanner (2000) showed that for three species (*Montastraea annularis*, *Agaricia agaricites* and *Leptoseris cucullata*), the levels of larval recruitment required to maintain populations at relatively "natural" (1977) levels increased significantly with time, but actual recruitment rate declined. Furthermore, the simulations showed that *Montastraea annularis* could survive long periods with minimal larval input (because of its life history traits), but recruitment failure was much more important to *Acropora agaricites* and *Leptoseris cucullata*. The simulations indicate that *Montastraea annularis*, and by extension *Montastraea*-dominated forereefs, will recover more slowly than other species because of the species' slow rates of recruitment and growth.

The remainder of this section is dedicated to variations in two key factors driving the recovery of coral populations: coral reproduction and recruitment. The growth of corals following recruitment has been addressed in Section 3.7. We have focused on coral reproduction and recruitment, as opposed to other components of the benthic community, because of the importance of corals in many reef processes and the fact that corals have received the most research effort. Habitat-specific functional values are only assigned for coral recruitment because there are insufficient data for coral reproduction.

3.9.1. Coral reproduction

Coral reproduction has been reviewed by Fadlallah (1983), Szmant (1986), Richmond and Hunter (1990), Harrison and Wallace (1990) and Richmond (1997). Within the body of literature on coral reproduction, there are few empirical data on how, or if, reproductive strategies and success vary across the seascape. Theoretically, it is possible to assess the reproductive potential of a given habitat based on the species present, their relative abundances and age structure (sexual maturity) and the ratio of brooders to broadcasters (Endean, 1976). However, it is conceivable that factors that vary between habitats might influence a given species' reproductive success such as interhabitat and intrahabitat competition, depth and water movement and these are poorly understood.

Szmant (1986) suggested that species in shallow disturbed habitats with much spatial rearrangement must withstand disturbance or rapidly recolonise by having high rates of local recruitment, resistant skeletons or a high rate of survival of fragments. Szmant (1986) concluded that iteroparous brooding is an optimal strategy in shallow water because it leads to high local settlement and is often used by species with a small adult size (i.e., have high adult mortality). The principles outlined by Szmant (1986) are well demonstrated by *Acropora* species, which are generally limited to shallow areas and largely depend on asexual reproduction caused by wave-induced fragmentation (Highsmith, 1982), along with some sexual recruitment. Johnson (1992) showed that *Manicina areolata*, commonly associated with seagrass and mangroves, is self-seeding and has life history characteristics suitable for life in a patchy chronically disturbed environment. *M. areolata* is a brooding species and is not reproductive until large enough to escape the high probability of mortality associated with small size. The restricted dispersal allows dense populations of *M. areolata* to develop in patchy but nutrient-rich environments such as reef flats. Furthermore, brooding species in shallow habitats may have different reproductive traits compared to those in deeper water. Van Moorsel (1983) demonstrated that differences between the reproductive strategies of two brooding *Agaricia* species were explained by the predictability of their preferred habitats. *Agaricia humilis*, which is found mainly in relatively disturbed shallow reef flats and dropoff zones (5–12 m), had an opportunistic reproductive strategy involving planulation throughout year, smaller maximum size, larger planulae production per unit of living tissue and smaller planulae volume. In contrast, *Agaricia agaricites* on the less-disturbed deeper reef slope (10–30 m) shed planulae in spring and summer and had the opposite traits to *A. humilis*.

3.9.2. Coral recruitment

Following coral larval production and their supply to a reefal area, recruitment to the reef is dependent on four major factors: (1) the phototactic behaviour of planulae; (2) the nature of the surface; (3) reproductive seasonality; and (4) the survival of spat under pressures of predation and competition (Baggett and Bright, 1985). The second and fourth factors are particularly influenced by habitat type and hence are within the scope of this review. The nature of the reef surface is especially important for larval settlement and the presence of crustose coralline algae are important metamorphosis cues. In laboratory experiments, Morse *et al.* (1988) showed that *Agaricia tenuifolia*, *humilis* and *danai* were induced to metamorphose by particular crustose coralline algal species, and in the field, this cue did not appear to vary between forereef, reef crest and back reef habitats in Bonaire. In Jamaica, *A. agaricites* settled and had the highest levels of metamorphosis on the coralline alga *Paragoniolithon typica*, with the coralline *Spongites* also an important cue, but little metamorphosis on bare rubble and none on coral fragments and filamentous algae (Carlon and Olson, 1993). Planulae generally do not settle on sediment and those that do have poor survival rates (Richmond, 1997). The presence of coralline algae on a consolidated substrate varies considerably between habitat types (see Section 3.3).

Habitat rugosity is a key factor influencing the spatial pattern of coral recruitment. The requisite rugosity may be at a very small scale and Gunkel (1997) showed higher recruitment to rough surfaces in the Bahamas and proposed that rough surfaces had a greater development of a bioorganic film compared to smoother surfaces. In contrast, Lewis (1974) showed *Favia fragum* had no preference for rough or smooth surfaces. The role of rugosity has generally been investigated at a larger scale than surface roughness, with many researchers reporting differential recruitment rates between vertical and horizontal surfaces. Overall, it seems that coral recruitment in shallow water is most frequent on downward facing surfaces or crevices to avoid high grazing pressure and sedimentation. In deeper water, recruitment is highest on upper (horizontal) surfaces to compensate for reduced light levels (Bak and Engel, 1979; Rogers *et al.*, 1984; Carleton and Sammarco, 1987). It has been hypothesised that recruitment probabilities are higher in microhabitats protected from surge or rapid water movement (Baggett and Bright, 1985). Furthermore, the general pattern of settlement preferences may not be uniform for all species in shallow and deep water; thus, *Agaricia tenuifolia* prefers shaded areas, but *Agaricia humilis* favours direct light (Morse *et al.*, 1988). However, the relative roles of coral larval settlement selection or postsettlement mortality in determining observed patterns of coral recruitment rates remain unclear. A high density of juvenile corals in a particular habitat may be caused by preferential settlement, low mortality rates or both. Examining the roles of settlement selection and postsettlement mortality is particularly difficult for corals, that broadcast their gametes, such as *Montastraea*, because of the rarity of juveniles found on a reef (reviewed by Mumby, 1999b).

Quantitative data on recruitment rates in a variety of habitats has been collected using both artificial (e.g., settlement tiles) and natural substrata. The link between densities of recruits on settlement plates and those found on reefs is equivocal, so here we assign functional values using surveys of natural substrata alone. On canyon walls at 9, 18, 27 and 37 m in St. Croix, there was a general decrease in the number of juveniles and species with increasing depth (Rogers *et al.*, 1984). Rogers *et al.* (1984) showed that recruits were most abundant at 9 m and 18 m (13–33 and 28–42 juveniles m^{-2}, respectively) with densities decreasing to 8–18 m^{-2} (27 m) and 3–5 m^{-2} (37 m). Also in the U.S. Virgin Islands, the median density of juvenile corals in a shallow (<6 m) boulder field with low coral cover was 0–8 0.25 m^{-2} (Edmunds, 2000, 2004). At a deeper forereef site in the U.S. Virgin Islands, along with forereef sites in Florida and Belize, densities were 1.8–44 juveniles m^{-2} with highest densities in the *Agaricia*-dominated Belize site and densities on *Montastraea* reefs were ~6 m^{-2} (Edmunds *et al.*, 1998). In high-relief spur and groove, relict reef flat and relict spur-and-groove habitats across a reef profile from 4 to 18 m in Florida, the number of species as juveniles was significantly greater in deeper (>10 m) relict spur-and-groove sites (2.81 juveniles m^{-2}) compared to the other two zones (1.61–1.65 m^{-2}) (Chiappone and Sullivan, 1996). The density of juveniles of spawning species (*M. annularis*, *M. cavernosa* and *Siderastrea siderea*) increased with increasing depth with a fivefold increase in the density of *M. cavernosa* from a shallow high-relief spur-and-groove habitat to a deeper relict spur-and-groove zone. Conversely the brooding *A. agaricites* decreased fourfold in abundance between the same habitats. On patch reefs and offshore bank reefs in Florida, juvenile densities using two methods were ~0.75–24.0 m^{-2} and ~0.75–10.0 m^{-2}, respectively (Miller *et al.*, 2000). Further data from macroalgal-dominated reefs in the Florida Keys gave relatively constant densities of 1.9–2.1 corals 0.25 m^{-2} at four depth intervals from 12 to 29 m (Edmunds *et al.*, 2004). At a shallow (5–8 m) control reef in Bermuda, Smith (1992) documented densities on the natural substratum of 18.0–21.1 recruits m^{-2}. Recruit density on an 8–10 m *Montastraea* reef in Belize was ~11–14.5 m^{-2}, which decreased to ~2.5 m^{-2} after a bleaching event and hurricane (Mumby, 1999a). At a series of spur-and-groove forereef sites in Mexico (~10 m depth), densities varied from 1.0 to 6.4 juveniles m^{-2} (Ruiz-Zárate and Arias-González, 2004). In Curaçao, densities of juvenile corals were 16.8 m^{-2} (shallow terrace, 3–9 m), 12.9 m^{-2} (dropoff, 9–17 m), 13.7 m^{-2} (upper slope, 17–26 m) and 17.9 m^{-2} (lower slope, 26–37 m) (Bak and Engel, 1979). Mean recruitment of *Manicina areolata* to a series of *Thalassia testudinum*–dominated carbonate reef flats in Panama was 1.62 m^{-2} (Johnson, 1992).

3.9.3. Habitat functional values (Figure 1)

Data on recruitment density to natural substrata are scarce and generally restricted to forereef habitats. Published densities for patch reefs, *Montastraea* reefs and escarpments range from 0.75–21.1 corals m^{-2} but are generally toward the higher end of this range and are assigned high functional values. Turbulent back reefs and reef crests and gorgonian-dominated forereef habitats are likely to have lower densities of recruits and are assigned putative medium functional values in the absence of quantitative data. Seagrass beds and mangrove stands are assigned low functional values as some recruitment is required to maintain the occasional colonies of hardy genera such as *Manicina*, *Porites* and *Siderastrea*. Forereef sand beds have no coral cover (poor recruitment to soft sediments; Richmond, 1997) and have no functional value.

3.10. Community biodiversity

Although maintenance of biodiversity is a major ecosystem process of coral reefs (Hatcher, 1997a), arguably the actual number of species or diversity in a habitat is a *property* of each community rather than a *functional value*. However, the biodiversity of Caribbean reef habitats is reviewed here because of the importance of this property. Biodiversity, along with conservation of fish stocks, is frequently cited as a key reason for establishing marine reserves (e.g., Roberts and Hawkins, 2000). Furthermore, research interest in the correlation between biodiversity and ecosystem functioning is expanding but is yet poorly understood in marine systems (Done *et al.*, 1996; Loreau *et al.*, 2002). It is likely, therefore, that researchers would wish to generate maps of biodiversity from standard habitat maps along with maps of functional values.

Despite a long history of describing reef zonation patterns (e.g., Goreau, 1959), the published literature describing the full diversity of a particular taxon across a range of habitat types is limited. Typically, descriptive papers list only the characteristic species for each habitat type documented or cover only part of a full shoreline-escarpment transect. For many taxa, inventories of species richness and diversity are limited by current taxonomic knowledge (Mikkelsen and Cracraft, 2001). Scleractinian corals are perhaps the best known and studied taxon, so variations in their diversity between habitats are reviewed here.

3.10.1. Scleractinian diversity

Scleractinians have well-established requirements of, for example, available space on a hard substratum for settlement (and possibly the presence of appropriate cues), limited sedimentation and some water movement to transport food and remove metabolic wastes (e.g., Sheppard, 1982; Morse *et al.*, 1988; Maida *et al.*, 1994; Sebens, 1997). Clearly the conditions within lagoons and mangrove stands are unsuitable for most coral species and these habitats have low scleractinian diversity. Only hardy species such as *Manicina areolata* and *Siderastrea radians* can survive in seagrass beds (e.g., Johnson, 1992).

The intermediate disturbance hypothesis (Connell, 1978) has frequently been invoked to explain the patterns of scleractinian diversity across hard-bottom habitats. This hypothesis posits that intermediate disturbance intensities (frequency and magnitude) may maintain benthic species diversity by reducing the abundance of competitive dominants, which may occur under low disturbance conditions. Similarly, high disturbance conditions limit the number of species that can become established compared to intermediate disturbance intensities. Across coral reefs, the effects of disturbance by hurricanes and wave action generally decrease with increasing water depth. However, the relationship between disturbance and diversity is confounded by a range of factors, particularly decreasing light intensity. Although it might be expected that diversity should be low in shallow (disturbed zones), high at intermediate depths and low in deeper zones (competitive exclusion), reduced light intensity (and perhaps other variables) appears to limit competitive exclusion by slowing growth rates (Huston, 1985c). Therefore, the intermediate disturbance hypothesis may only be applicable across relatively shallow reef zones subject to varying disturbance regimens (Rogers, 1993b). Such a pattern across a single habitat (shallow spur-and-groove zone) has been shown by Aronson and Precht (1995) in Belize. At a landscape scale (>10 m^2), coral diversity was highest (Shannon-Wiener diversity $\sim$1.2 compared to a minimum of $\sim$0.2) at intermediate levels of disturbance, as measured by substratum topographical complexity. Disturbance reduced the percentage cover of the competitive dominant *A. tenuifolia* (Aronson and Precht, 1995).

Jamaican reefs, particularly those close to Discovery Bay, are some of the best studied in the Caribbean and provide data on patterns of scleractinian diversity across whole reefs. Huston (1985a) provides data showing that coral diversity was relatively low at the reef crest and increased with increasing depth to a maximum between 15 and 30 m. Shannon–Wiener diversity values were 0.01 (reef crest), 0.75–1.18 (5 m), 1.57–1.68 (10 m), 1.65–2.12 (15 m), 1.54–2.16 (20 m) and 1.26–1.81 (30 m). As predicted, these data support the intermediate disturbance hypothesis at shallow depths but suggest that increasing diversity with increasing depth is caused by limits to competitive dominance. Liddell *et al.* (1984) provided further data from Discovery Bay at depths below the maximum limit of the study by Huston (1985a). Liddell *et al.* (1984) showed that coral diversity, using the Shannon–Wiener index, increased from 15 m (1.87) to 22 m (2.12) and then decreased at 30 m (1.54), and minimum values were found at 56 m (1.49) on the unstable steeply sloping escarpment. Surveys on the same reefs following *Diadema* mortality and hurricane disturbance document the same patterns of coral diversity, despite significant changes to community structure (Andres and Witman, 1995).

Data on interhabitat coral diversity patterns, all using the Shannon–Wiener index, are also available from other reef systems. Sullivan *et al.* (1994b) reported no discernible trends between diversity and evenness indices for linear patch reef (diversity 2.09), transitional reef (2.19) and high- and low-relief spur-and-groove zones (2.17) in the Turks and Caicos Islands. Mean diversity values for a reef in Florida (taken in 1975 and again in 1982) were 0.66–0.68 (reef terrace), 0.48–0.52 (gorgonian zone), 0.46–0.47 (ridge/trough zone), 0.4–0.5 (*A. palmata* zone) and 0.35–0.36 (reef flat)

(Dustan and Halas, 1987). Further assessments of diversity for sponge/octocoral habitats in Florida were 0.49–1.36 (Sullivan and Chiappone, 1993). Work in Mexico showed that the highest coral diversity was on the forereef (1.78 at 5 m; 2.03 at 10 m; 1.66 at 15 m; 1.72 at 20 m; 1.76 at 25 m) compared to the breaker (reef crest, 1.40) and rear (back reef, 1.62) zones (Jordan *et al.*, 1981). Diversity on a *Montastraea* reef (10.7–12.7 m) in St. John before and after Hurricane Hugo in 1989 was 1.94–2.13 (Rogers *et al.*, 1991) and 1.44–1.81 before and after Hurricane David (1979) in St. Thomas (Rogers *et al.*, 1983). Mean diversity for three types of patch reefs in the Bahamas was 1.56 (Chiappone and Sullivan, 1991). For spur-and-groove zones (12–15 m) in Belize, Jamaica and Florida, diversity values were 1.04–1.81 (Aronson *et al.*, 1994). For two sites on a Puerto Rican forereef (8–17 m), diversity was 1.89–2.20, compared to 1.97 at 18–20 m (Loya, 1976).

3.10.2. Habitat functional values (Figure 1)

Highest diversities (Shannon–Wiener index generally >1.5) have been reported from patch reefs, *Montastraea* reefs and escarpments and are assigned high functional values. Diversity values for back reefs, reef crest and gorgonian-dominated forereefs are generally <1.5 and are given medium functional values. Seagrass beds and mangrove stands are assigned low functional values because they may contain occasional colonies of hardy genera such as *Manicina*, *Porites* and *Siderastrea*. Forereef sand beds have no coral cover and have no functional value.

4. FUNCTIONAL LINKS BETWEEN HABITATS

We have so far concentrated on how functional values vary between habitat types, but there are also numerous functional links between habitats. For example, the reef crest dissipates a significant proportion of wave energy and this influences conditions in the back reef and lagoon zones. Similarly, upstream habitats affect the nutrient concentrations reaching downstream zones, and the internal fabric of a given part of a reef can be largely composed of debris and carbonate sediments from elsewhere. Furthermore, many species undertake ontogenetic shifts, with juveniles and adults having different habitat preferences and individuals migrating between habitats as they grow older. However, interhabitat functional links have received relatively little research attention. For example, there is limited insight into questions such as whether the biomass or behaviour of a species in its preferred habitat varies depending on the nature of adjacent habitats or the role of "corridors" of suitable habitat during ontogenetic shifts. Advances in landscape ecology (see Gutzwiller, 2002, for a review of this topic) may assist with a better understanding of the consequences of particular habitat patterns. The remainder of this section explores the links between reefs, mangroves and seagrass beds, which exemplify functional interactions between tropical marine habitats.

4.1. Links between reefs, seagrass beds and mangroves

The link between reefs, seagrass beds and mangroves is multifaceted and includes reefs acting as breakwaters that lead to low-energy environs for mangroves and seagrass beds (see Section 3.1). Seagrass beds and mangroves buffer reefs from excessive nutrients (Done *et al.*, 1996) and sediment load (Ogden, 1997) but supply detritus and essential nutrients. Mangroves may also cause more nutrients to be available to adjacent seagrass beds, but this does not appear to increase seagrass net community primary productivity (Koch and Madden, 2001). Seagrass beds are used by some reef fishes for foraging, and both seagrass and mangroves are used by many fish species as nurseries before juveniles undertake ontogenetic shifts to reef habitats (Mumby *et al.*, 2004a). A full review of the links between reefs, seagrass beds and mangroves is beyond the scope of this chapter, but we illustrate the interactions by highlighting the movement of organic matter, ontogenetic shifts from nursery areas and trophic connections.

The export of organic production from seagrass beds and mangrove stands to reefs is dependent on a range of factors. A mangrove stand inundated by frequent large tides and strong currents will lose more of its litter production than a stand in a more sheltered environment (Hogarth, 1999). However, there appears to be a net movement of dissolved organic matter from mangroves to seagrass beds and then to reefs. Despite the export of inorganic and organic material from mangroves, the productivity of downstream systems is rarely enhanced (Ogden, 1997). Even 1 km away from a mangrove swamp in the Bahamas, only ~10% of dissolved organic matter was attributable to the vascular plant-derived material (Moran *et al.*, 1991). Hogarth (1999) also indicates that mangroves tend to have significant net imports of soluble forms of nitrogen (and phosphorus) but a net export of particulate nitrogen. In contrast, it has been estimated that export from Caribbean seagrass beds ranged from up to 10% of leaf productivity from *Thalassia*-dominated areas to >60% for *Syringodium* beds (Greenway, 1976; Zieman *et al.*, 1979). The lower export rate of *Thalassia* is caused by herbivore bites having little effect on the whole blade, but a similar bite on *Syringodium* severs the blade and the upper portion is carried away from the site of growth by water movement (Thayer *et al.*, 1984).

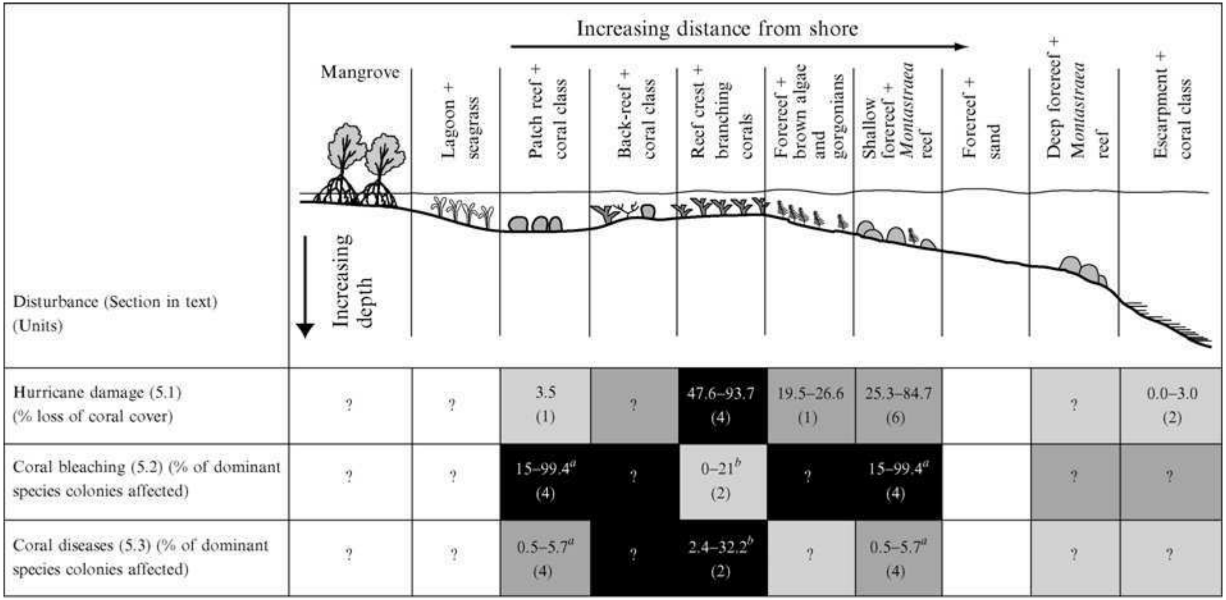
A seagrass bed or mangrove stand acts as a nursery if "its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur" (Beck *et al.*, 2001). Creeks, mangroves and seagrass beds intercept large numbers of fish larvae and provide abundant food resources and protection from predators (e.g., Eggleston, 1995; Nagelkerken *et al.*, 2000a,c). Fishes eventually migrate to near-shore patch reefs and offshore reefs as they mature so that few adults are seen. As noted by Adams and Ebersole (2002), for species that use lagoons as nurseries, these habitats must provide advantages that offset the energy expense and predation risk incurred by incoming larvae both when travelling across the reef to the lagoon and subsequently when returning to the reef. Evidence is provided by both Shulman (1985) and Sweatman and Robertson (1994) that at least part of the advantage of nursery habitats lies in the reduced predation risk associated with settling in seagrass areas compared to the edges of a bank-barrier reefs or patch reef. As recruits grow larger, the seagrass blades no longer offer concealment, but the animals are faster swimmers, may manoeuvre with more agility and achieve a size refuge from predators, which facilitates a move to favourable hard-bottom areas (Shulman, 1985). In Bonaire, van der Velde *et al.* (1992) showed that seagrass beds were important for juvenile *Haemulon flavolineatum*, *H. sciurus*, *Ocyurus chrysurus*, *Sparisoma viride* and *Acanthurus chirurgus*. Mangroves were particularly used by *Lutjanus apodus*, *L. griseus*, *Sphyraena barracuda* and *Chaetodon capistratus*. Nagelkerken *et al.* (2000a) showed that in a Curaçao bay, variations in the density of juveniles within seagrass and mangrove habitats were caused by the distance to the mouth of the bay, water transparency, amount of shelter and structural complexity. Mumby *et al.* (2004a) show that the presence of mangroves significantly affects fish community structure on nearby reefs and increases the biomass of many species compared to reefs without adjacent mangroves. Nagelkerken *et al.* (2000c) demonstrated that although most species had habitat preferences, many used multiple biotopes.

Trophic links, particularly between seagrass beds and hard-bottom communities, have received considerable attention and are an important component of tropical marine food webs. For example, patch reef–associated predators such as *Epinephelus striatus* are significant predators of nocturnally foraging crabs in adjacent seagrass meadows and are an important trophic link between these habitats (Eggleston *et al.*, 1998a). At a lower trophic level, Kirsch *et al.* (2002) showed that small vertebrate grazers consumed substantial amounts of seagrass production in the Florida Keys. Vertebrate grazing led to a large amount of primary production reaching higher consumers, some of which enter seagrass beds from surrounding reefal areas to feed. Grazing of seagrass beds by both fishes and sea urchins, aided by wave and current action, around patch reefs creates the "halos" of sand where seagrass blades have been removed (e.g., Randall, 1965; Ogden and Zieman, 1977). Herbivorous fishes also recycle nutrients (largely ammonium) from feeding on seagrass blades by defaecation on adjacent reef resting areas rather than the feeding areas themselves (Thayer *et al.*, 1984). Not only does the defaecation process transfer nutrients from seagrass beds to reefs, it is also more rapid than rates of natural seagrass decay.

The trophic link between reefs and seagrass beds is perhaps best demonstrated by grunts (Haemulidae), which feed on seagrass beds by night and cause an enhanced biomass on reefs near seagrass (Ogden and Zieman, 1977). Reefs near seagrass experience a strong reduction in fish density and richness at night as fishes migrate to areas with a high availability of preferred food (Nagelkerken *et al.*, 2000b). The dusk and dawn migration distances of *Haemulon plumieri* may be up to 560 m and increase with increasing fish size (Tulevech and Recksiek, 1994). Helfman *et al.* (1982) showed that on patch reefs in St. Croix, small, medium, transitional and large juvenile stages of *Haemulon flavolineatum* and *H. plumieri* each differed in age, size, colouration, habitat preference, diel foraging patterns and twilight migratory behaviour, concluding that ontogenetic differences may be caused by learning and development of visual apparatus. The route of migration paths are also affected by interspecific differences in foraging habitat preferences. Burke (1995) studied *H. flavolineatum* and *H. sciurus* leaving a back reef in Belize; *H. flavolineatum* preferentially used sand flats, whereas *H. sciurus* were usually found in seagrass beds. Working in St. Croix, Meyer *et al.* (1983) showed that juvenile grunts (Haemulidae), which feed in seagrass beds at night, excrete substantial quantities of ammonium, particulate nitrogen and phosphorus onto their daytime resting sites (generally coral heads). Furthermore, excreted nutrients were demonstrated to be more beneficial to corals than had previously been assumed and those colonies with resident fish schools grew faster than those without. Further work (Meyer and Schultz, 1985) showed that the excretions were rich in nitrogen (mainly ammonium), whereas faecal matter was richer in phosphorus and half of a fish's daily excretion and defaecation was during the first 4 hr after return to the reef, doubling the amount of ammonium available to corals.

5. SUSCEPTIBILITY OF TROPICAL MARINE HABITATS TO DISTURBANCE

The susceptibility of a range of habitat types to hurricanes and coral bleaching and diseases is addressed in separate subsequent sections as key examples of spatial variation in disturbance regimens (summarised in Figure 2). Synergistic interactions between different types of disturbances are poorly



Disturbance (Section in text) (Units)	Mangrove	Lagoon + seagrass	Patch reef + coral class	Back-reef + coral class	Reef crest + branching corals	Forereef + brown algae and gorgonians	Shallow forereef + *Montastraea* reef	Forereef + sand	Deep forereef + *Montastraea* reef	Escarpment + coral class
Hurricane damage (5.1) (% loss of coral cover)	?	?	░ 3.5 (1)	▓ ?	■ 47.6–93.7 (4)	▓ 19.5–26.6 (1)	▓ 25.3–84.7 (6)		░ ?	░ 0.0–3.0 (2)
Coral bleaching (5.2) (% of dominant species colonies affected)	?	?	■ 15–99.4[a] (4)	■ ?	░ 0–21[b] (2)	■ ?	■ 15–99.4[a] (4)		▓ ?	▓ ?
Coral diseases (5.3) (% of dominant species colonies affected)	?	?	▓ 0.5–5.7[a] (4)	■ ?	■ 2.4–32.2[b] (2)	░ ?	▓ 0.5–5.7[a] (4)		░ ?	░ ?

[a] *Montastraea annularis* complex.
[b] *Acropora palmata*.

Figure 2 Susceptibility of habitats to disturbances across a schematic profile of a Caribbean tropical marine seascape, derived from empirical literature reviewed in the text. Black, dark grey, light grey and no shading indicate high, medium, low and no susceptibility, respectively. Figures represent range of published values. The number of studies (some of which may contribute more than one value) used to derive the ranges are in parentheses. ? indicates a putative class but quantitative data have not been found in the literature.

understood, but Figure 2 summarises the patterns of susceptibility that can form the basis of maps and models of reef resilience to disturbance. In addition to hurricanes and coral bleaching and diseases, other disturbances affect Caribbean reef habitats. The effects of oil pollution are generally most severe in shallow areas, which are the only zones where the oil, which is less dense than water, can accumulate in close contact with the benthos. Jackson *et al.* (1989) documented damage to intertidal reef flats in Panama, which was most extensive at the seaward border where oil accumulated at low tide and caused a bloom of microalgae. Zooanthids, *Millepora* spp., *Porites* spp. and *Echinometra* urchins were also severely affected by the oil. The effects of oil were also seen on shallow subtidal reefs where coral cover decreased by 76%. Similar damage of shallow reefs was seen in Aruba by Bak (1987) as a result of chronic effects from an oil refinery. The *Acropora palmata* zone at ~2 m was affected, and this habitat appears to be particularly susceptible because of the sensitivity of the characteristic species to oiling (Bak, 1987; Guzmán *et al.*, 1991; Brown, 1997).

Sediment rejection is a function of colony morphology, orientation, growth habit and behaviour (e.g., Stafford-Smith and Ormond, 1992). Heavy sedimentation can lead to reduced coral species richness and cover, lower coral growth rates, reduced recruitment, decreased calcification, decreased net productivity of corals and slower rates of reef accretion and affects the structure and function of coral reef ecosystems by altering both physical and biological processes (e.g., Loya, 1976; Rogers, 1990). Most empirical research on the effects of sedimentation has been focused on comparing sedimented habitats to nonsedimented areas or interspecific variations of corals in susceptibility to sediment damage. Such data are difficult to interpret in terms of habitat-specific sedimentation effects and hence are not discussed in detail in this chapter. Furthermore, sedimentation has a wide variety of effects and is referenced elsewhere as appropriate (e.g., the effects on settlement of coral recruits). However, corals such as *Siderastrea radians*, *S. siderea*, *Diploria strigosa* and *Meandrina meandrites* appear tolerant of heavy sediment regimens (e.g., Loya, 1976) and habitats dominated by these species are likely to be sedimentation resistant. Similarly, the most profuse coral growth in Jamaica occurred where sediment drainage was most efficient (Goreau and Wells, 1967). More generally, Stoddart (1969) suggested that the main controls of natural sedimentation on a reef are reef geometry and wave energy.

There is a huge literature devoted to increases in global concentrations of CO_2 (and other gases) caused by human activities, particularly burning fossil fuels and changes in land use, leading to rising atmospheric temperatures (e.g., Vitousek, 1992; Houghton, 1997; IPCC, 2001). Rising temperatures have been predicted to lead to changing sea levels, but there is little empirical research on how sea-level rise will affect tropical marine ecosystems. However, there have been a number of proposed consequences of rising sea level and it is suggested that shallow reef habitats will be most affected. For example, the areal extent of reef flats could increase because of the release from sea-level constraints of further growth and the putative expansion of reef flats may cause concomitant changes in the fauna and flora of their communities (Cubit *et al.*, 1986; Smith and Buddemeier, 1992). Brown (1997) suggests that reef flats currently constrained by present sea levels in protected waters might be expected to show increases in diversity and productivity. However, the increases in diversity and productivity will be swamped by natural variations in the short term. Empirical evidence of the effects of sea-level rise on shallow water communities is scarce, but predictions are supported by evidence from Panama where movement of a zone of *Laurencia papillosa* at the seaward edge of a reef flat has been linked to sea-level change (Cubit, 1985). The effects of sea-level rise on deeper habitat types is unclear, but they may become subject to greater wave action (Brown, 1997). Furthermore, an increase in the partial pressure of atmospheric CO_2 will decrease the saturation states of calcite, aragonite and Mg-calcite (e.g., Smith and Buddemeier, 1992). Aragonite is deposited by scleractinians and calcareous green algae, and Mg-calcite is commonly precipitated by coralline red algae and many other taxa. The effects of the changes of saturations states on coral reef communities are poorly understood, but it seems likely that calcification rates will decrease and there may be a shift to noncalcifying organisms and bioeroders (Smith and Buddemeier, 1992; Kleypas *et al.*, 1999a).

In lagoonal habitats, sea-level rises may affect seagrass and mangrove habitats. Short and Neckles (1999) indicated that there may be shifts in seagrass bed distributions and community structures because of changes in water depth and movement. A key factor of the response of mangrove forests will be the balance between sedimentation and sea-level rise and the geometry of the shoreline (Woodroffe, 1995; Nicholls *et al.*, 1999). If sediment accumulates at the same rate as sea-level rises, the coastal wetland will grow upwards in place. If accretion is too slow, wetlands are submerged longer during tidal cycles and may die because of water logging (Nicholls *et al.*, 1999). More generally, wave inundation will threaten the buffering capacity of coastal systems because seagrass beds and mangroves will be eroded (Ogden, 1997). In enclosed lagoons, sea-level rise may increase the similarity between the properties of lagoonal seawater and those of local oceanic water and reduce the environmental extremes that limit reef development (Smith and Buddemeier, 1992).

Habitats rich in branching corals are generally the most susceptible to degradation from breakage caused by reef walkers, snorkellers, divers and boat anchors, but much of the work on mechanical breakage has been undertaken in the Red Sea and Indo-Pacific. In Bonaire, Hawkins *et al.*

(1999) showed that sublethal effects of diver damage may alter coral communities; direct physical damage was relatively minor, but diving pressure was causing the proportion of branching corals to increase and reducing the number of large massive colonies. Hawkins *et al.* (1999) hypothesised that there were synergistic effects between diver-induced abrasions, rather than actual breakages, and subsequent coral diseases, on mortality. In the Florida Keys, Davis (1977) showed that 20% of an extensive *A. cervicornis* reef was damaged by boat anchors and suggested that anchor-sensitive areas should be identified and closed to anchoring.

5.1. Susceptibility to hurricane disturbance

There is a large body of literature on the role of hurricanes in Caribbean reef systems, highlighting that the damage to each habitat type is dependent on factors such as benthic community composition, reef topography, previous disturbance regimens and storm type, but we use percentage loss of coral cover to assess susceptibility of different habitats. The most obvious pattern of hurricane effects is the damage to shallow habitats compared to deeper reef areas. Wave energy is highest in shallow water, and many authors describe damage to reef crests while deeper forereefs are less affected (e.g., Woodley *et al.*, 1981). Within shallow areas, *Acropora*-rich habitats are repeatedly reported to be most affected because of the susceptibility of these branching species to breakage compared to massive poritids and faviids (e.g., Stoddart, 1985; Brown, 1997). Severe damage to *Acropora* communities has been reported in many locations including Jamaica (76% loss, Woodley *et al.*, 1981; 93.7% at depths of 3–8 m, Crawford, 1995), Puerto Rico (Armstrong, 1981), Belize (Stoddart, 1965, 1974), the U.S. Virgin Islands (mean of 3.9 broken branches m^{-2}; Rogers *et al.*, 1982), Mexico (82% loss; Jordán-Dahlgren and Rodríguez-Martínez, 1998) and Florida (>90% colonies damaged; Lirman and Fong, 1997). Shallow water *A. palmata* is particularly susceptible to breakage because of its high surface area to volume ratio (e.g., Lirman and Fong, 1997).

Although shallow zones are most affected by hurricanes, reef disturbances have been recorded to 20–30 m (Highsmith *et al.*, 1980; Kjerfve *et al.*, 1986; Scoffin, 1993) and occasionally 50 m (Woodley *et al.*, 1981). After Hurricane Allen in Jamaica (1980), Crawford (1995) reported decreases in coral cover of 84.7% in a mixed zone of *Montastraea* and *Acropora cervicornis* (5–11 m) and 78.9% in an *A. cervicornis* zone (8–25 m). The loss of coral cover in a similar Jamaican mixed zone after Hurricane Allen was assessed as 62.5% by Steneck (1994). In St. Croix, loss of coral cover on a shallow (4-m) *Diploria*-dominated forereef was ~96.9% but was only ~28% on a deeper (7 m) *Montastraea* reef (Bythell *et al.*, 2000). On St. John, the loss of coral cover on a *Montastraea* reef (10.7–12.7 m) after Hurricane Hugo (1989) was ~40% (Rogers *et al.*, 1991) but insignificant after Hurricanes Luis and Marilyn in 1995 (Rogers *et al.*, 1997). Mean loss of coral cover on St. Thomas after Hurricane David (1979) at four *Montastraea* reef sites (4–6 m deep) was 25.3% compared to 0% on a steep wall in St. Croix (Rogers *et al.*, 1983). On a foliaceous coral–dominated wall following Hurricane Allen, coral cover was reduced by only 0–3% (Woodley *et al.*, 1981).

In addition to direct wave effects, hurricanes cause a "domino effect," where if one colony is shattered, fragments can cause a cascade of damage to its neighbours (Lirman and Fong, 1996, 1997). The fragments of a coral shattered in one habitat may break corals in both the same habitat and adjacent habitats. Lirman and Fong (1996) document Hurricane Andrew in South Florida causing corals, mainly *Acropora palmata*, from the reef flat to break corals in the rubble zone. Scoffin (1993) highlights that some deeper corals can be broken by colonies "falling" from the shallows. Whether breakage is caused directly by waves or indirectly by collisions between colonies, bioerosion can weaken colonies and introduce further spatial variability to patterns of hurricane damage. Kjerfve *et al.* (1986) noted the importance of bioerosion weakening *Acropora* and making colonies more susceptible to damage. Secondary tissue damage of corals is caused by sand scouring in turbulent water, especially to colonies close to sandy areas (Highsmith *et al.*, 1980; Scoffin, 1993). Layers of sand are also a significant factor in the damage caused to sponges by hurricanes (Fenner, 1991).

Tissue mortality following mechanical breakage by hurricanes is spatially variable within shallow water *Acropora* communities. Knowlton *et al.* (1981, 1990) suggested that during the 5 mo after Hurricane Allen, secondary mortality was >1 order of magnitude more severe than the immediate effects of the storm and eliminated >98% of the original survivors. The complex pattern of mortality involved disease and predation, with predation by *Coralliophila* particularly severe in shallow water. However, patterns of mortality on sections of the back reef epitomised the complex spatial variables that affect coral survival. Some sections of the back reef were protected by *A. palmata* reef crest that survived the hurricane. In protected sections, the mean volume of 22% of patches of *A. cervicornis* remained unchanged or increased in volume and only 9% was reduced to rubble (Williams, 1984). The increase in broken *A. cervicornis* then led to an increase in the abundance of *Diadema* (additional food available) and *Stegastes planifrons* (which are negatively correlated with *A. cervicornis* patch size). There was a competitive interaction between the fish, and urchin species and coral patches occupied by both *Diadema* and *S. planifrons* had a high proportion of living tissue. Coral patches dominated solely by one of the species were overgrazed and <5% of the substratum was covered by living coral (Williams, 1984). In Florida, survival of fragments of *A. palmata* on a patch reef was influenced by the distance from a patch of mature (standing) *A. palmata* (Lirman and Fong, 1997). Standing *A. palmata* may have protected regenerating fragments from wave removal.

Reef topography, the location of the reef relative to the path of the storm, reef orientation with respect to wave direction, the character of prestorm communities and ecological history are important factors determining hurricane damage to reef habitats (e.g., Rogers, 1993a; Bries *et al.*, 2004). For example, the prevalence of reefs on the southwestern coast of Cozumel reduced the impact of Hurricane Gilbert (1988) because the largest waves approached from the east, and there is a limited fetch between the western side of the island and the Yucatan Peninsula (Fenner, 1991). Mean loss of coral cover in Cozumel was 47.6% (shallow fringing reefs), 61.2% (deep fringing reefs), 3.5% (patch reefs), 58.5% (top of shelf-edge reefs) and 30.7% (slopes of shelf-edge reefs). At a smaller scale, reef topography is particularly important as it has a direct effect on wave height and hence energy dissipation. Hindcasting of Hurricane Allen in Jamaica demonstrated a correlation between the tallest breaking waves and maximum damage (Kjerfve *et al.*, 1986). The eastern forereef at Discovery Bay had the tallest waves because of a greater seaward extension of the reef and the effect was exacerbated by the storms being from the east. Furthermore, flow deflection by reef topography was important because this creates high turbulence that breaks *Acropora palmata* as the water moves in untypical directions (Kjerfve *et al.*, 1986). Spur-and-groove formations appear to baffle wave energy more effectively than areas with less topographical relief (Scoffin, 1993). Woodley *et al.* (1981) stated that hurricane damage was more significant on sloping or level areas of reef in Jamaica compared to vertical sections, presumably because vertical areas are generally found in deeper water and wave energy is higher on sloping forereefs. Hurricane damage is also dependent on the distance of a reef from shore. Blair *et al.* (1994) found that in Florida after Hurricane Andrew in 1992, the forereef slope of an offshore reef (between 17 and 29 m) was most heavily affected (26.6% loss) with lesser impacts on a middle reef (21.7%; 11–17 m) and least damage on an inner reef (19.5%; 8–12 m), although all sites initially had low coral cover and could be classified as gorgonian dominated.

Disturbance history is an important consideration in predicting hurricane damage of reef habitats. Hughes and Connell (1999) state that the effect of a given disturbance is significantly affected by previous disturbances and "blurs the line" between single and multiple disturbances. Bythell *et al.* (2000) provide data for the effects of three hurricanes within 6 yr on benthic communities in a protected area in St. Croix, a system with relatively low levels of anthropogenic impacts. Data from three sites (7 m diverse but moderate coral cover; 4 m, high coral cover; 3 m, dominated by dead *A. palmata*) showed that only the 7 m site experienced significant changes in community composition. The change was caused by the interaction of hurricane-induced mortality, some recovery of coral cover, recovery of species richness to higher than prehurricane levels and the role of a major coral recruitment event after the first hurricane. However, variations in community composition between sites (effectively habitats) were much greater than changes over time and landscape community composition appears to remain stable. Bythell *et al.* (2000) conclude that coral communities in St. Croix are resilient to repeated hurricane impacts over a period of 10 yr. The severe damage to shallow water communities during Hurricane Allen in Jamaica (1980) might be atypical because *Acropora palmata* may have been so abundant only because of lack of hurricanes in the preceding years (Woodley, 1992).

5.1.1. Habitat susceptibilities (Figure 2)

Reef crests are clearly the most susceptible habitats to hurricane damage with generally >60% of coral cover lost (high susceptibility). We assign medium susceptibility to coral loss of generally 10–60% (shallow *Montastraea* reefs and gorgonian-dominated forereefs). Note that although gorgonian-dominated forereefs appear to lose 10–60% of their corals during hurricanes, *Montastraea* reefs have higher initial coral cover, so absolute losses of cover are greater. Although there are few data, shallow back reefs are also assigned medium susceptibility as large coral heads are broken, but some patches of *Acropora cervicornis* may receive limited damage (Williams, 1984). Low susceptibility is defined as loss of coral cover of generally 1–10% (patch reefs and escarpments). Deep *Montastraea* reefs are also assigned low susceptibility, although data are scarce. Mangroves, seagrass beds and sand channels are assigned no susceptibility because coral colonies are only very occasional or absent.

5.2. Susceptibility to coral bleaching

Mass coral bleaching involves the loss of symbiotic zooxanthellae following chronic photoinhibition, and more frequent bleaching events may represent a symptom of global climate change (see Hoegh-Guldberg, 1999). Bleached coral colonies may recover by regaining zooxanthellae after initial bleaching, but rates of mortality are generally positively correlated with initial susceptibility. Patterns of bleaching susceptibility may be at least partially explained by different tolerances of zooxanthellae (Fitt and Warner, 1995). However, tolerances of different clades of zooxanthellae, how the clades are distributed intraspecifically and interspecifically and whether particular zooxanthellae will spread across reefs to make corals in a range of habitats more tolerant of bleaching (and hence alter the susceptibility values presented here) is the subject of intense research and speculation (e.g., Baker *et al.*, 2004; Rowan, 2004; Sotka and Thacker, 2005).

Between 3.4 and 8.7% of corals were bleached in four reef sites in Panamá following the 1982–1983 El Niño event (Glynn, 1984). Across a series of Caribbean sites 3–4 mo after the 1987 bleaching event, mean percent of all "pale" corals was 19.9% on patch reefs and 21.7% on forereefs (Lang *et al.*, 1992). The 1995 bleaching event in Belize affected 52% of coral colonies and caused 10–25% of bleached colonies to experience at least partial tissue mortality with a 10–13% loss of coral cover (McField, 1999; Kramer *et al.*, 2000). The proportions of corals affected in Belize were ~43% (back reef), ~50% (forereef) and ~57% (patch reef) (McField, 1999). Following the 1998 bleaching event in Belize, there was an average of 18% mortality on shallow reefs and 14% on forereefs across the Mesoamerican Barrier Reef System but reached 75% in some locations (Kramer *et al.*, 2000).

However, most research on the effects of bleaching has tended to focus on interspecific comparisons of susceptibility, but this work does indicate which habitat types are most affected. The major reef builder *Montastraea annularis* typically has the highest rates of both initial bleaching and tissue mortality (e.g., Goenaga *et al.*, 1989; 90% of colonies at 30 m and 14% at 46 m, Ghiold and Smith, 1990; 76% of colonies affected, McField, 1999; 25–50% mortality, Kramer *et al.*, 2000). CARICOMP (1997a) gave an extensive assessment of bleaching across the Caribbean following the 1995–1996 bleaching event, and bleaching in *Montastraea* varied from 15 to 99.4% (mean ~70%) and tissue mortality ranged from 0 to 30%. Other taxa regularly affected by bleaching are *Millepora* spp., *Agaricia* spp., *Colpophyllia natans*, *Diploria* spp. and *Porites* spp. and *Siderastrea siderea* (Glynn, 1984; Ghiold and Smith, 1990; Lang *et al.*, 1992; CARICOMP, 1997a; McField, 1999). For example, *Agaricia tenuifolia* underwent almost total mortality at all depths in Belize after the 1997–1998 bleaching event (Aronson *et al.*, 2000), and *A. agaricites* was significantly affected by bleaching in 1995–1996 on patch reefs in the Bahamas (McGrath and Smith, 1998). Similarly, all *Agaricia undata* colonies were bleached at 46, 62 and 77 m in the Cayman Islands, and only *A. palmata* escaped severe bleaching (Ghiold and Smith, 1990). *Acropora* was also only minimally affected by bleaching in Jamaica and the Mesoamerican Barrier Reef System (Goreau, 1990; Kramer *et al.*, 2000), although up to 21% of *palmata* colonies and up to 54% of *cervicornis* colonies have been affected at specific locations (CARICOMP, 1997a).

Intraspecific variations of bleaching susceptibility and subsequent mortality are in part caused by water depth. Depth is important because of its effects on attenuating light and hence thermal stress from radiative energy (e.g., Mobley, 1994). Bleaching mortality generally decreases with increasing depth, and this has been recorded in, for example, the Cayman Islands (Ghiold and Smith, 1990) and Panama (Glynn, 1984). However, shallow water corals may be able to adapt or acclimatise to high temperatures and light intensities. Brown (1997) states that hardy reef-flat and shallow water corals may show considerable scope for nongenetic adaptations to bleaching-induced mortality, which may be much reduced in species living subtidally. For example, in the Florida Keys and Bahamas, colony recovery rates from initial bleaching seemed more rapid in shallower habitats (Lang *et al.*, 1992). Shallow water adaptations to high temperatures and light intensities may vary between species; a comparison of initial bleaching rates in Belizean back reefs and forereefs and demonstrated that *Siderastrea siderea* and *Montastraea annularis* colonies had higher rates in the forereef, but *Porites porites* and *Agaricia* spp. had higher rates in the back reef (McField, 1999).

5.2.1. Habitat susceptibilities (Figure 2)

There are insufficient habitat-specific data to assess the effects of bleaching in terms of loss of coral cover across whole communities. Therefore, we assign susceptibility values using the proportion of colonies of the dominant coral species that is typically affected during bleaching events. *Montastraea annularis* is one of the most susceptible species, with ~70% of colonies affected in a Caribbean-wide survey (CARICOMP, 1997a), and shallow *Montastraea* reefs and patch reefs (where *Montastraea* is commonly a major frame building coral along with susceptible *Agaricia* species) are assigned high susceptibility. Deep *Montastraea* reefs are assessed as having medium susceptibility, as the effects of bleaching generally decrease with increasing depth. Similarly, escarpments are assigned medium susceptibility, as they are in deeper water, but characteristic species such as *Agaricia undata* may be severely bleached (Ghiold and Smith, 1990). *A. palmata* is generally resistant to bleaching, and reef crests are assessed as having low susceptibility. *Acropora* may also be present in back reefs but are typically dominated by a mix of susceptible species (e.g., *Agaricia* spp., *Millepora* spp. and *Porites* spp) and are assessed as having high susceptibility. Similarly, the corals present in gorgonian-dominated forereefs are generally susceptible species, and this habitat is assigned high susceptibility, although the coral cover is low. Seagrass beds, mangroves and sand beds have no susceptibility because corals are only occasional or absent.

5.3. Susceptibility to coral diseases

Diseases are defined as any impairment of vital body functions, systems or organs (Peters, 1997). Incidents of coral diseases may be increasing in frequency because of anthropogenic stresses to reef systems (Peters, 1997;

Green and Bruckner, 2000) and appear to be having deleterious impacts on reef communities. A range of diseases have been defined in the Caribbean, such as white pox (Patterson *et al.*, 2002) and yellow band (Santavy and Peters, 1997), but here we concentrate on two that are perhaps best studied: black band and white band (e.g., Peters *et al.*, 1983; Rützler and Santavy, 1983).

Diploria strigosa and the *Montastraea annularis* complex are most prone to black band disease, and typically ~0.5–1.0% of the population is affected (Antonius, 1981; Peters, 1997; Green and Bruckner, 2000). Antonius (1981) found that *Montastraea cavernosa*, *Diploria labyrinthiformis* and *D. clivosa* are also relatively susceptible, whereas *A. palmata*, *A. cervicornis* and *A. prolifera* appear totally resistant. In Jamaica, Bruckner and Bruckner (1997) documented similar interspecific patterns of black band susceptibility, with the addition of effects to *S. siderea*. A summary of data from across the Caribbean for colonies >25 cm in diameter gave incidence rates as follows: *M. annularis* 1.0%, *faveolata* 1.0, *franksi* 3.7% and *cavernosa* 0.6%, *Siderastrea siderea* 0.8%, *Diploria strigosa* 0.5%, *Agaricia* spp. 0.1%, *Colpophyllia natans* 1.5%, *Diploria labyrinthiformis* 0.6%, *Agaricia agaricites* 0.3%, *Montastraea complanata* 0.4%, *Stephanocoenia intersepta* 1.5% and *Meandrina meandrites* 1.3% (Kramer, 2003). Bruckner and Bruckner (1997) showed that black band disease was rarely found below 10 m, that 47.9% of infected coral died and that the loss of coral was greatest in the back reef, which was exposed to physiological and environmental stresses. Bleached corals may also be more susceptible to black band disease with 34% of *Montastraea faveolata* colonies in Honduras infected after the 1995 bleaching event (Kramer *et al.*, 2000).

Corals of the genus *Acropora* are most, and possibly exclusively, susceptible to white band disease (Gladfelter, 1982; Peters, 1997; Aronson and Precht, 2000, 2001). Other species have been reported as being affected by white band, but it seems likely that these reports are misidentifications of the disease (Green and Bruckner, 2000). A summary of data from across the Caribbean for colonies >25 cm in diameter gave incidence rates of 2.4% for *A. palmata* and 12.4% for *A. cervicornis*, with the disease not reported for any other species (Kramer, 2003), but these values inevitably reflect the severe depletion of *Acropora* populations. In 1977–1979 in St. Croix, 32.2% of 90 *A. palmata* colonies were diseased, with a further 41.1% dead (Gladfelter, 1982) and can reach 64% for *Acropora* communities (Peters *et al.*, 1983). Aronson and Precht (2001) suggest that white band disease has probably been the primary factor reducing populations of acroporids, with hurricane damage also important on some reefs, and that this event is unique in the late Holocene. The effects of white band disease were documented by Aronson and Precht (2000) in Belize where coral cover decreased in a relatively deep spur-and-groove zone dominated by *A. cervicornis*. In comparison, a shallower spur-and-groove zone was less affected because the resistant *Agaricia tenuifolia* was the dominant coral. In St. Croix, white band disease in *Acropora palmata* facilitated access to coral skeletons for a variety of boring organisms so that colonies were weakened and collapsed (Clarke, 1996). The massive mortality of *A. palmata* in shallow habitats will have consequences including reduced carbonate deposition, increased wave energy reaching shorelines, mangroves and seagrass beds and affect sand production and beach dynamics (Gladfelter, 1982; Bythell and Sheppard, 1993).

5.3.1. Habitat susceptibilities (Figure 2)

There are insufficient, habitat-specific data to assess the effects of white and black band diseases in terms of loss of coral cover across whole communities. Therefore, we assign susceptibility values using the proportion of colonies of the dominant coral species that is typically infected. White band disease causes the greatest loss of coral cover, and *Acropora palmata* is highly susceptible (2.4–32.2% of colonies infected) and reef crests and back reefs are assessed as having high susceptibility. The *Montastraea annularis* complex is one of the most susceptible species to black band disease, with ~0.5–5.7% of colonies affected, and shallow *Montastraea* reefs and patch reefs (where *Montastraea* is commonly a major frame building coral) are assigned medium susceptibility, although both these communities would previously have also supported *Acropora cervicornis* communities that would have been susceptible to white band disease. Deep *Montastraea* reefs are assessed as having low susceptibility, as black band disease is rarely found below 10 m (Bruckner and Bruckner, 1997). Escarpments are also assigned low susceptibility, as they are in deeper water with small populations of *Acropora* and *Montastraea*. Similarly, the few corals present in gorgonian-dominated forereefs are generally tolerant of disease, and this habitat is assigned low susceptibility. Seagrass beds, mangroves and sand beds have no susceptibility because corals are only occasional or absent.

6. EXAMPLE MAPS AND MODELS UTILISING FUNCTIONAL VALUES

6.1. Maps of functional values

One of our key aims is to review the empirical data that are available in published literature to assist the generation of maps that facilitate further insight into ecosystem processes and aid conservation. Static maps can be created using a combination of remotely-sensed imagery and the proposed functional values (Figure 1) and individual maps, or combinations of data layers, will have a range of applications. We develop this concept by generating maps of "hot spots" of functional value for populations of the commercially important *Epinephelus striatus*, *Panulirus argus* and *S. gigas* (Figure 3). The traditional habitat map used (Figure 3A) is from Andros Island, Bahamas, created using IKONOS imagery with three spectral bands and resampled to 100 m^2 pixels. The map shows a typical barrier reef zonation (total of 15 habitat types) with mangroves (pink), lagoonal seagrass beds (green) and patch reefs (blue) in shallow water behind the reef crest

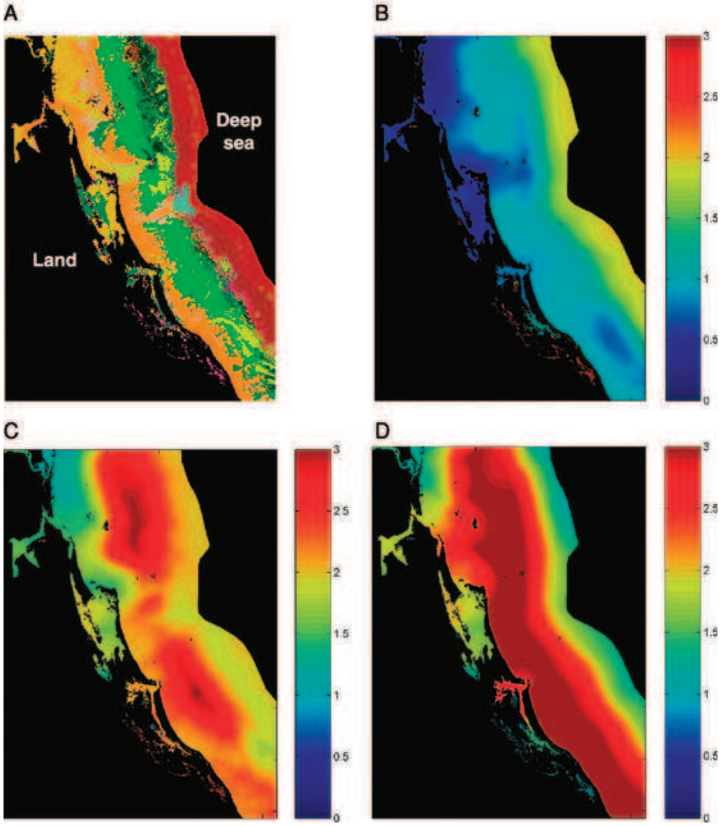


Figure 3 Maps of (A) habitat types off the east coast of Andros Island (Bahamas) and mean functional values of the seascape for populations of (B) *Epinephelus striatus*, (C) *Panulirus argus* and (D) *Strombus gigas*. Mean functional values calculated using 2-km^2 windows centred on each pixel. Colour bars show mean functional value (no functional value = 0; low = 1; medium = 2; high = 3). Functional value of each habitat taken from Figure 1. Area represented is 14.3 × 10.5 km and centred on 24°51′41″ N, 77°53′49″ W.

(purple) and offshore gorgonian-dominated and *Montastraea* reefs (brown shades). For details on standard processing techniques of remotely sensed imagery, see Green *et al.* (2000).

The three derived layers (Figure 3B–D) were generated by first assigning each pixel a functional value based on its habitat type (none = 0, low = 1, medium = 2, high = 3; derived from Figure 1). Note that the use of satellite imagery does not allow the parameterisation of steeply sloping habitats, such as escarpments, and their functional values are significantly underestimated in Figure 3. Additional data, such as those generated by an acoustic ground discrimination system (White *et al.*, 2003), could be used to ensure escarpments are correctly represented in assessments of functional value. The mean functional value was then calculated in 2-km^2 "windows" (an arbitrary size to demonstrate the approach) centred on each pixel using a bespoke computer algorithm. The windows grew outwards from the initial centre "seed" pixel in a method analogous to conducting a pixel-to-pixel random walk in all possible directions simultaneously. The walk was iterated until the number of pixels in the locality window was equal to the required number (i.e., the desired area of the window was achieved). In an entirely marine area this method generated circular windows, and when land was encountered, the shape of the window "grew" around, for example, headlands and small islands. Mean functional values (minimum 0, maximum 3) were then assigned to each pixel. Although traditional maps allow the identification of locations of habitats with high functional value (e.g., patch reefs for *Epinephelus striatus*), the maps in Figure 3 allow quantitative identification of areas with consistently high functional values across multiple habitats. Furthermore, the hot-spot areas are at a scale appropriate for management and could assist managers to identify priority sites for marine reserves, particularly if used in combination with maps of susceptibility to disturbance that could be generated from both Figure 2 and location-specific data (e.g., fishing pressure).

6.2. Models of ecosystem processes

Of the published habitat-scale ecological models, perhaps only that of Wolanski *et al.* (1984) can be considered a seascape model; most focus on a specific habitat within an ecosystem. Given the obvious patchiness in our habitat-level understanding of processes, it still remains a considerable challenge to create meaningful models of individual tropical marine ecosystem habitats. However, habitat-level models provide useful insights into processes and management of marine resources, particularly when the habitat being modelled is widely used for extractive activities. For example, Mumby and Dytham (2006) used a spatial-simulation model to explore the link between resilience of *Montastraea* reefs and one of the proxies of secondary production reviewed in this chapter (density of parrotfishes). In the absence of the sea urchin *Diadema antillarum* (Lessios *et al.*, 1984), Caribbean forereefs are largely dependent on parrotfishes to control the cover of macroalgae. Even relatively minor depletions of grazer density can reduce the resilience of *Montastraea* habitats, leading to a reduction in coral cover, which, if left unresolved, will cause a decline in the structural complexity and quality of the habitat (Glynn, 1997). The papers reviewed here on secondary production and coral recruitment and growth, along with new data, allowed parameterisation of the model and similar efforts could be undertaken both for different processes within this habitat and for other habitats. Extending individual-habitat models to seascape scales, either by varying the parameters (e.g., depending on the presence of adjacent nurseries areas) or by linking dynamic models of different habitats using established functional links, will reveal potentially surprising but important phenomena. More importantly, seascape-level models are more likely to become decision-support tools because they must, by definition, embody suitably large spatial scales, such as entire reefs. Reconciling the competing needs of multiple users at these scales is the very essence of coastal management.

7. CONCLUSIONS

7.1. Current status of empirical knowledge

The last 50 years of research on coral reefs has led to great increases in understanding their biology, ecology and underlying processes. However, perhaps the most obvious conclusion from this chapter is the disparate nature of empirical research that has limited attempts to synthesise overarching principals of how whole reef seascapes function spatially and temporally. It is obvious that, even for well-researched processes, there are few documented patterns of how functional values change between habitats and affect the resulting interactions and emergent properties. This chapter has attempted to draw together the disparate and extensive literature and provide spatially-explicit functional values of typical Caribbean habitat types to some ecosystem processes clearly derived, where possible, from quantitative data (Figure 1). We have also generated assessments of susceptibility of each habitat to three important disturbances (Figure 2).

Hatcher (1988) provided a review of rates of primary productivity in a range of geomorphological zones and benthic communities and showed that data were relatively abundant for back reef, reef crest and shallow forereef areas, but there was very little information available for deeper forereefs and escarpments. The relative lack of data for deeper reef areas has been borne out by this chapter for other processes and represents a significant gap in the framework of data required for mapping and modelling these processes across tropical marine seascapes. The lack of information in deeper reef zones is largely caused by experimental difficulties, but with considerable coral growth possible to at least 40 m and remotely sensed imagery able to discriminate habitats beyond 20 m in good conditions (Green *et al.*, 2000), additional experimental work is imperative. Incorporating the functional values of mangrove and seagrass habitats is also impeded by a lack of empirical data, despite their importance in a number of processes. The limited data available for mangrove stands and seagrass beds has been highlighted previously (e.g., Hatcher *et al.*, 1989).

In addition to a lack of data for particular habitat types, many of the published data are essentially related to clear water ("optimal") environmental conditions. There are very few empirical data on how functional values change when environmental parameters are altered by natural or anthropogenic influences (e.g., increased turbidity). Furthermore, much of the key empirical data on the functional values of many habitats pre-dates significant changes to Caribbean coral reefs. It is clear that the mass mortality of *Diadema* in the early 1980s (e.g., Lessios, 1988) catalysed a shift from coral domination to algal domination in some parts of the region (e.g., Hughes, 1994). Such changes will have profound effects on processes such as biological production, biogeochemical cycling and accretion, and further empirical work may be required for these "modified" habitats to parameterise models. Similarly, populations of *Acropora palmata* and *A. cervicornis*, which were previously dominant in many reef crest and forereefs zones, have decreased significantly throughout the Caribbean because of white band disease (e.g., Aronson and Precht, 2001). Again, the loss of many *Acropora* stands will have significant effects on rates of, for example, calcification and wave-energy dissipation, and previous data may no longer be applicable. An understanding of the changes caused by the loss of *Acropora* in shallow water seems particularly important because of the importance of coral-rich reef crests in many of the processes reviewed in this chapter (Figure 1). Despite the importance of research on the changing nature of reef crests, few empirical data have been published since, for example, Bythell and Sheppard (1993) highlighted the mortality of *A. palmata* in the British Virgin Islands and raised concerns about increased wave energies reaching shorelines and alterations to patterns of sand production, beach dynamics and erosion.

The functional values presented in this chapter must also be placed in a longer-term historical context. It is easy, particularly in a relatively new discipline such as tropical marine science, to view recent data as the baseline for monitoring subsequent changes when in fact the current status is dramatically altered from the "natural" situation (the "shifting baseline" syndrome). Fossil data are important to provide historical context and show that, for example, the decline of *Acropora* is indeed unique in the late Holocene (Aronson and Precht, 2001). In the context of this chapter, the *relative* pattern of many functional values has probably remained similar over long timescales. For example, coral-rich forereef habitats have always had higher calcification rates than gorgonian-dominated habitats, although the actual calcification rates have decreased in coral-rich habitats since the loss of *Diadema* and subsequent decline in coral cover (e.g., Hughes, 1994). However, there are certainly examples of how relative functional values have changed so that patterns described in this chapter represent an "unnatural" scenario. Perhaps the best example of changing patterns is the dramatically reduced densities of megavertebrates (e.g., manatee and green turtle). The loss of these vertebrates cannot be compensated for by fishes and invertebrates and must have altered herbivory in seagrass beds (now significantly lower), patterns of loss of production to adjacent ecosystems and the structure of food chains (Jackson, 1997).

We recognise that the functional value of a given habitat will vary significantly across the seascape. Perhaps most obviously, the functional value of a specific habitat will be affected by its spatial context within the seascape. For example, a patch of habitat may not fulfil an "adult microhabitat" function for a given species if the patch is isolated from the species' juvenile microhabitat (e.g., Acosta, 1999). Lindeman *et al.* (1998) provide a demonstration of how settlement rates of lutjanids and haemulids to a habitat type will vary depending on its cross-shelf position. At a larger scale, the benthic communities of reef crests (and hence functional values) have been shown to vary dramatically depending on wave energy and storm frequency (Hubbard, 1997). Further complications in describing the functional value of a habitat arise because multiple processes may be linked across habitat boundaries. Wave-energy dissipation varies across different types of reef crests, which then affects primary production, grazing pressure, calcification rates and bioerosion rates in back reefs and lagoons (e.g., Smith and Kinsey, 1976; McGehee, 1994; Hatcher, 1997b). Thus, the functional value of a habitat is far from consistent across a whole seascape and may depend on its size and spatial context. The effects of habitat configurations have been reported where possible, but studies rarely address spatial changes in a habitat's functional value depending on the nature of adjacent areas. Models of reef processes will need to incorporate such intrahabitat variation and it is likely that the application of landscape ecology approaches (e.g., Liu and Taylor, 2002) will be profitable.

Despite the inevitable caveats associated with Figure 1, it does represent the first time that functional values have been summarised for such an extensive range of processes and habitats. Furthermore, it raises a number of important questions: Which habitats are the most "important" overall and how is their importance influenced by their areal extent? What are the effects of anthropogenic impacts to functional values? Can functional values be weighted depending on their importance to overall reef ecosystem health? Such questions are beyond the scope of this chapter and require specific targeted research programmes. However, it is possible to gain some insight into overall functional roles of habitats by converting functional values to ordinal values (no functional value = 0, low = 1, medium = 2, high = 3; derived from Figure 1 and using pre-1983 densities of *Diadema antillarum*) and generating an ordination using nonmetric multidimensional scaling (MDS; Figure 4) (see Clarke, 1993, for more details). Sand is so different from the other habitats that it is omitted from the MDS for clarity. Perhaps the most striking feature of the ordination is the spread of habitats, indicating that each habitat has a relatively unique set of functional values. The "Reef crest + branching corals" and "Back reef + coral class" are close together, showing that they have similar functional values for each process. Rather than representing any kind of "habitat redundancy," we would suggest that this pairing actually represent limitations of the empirical data where such habitats are frequently grouped together. Care must also be taken when suggesting that the ordination shows that each habitat is equally "important." However, even this basic

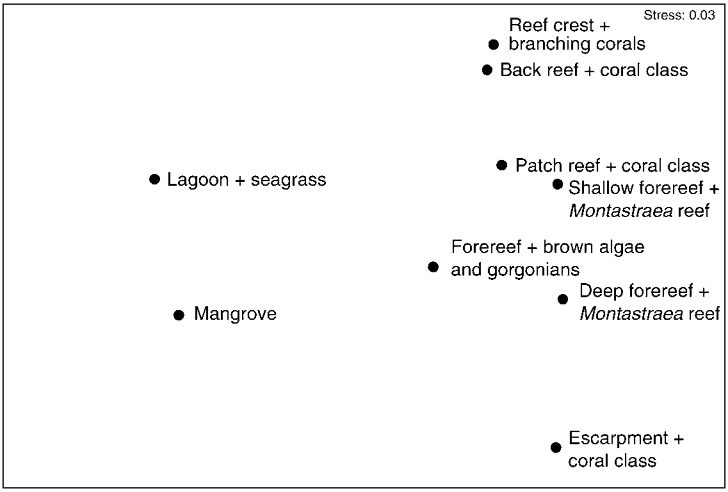


Figure 4 Ordination of nine of the generic habitats (sand omitted) assigned functional values (Figure 1). Variables used were those represented in Figure 1, with the exception of post-1983 *Diadema* densities. Functional values for each variable were converted to an ordinal value (no functional value = 0; low = 1; medium = 2; high = 3). The relatively low stress indicates that the two-dimensional distances are a good representation of the multidimensional similarity between habitats.

analysis, which requires much further research to fully explore, appears to show how different habitats may have different and specific functional roles that combine to maintain ecosystem functioning.

7.2. Limitations of the review

The complexity of the processes reviewed in this chapter is such that dividing them into separate sections is often artificial. For example, primary productivity and the density of secondary producers (herbivores) are inextricably linked, as are calcification rates and patterns of reef recovery, and indeed multiple processes might be investigated within a single research paper. Some of the most obvious links between processes have been addressed by cross-referencing between sections, but others are not made explicitly in deference to the readability of the text. Finally, space limitations meant that we have limited our review to what we consider the most ecologically and economically important functions. Readers will be aware that, for example, all habitats across a reef seascape function as nursery or adult habitats for a whole range of taxa in addition to the key primary, secondary and tertiary producers discussed.

The functional value of a habitat will vary at a range of temporal scales. Algal communities (and hence primary productivity) vary between seasons (e.g., Lirman and Biber, 2000) and the calcification rates of *Acropora palmata* in Jamaica were anomalously high in the 1970s because of the unusual infrequency of major hurricanes in preceding years (Woodley, 1992). Temporal aspects of processes are arguably better understood than the importance of spatial context, but we have not attempted to review temporal variation. Modelling of reef processes is at such a nascent stage that the inclusion of spatial information alone remains problematic.

7.3. Research priorities and future directions

This chapter aimed to provide a basic framework of information on the functional value of different habitats, particularly those that can be delineated by remotely-sensed imagery, in a range of reef processes. Figure 1 highlights clear gaps in our knowledge, which could guide future research. In the context of building maps or models of reef processes, studies working simultaneously in multiple habitats will be particularly important because they provide directly comparable functional values. Ideally, such studies would also include an assessment of functional links between habitats and across their boundaries because these links are poorly understood. If links have been studied, it is normally at large scales between major habitat types (e.g., seagrass beds, mangroves and reefs). Currently, understanding of reef processes is inhibited by a "dearth of system-level information about coral reefs and a poor understanding of how population and community parameters relate to functions at the system level" (Johnson *et al.*, 1995). An alternative approach is to take existing framework models of reef processes and make them spatially explicit. For example, a trophic model has been developed (ECOPATH with Ecosim, e.g., Christensen and Pauly, 1992) and has been parameterised to study trophic structure (and energy flows) of the back reef, reef front and slope zones of three coral reef complexes in the Mexican Caribbean (Arias-González, 1998).

Individual researchers will inevitably have specific aims during their work and may not be concerned with building maps and models of reef processes across multiple habitats. However, most data collected are useful for modelling reef processes if it is clear which habitats were the basis for their experiments. It was clear while reviewing literature for this chapter that the particular habitat used for many studies received only a cursory description or was commonly limited to a geomorphological zone (e.g., "forereef"), even though the benthic community in a given zone can vary widely. We would encourage researchers to provide enough information so that their study site could be allocated to a habitat within a typical classification scheme for remotely sensed imagery.

There are clear limitations in our understanding of how each Caribbean marine habitat contributes to important reef processes and how these functional values are affected by the spatial context of the habitat. However, it does seem that there is sufficient empirical data to combine with remotely-sensed imagery and to start building spatially explicit maps and models of reef processes. We feel that such maps and models represent an exciting direction for furthering our understanding of these complex environments. A transect from shore to reef wall encompasses such a panoply of biotopes that it is of interest to even the casual observer how these habitats function together so that reefs are so much more productive and diverse than the open ocean. Perhaps more pertinently, the functional values of reef habitats are increasingly under threat from a suite of factors and a more sophisticated understanding of the implications of these changes, and how to mitigate and reverse them, is vital for the ecological and economic health of tropical marine ecosystems.

ACKNOWLEDGEMENTS

This work was supported by a grant (OCE-0119976) from the U.S. National Science Foundation's Biocomplexity in the Environment Program and is a publication of the Bahamas Biocomplexity Project. We thank Nicholas

Polunin and John Turner for reviews that significantly improved the manuscript.

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Southern Ocean Cephalopods

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ADVANCES IN MARINE BIOLOGY VOL 50
0065-2881/06 $35.00
DOI: 10.1016/S0065-2881(05)50003-8

The Southern Ocean cephalopod fauna is distinctive, with high levels of endemism in the squid and particularly in the octopodids. Loliginid squid, sepiids and sepiolids are absent from the Southern Ocean, and all the squid are oceanic pelagic species. The octopodids dominate the neritic cephalopod fauna, with high levels of diversity, probably associated with niche separation. In common with temperate cephalopods, Southern Ocean species appear to be semelparous, but growth rates are probably lower and longevity greater than temperate counterparts. Compared with equivalent temperate species, eggs are generally large and fecundity low, with putative long development times. Reproduction may be seasonal in the squid but is extended in the octopodids. Cephalopods play an important role in the ecology of the Southern Ocean, linking the abundant mesopelagic fish and crustaceans with higher predators such as albatross, seals and whales. To date Southern Ocean cephalopods have not been commercially exploited, but there is potential for exploitation of muscular species of the Family Ommastrephidae.

1. INTRODUCTION

The Southern Ocean, which surrounds the Antarctic continent, consists of a system of deepsea basins, separated by three systems of ridges: the Macquarie Ridge (south of New Zealand and Tasmania), the Scotia Arc (between the Patagonian shelf and the Antarctic Peninsula) and the Kerguelen Ridge (Carmack, 1990) (Figure 1). It is bounded to the north by the Antarctic Polar Front (APF) or Antarctic Convergence (Figure 1) and occupies an area of $\sim 38 \times 10^6$ km^2 (Carmack, 1990). The location of the APF, where cold Antarctic surface water meets warmer sub-Antarctic water flowing southeast, varies temporally and spatially (between 47 and 63°S) and is characterised by a distinct change in temperature (2–3°C) and other oceanographic parameters (Carmack, 1990). It acts as a biological barrier, making the Southern Ocean a largely closed system. The main surface currents are the Antarctic Circumpolar Current, which flows in an easterly direction encircling the Antarctic continent, and the east wind drift, which flows in a westerly direction, close to the Antarctic continent (Lutjeharms *et al.*, 1985). Seasonal and regional variations in water temperature in the Southern Ocean are small (+3 to −2 °C). Sea ice covers large areas of the Southern Ocean, the extent varying seasonally from ~10% in summer to 50% of the total area in winter (Carmack, 1990). Within the Southern Ocean, sub-Antarctic Islands, such as South Georgia, Kerguelen and Heard, are areas of enhanced productivity and support large populations of higher predators such as whales, seals and seabirds (Atkinson *et al.*, 2001), as well as fisheries for toothfish, krill and icefish (Kock, 1992; Agnew, 2004).

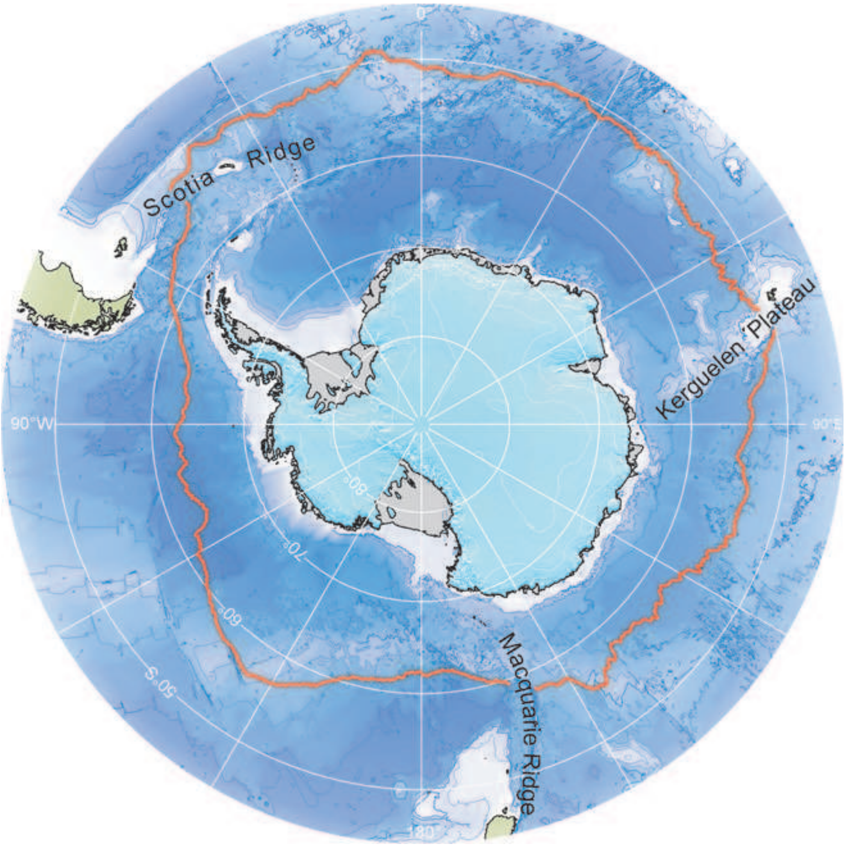

Figure 1 Polar projection of the Antarctic continent to 45 °S, showing the approximate location of the Antarctic Polar Front and the locations of the Scotia Ridge, Macquarie Ridge and Kerguelen Plateau.

The ecology of the Southern Ocean, particularly in the southwest Atlantic sector, is dominated by Antarctic krill (*Euphausia superba*), which is considered the keystone species linking primary production to the abundant higher predators. However, evidence from predators such as toothed whales, penguins, albatross and elephant seals has also highlighted the importance of cephalopods (particularly squid) in the Antarctic system, leading Rodhouse and White (1995) to propose an alternative oceanic food-web linking planktivorous mesopelagic fish to squid and predators. The abundance of cephalopods in predator stomachs has not been replicated in net samples, which rarely produce significant quantities of squid, probably as a consequence of the small size of scientific nets and their avoidance by mobile large squid (see Clarke, 1977).

Investigations of Southern Ocean cephalopods began with the pioneering expeditions of HMS *Challenger*, the Scottish Antarctic Expedition on HMS *Alert* and the German *Valdivia* cruise (Hoyle, 1886; Odhner, 1923). Small numbers of cephalopods were collected on these early expeditions, and many of the early descriptions of Southern Ocean cephalopods were based on fragments of specimens or remains found in predator stomachs (Thiele, 1920; Odhner, 1923; Robson, 1925). In the 1960s, Clarke (1962a,b) developed the use of beaks to identify cephalopod remains in predator stomachs, and this highlighted the importance of cephalopods in the diet of many predators, particularly sperm whales. In fact the stomachs of predators were the main source of cephalopods for many years, with sperm whales much better samplers of large adult squid than any nets (Clarke, 1980), but this source of material has been limited since the cessation of commercial whaling. During the 1960s, the former Soviet Union began a series of cruises, initially on the purpose-built RV *Academic Knipovitch*, to search for new fishery resources in the Scotia Sea. Cephalopods were not targeted but were often taken as "by-catch." The results of the Soviet work are largely in grey literature (and in Russian), but Filippova (2002) reviewed some of the important findings of the Russian studies. Since the 1970s, there has been considerable research effort in the Southern Ocean, both ship-based research, using scientific and commercial-scale fishing nets, and land-based studies of predator diets. Whilst few of these studies have focused specifically on cephalopods, they have yielded considerable new data on their distribution and ecology in the Southern Ocean.

In 1982 the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) was established in response to concerns about the ecosystem effects of exploitation of Antarctic marine resources. The focus of CCAMLR has been primarily krill and exploited finfish, but commercial exploitation of cephalopods has also been the subject of interest in the Southern Ocean, with some exploratory fishing for the squid *Martialia hyadesi* having been undertaken around South Georgia (Rodhouse *et al.*, 1993; Gonzalez *et al.*, 1997; Rodhouse, 1997; Gonzalez and Rodhouse, 1998).

In this review we deal with the biology and ecology of the Southern Ocean cephalopods including species that spend part of their life cycle south of the APF. However, considerably more is known about the biology of species that are also caught north of the APF, such as *M. hyadesi* and *Moroteuthis ingens* than the species that are generally restricted to south of the APF and this is reflected in the text.

2. CEPHALOPOD BIODIVERSITY AND ORIGINS OF THE ANTARCTIC CEPHALOPOD FAUNA

The high-latitude Southern Ocean cephalopod fauna is highly distinctive, differing greatly from that of the temperate zone. The fauna includes oegopsid squids, cirrate and incirrate octopods, but the sepiids, sepiolids and loliginid squid, which dominate the cephalopod fauna in the neritic zone of temperate and tropical regions, are entirely absent. The reasons for this absence are not clear but could be related to putative long development times in cold water (Boletzky, 1994), making the relatively unprotected benthic egg masses of these groups more susceptible to predation and ice scour. The oegopsid squids, which are present in the Southern Ocean, are exclusively pelagic or benthopelagic and most have circum-Antarctic patterns of distribution, a consequence of which may be the relatively small number of species (see later discussion). In contrast, the incirrate octopodids are highly speciose, with each species typically occupying a rather limited geographic distribution (see Allcock and Piertney, 2002; Allcock *et al.*, 2003b; Allcock, 2005). The difference in distribution and diversity patterns between the two groups is probably a result of differences in habitat and reproductive strategy. Adult squid are generally highly mobile, with planktonic eggs and larvae, permitting a high degree of dispersion. The octopodids, on the other hand, produce large, direct developing eggs and the adults are, with the exception of some of the cirrates, benthic, reducing the opportunity for dispersal.

The distinct Southern Ocean fauna includes high levels of endemism in both the squid (two endemic families, Psychroteuthidae and Batoteuthidae, and six endemic genera, *Mesonychoteuthis, Psychroteuthis, Kondakovia, Alluroteuthis, Slosarczykovia* and *Batoteuthis*) and the incirrate octopods (five endemic genera: *Pareledone, Megaleledone, Adelieledone, Prealtus* and *Bathypurpurata*). The endemic incirrates are thought to have evolved after the separation of the Antarctic continent and the subsequent formation of the Antarctic circumpolar current (25–28 my BP) and the APF (22 my BP) (Allcock and Piertney, 2002), which produced a distinct thermal barrier for the shallow fauna. This mirrors what is found in the Antarctic fish, where the notothenioids are largely endemic to the Southern Ocean (Eastman and Clarke, 1998). There is also evidence that the incirrate octopods have diversified into species flocks in a similar way to that of the notothenioids (Allcock and Piertney, 2002).

At present, the extant Southern Ocean octopod fauna (known to science) includes seven cirrate and 27 incirrate species (Figures 2 and 3; Table 1). *Paraeledone* is the most speciose and abundant genus, with 13 species recognised (Allcock, 2005). It is becoming apparent that the diversity of

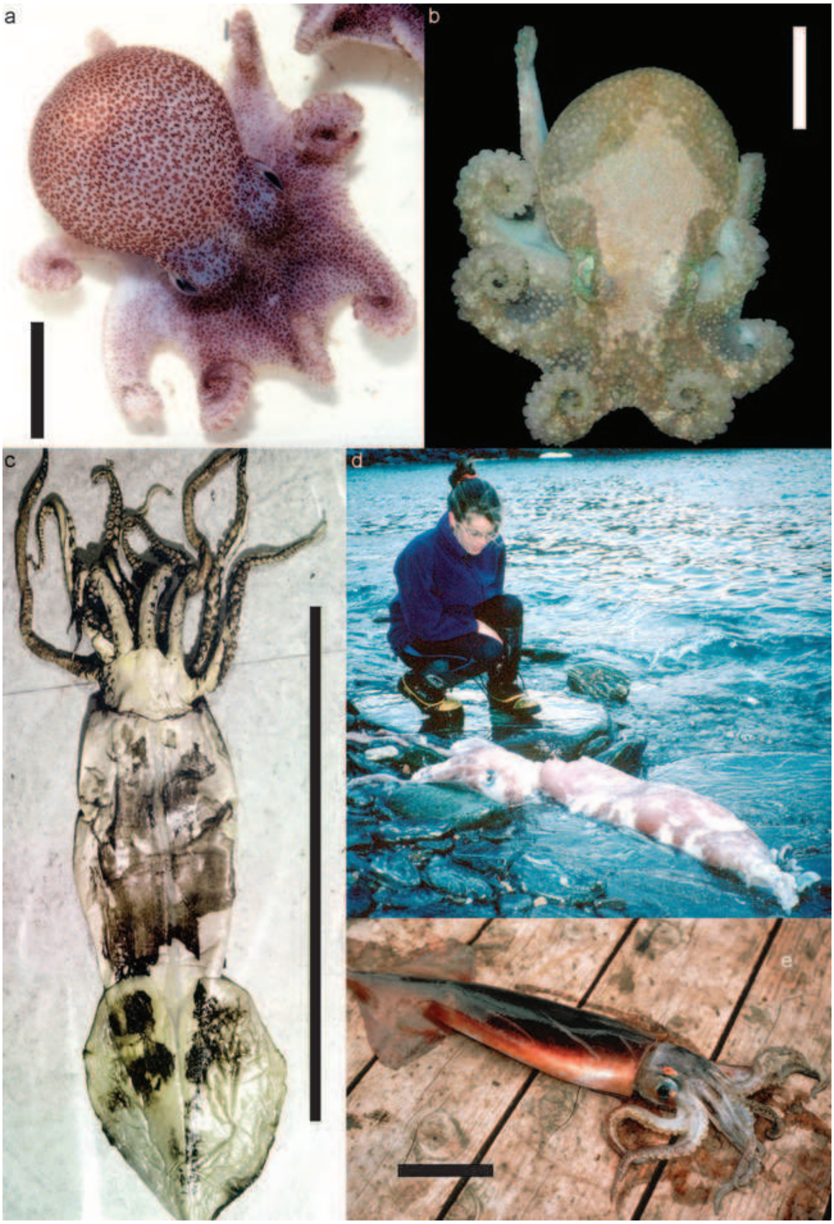

Figure 2 Photographs of Southern Ocean cephalopod fauna: (a) *Thaumeledone gunteri*: scale bar 50 mm, (b) *Pareledone charcoti*: scale bar 50 mm (c) *Mesonychoteuthis hamiltoni* scale bar 1000 mm (d) *Kondakovia longimana*, washed ashore on Signy Island (South Orkneys), (e) *Martialia hyadesi*: scale bar 100 mm.

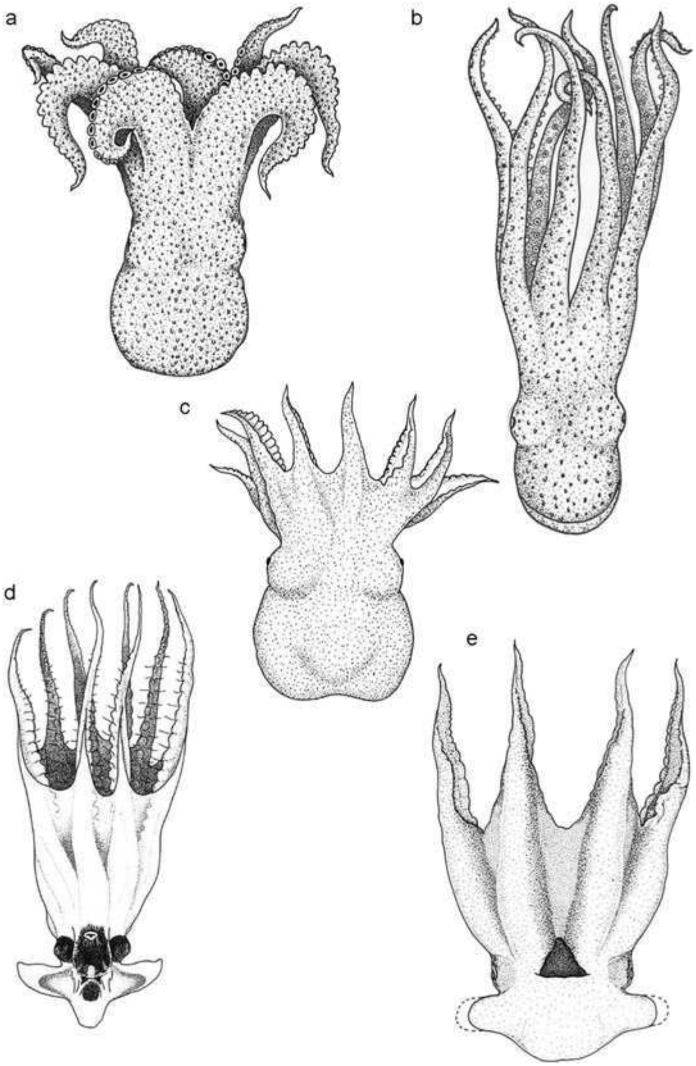

Figure 3 Southern Ocean octopod fauna (a) *Pareledone turqueti* (b) *Graneledone* sp., (c) *Thaumeledone gunteri*, (d) *Stauroteuthis gilchristi* and (e) *Opisthoteuthis hardyi*.

incirrate octopods, particularly the genus *Pareledone*, is much greater than previously thought. In common with the endemic notothenioid fish families (e.g., Channichthyidae, Artididraconidae, Bathydidraconidae), *Pareledone* has undergone extensive radiation in the Southern Ocean, probably a

Table 1 Bathymetric and geographic distribution of Southern Ocean Octopoda

Family	Species	Geographic range	Bathymetric range (m)	Sources
Opisthoteuthidae	*Opisthoteuthis hardyi* Villanueva *et al.*, 2002	South Georgia	~1000	Villanueva *et al.*, 2002
	Cirroctopus glacialis Robson, 1930	South Shetlands; Antarctic Peninsula	>330	Robson, 1930; Hardy, 1963; Vecchione *et al.*, 1998
	Cirroctopus mawsoni (Berry, 1917)	Indian Ocean sector	526–911	O'Shea, 1999
	Cirroctopus antarctica (Kubodera and Okutani, 1986)	Pacific sector		Kubodera and Okutani, 1986; Vecchione *et al.*, 1998; O'Shea, 1999
Cirroteuthidae	*Cirrothauma magna* (Hoyle, 1885)	Prince Edward/Crozet	Bathyal	Guerra *et al.*, 1998
	Cirrothauma murrayi Chun, 1910	Scotia Sea, Drake Passage	Bathyal	Collins, unpublished; Roper and Brundage, 1972
	Stauroteuthis gilchristi (Robson, 1930)	South Georgia	~1000	Collins and Henriques, 2000
Octopodidae	*Graneledone antarctica* Voss, 1976	Ross Sea, Antarctic Peninsula	1500–2341	Voss, 1976; Vecchione *et al.*, 2005
	Graneledone macrotyla Voss, 1976	Drake Passage	1647–2044	Voss, 1976
	Graneledone gonzalezi Guerra *et al.*, 2000	Kerguelen	510–540	Guerra *et al.*, 2000
	Bathypurpurata profunda Vecchone *et al.*, 2005	South Shetlands	509–565	Vecchione *et al.*, 2005
	Pareledone turqueti (Joubin, 1905)	West Antarctic	25–640	Kuehl, 1988; Allcock, 2005

Pareledone antarctica (Thiele, 1920)	Probably junior synonym of *P. harissoni*		Lu and Stranks, 1994
Pareledone charcoti (Joubin, 1905)	Antarctic Peninsula, South Orkneys, South Shetlands	Shallow to 392	Allcock, 2005
Pareledone aurorae (Berry, 1917)	Queen Mary Land	200	Allcock, 2005
Pareledone framensis Lu and Stranks, 1994	Fram Bank, East Antarctica	145–319 (2.2 to −2.1 °C)	Lu and Stranks, 1994
Pareledone aequipapillae Allcock, 2005	South Shetlands	110–465	Allcock, 2005
Pareledone albimaculata (Allcock, 2005)	South Shetlands	190–465	Allcock, 2005
Pareledone aurata Allcock, 2005	South Shetlands	89–465	Allcock, 2005
Pareledone cornuta Allcock, 2005	South Shetlands	130–454	Allcock, 2005
Pareledone panchroma Allcock, 2005	South Shetlands	427–804	Allcock, 2005
Pareledone serperastrata Allcock, 2005	South Shetlands	130–454	Allcock, 2005
Pareledone subtilis Allcock, 2005	South Shetlands	190–427	Allcock, 2005
Pareledone prydzensis Lu and Stranks, 1994	Prydz Bay, East Antarctica	526–676 (2.1 to −0.6 °C)	Lu and Stranks, 1994
Pareledone harrissoni (Berry, 1917)	East Antarctic	25–743 (2.1 to −0.6 °C)	Lu and Stranks, 1994
Adelieledone polymorpha (Robson, 1930)	West Antarctic	15–862	Kuehl, 1988; Allcock *et al.*, 2003b

(Continued)

Table 1 (Continued)

Family	Species	Geographic range	Bathymetric range (m)	Sources
	Adelieledone adelieana (Berry, 1917)	30 E to 90 E	139–680	Lu and Stranks, 1994; Allcock *et al.*, 2003b
	Adelieledone piatkowski Allcock *et al.*, 2003	Antarctic Peninsula	612–1510	Allcock *et al.*, 2003b
	Thaumeledone gunteri Robson, 1930	South Georgia only	364–964 possibly deeper	Yau *et al.*, 2002; Allcock *et al.*, 2004
	Thaumeledone rotunda (Hoyle, 1885)	Circum-Antarctic	2900–3500	Allcock *et al.*, 2004
	Thaumeledone peninsulae Allcock *et al.*, 2004	Antarctic Peninsula	377–1512	Allcock *et al.*, 2004
	Megaleledone setebos (Robson, 1932)	Circum-Antarctic	32–850; 1.9 to −1.4 °C	Lu and Stranks, 1994; Allcock *et al.*, 2003a
	Benthoctopus levis (Hoyle, 1885)	Heard Island, Weddell Sea?	140	Piatkowski *et al.*, 1998; Allcock *et al.*, 2001
	Benthoctopus thielei Robson, 1932	Kerguelen		Bustamente *et al.*, 1998; Cherel *et al.*, 2002
	Bentheledone albida (Berry, 1917)	*Nomen dubium*		Allcock *et al.*, 2004
	Praealtus paralbida Allcock *et al.*, 2004	Antarctic Peninsula	2986–3222	Allcock *et al.*, 2004

consequence of the isolated areas of shelf associated with different island groups (Allcock *et al.*, 2001; Allcock, 2005). At South Georgia, the only peri-Antarctic island where the octopod fauna has been extensively studied, there is just one species of *Pareledone*, perhaps as this represents the edge of the range of this genus.

The cirrate octopods, characterised by the presence of cirri on the arms, paired fins and a well-developed internal shell, are generally deepwater forms. Endemism is less apparent in the cirrates, with no endemic genera, which is probably a consequence of the greater mobility of the adults and their deepwater habitat, to which the polar front is less of a barrier. To date, the deep waters of the Southern Ocean have been poorly investigated and further work will probably reveal greater diversity in both the incirrate and the cirrate octopods.

The 22 species of Southern Ocean squid include representatives of 13 oegopsid families (Figures 2 and 4; Table 2). It is notable that, as well as the absence of the myopsids from the Southern Ocean, many families of oegopsids that are abundant in temperate oceanic areas such as the Enoploteuthidae are also absent. The squid fauna can be divided into species that are entirely Antarctic (*Psychroteuthis, Alluroteuthis*) and those that span the APF. The species that cross the APF are either mobile migratory species that undertake feeding migrations (*M. hyadesi, M. ingens*) or deepwater species to which the APF is not such a distinct barrier (*Chiroteuthis veranyi*). A number of other squid species have been recorded in the diets of Southern Ocean predators but were probably taken when predators forage north of the polar front and are excluded from Table 2.

3. DISTRIBUTION

3.1. Determining distribution

The distribution of Southern Ocean cephalopods has largely been determined from relatively small scientific nets, which can be opened and closed and are useful in determining the vertical distribution of species but tend to catch only juvenile cephalopods. Rodhouse *et al.* (1996) used a large pelagic trawl at the APF and caught larger specimens of *M. hyadesi, Slosarczykovia circumantarctica* and *Galiteuthis glacialis* than those caught in scientific nets.

Predators, such as seabirds, whales, seals and fish, can also be used to provide information on the distribution of cephalopods. However, squid beaks are often retained in predator stomachs for a long time (e.g., sperm whales), and because some predators have extended foraging ranges, the

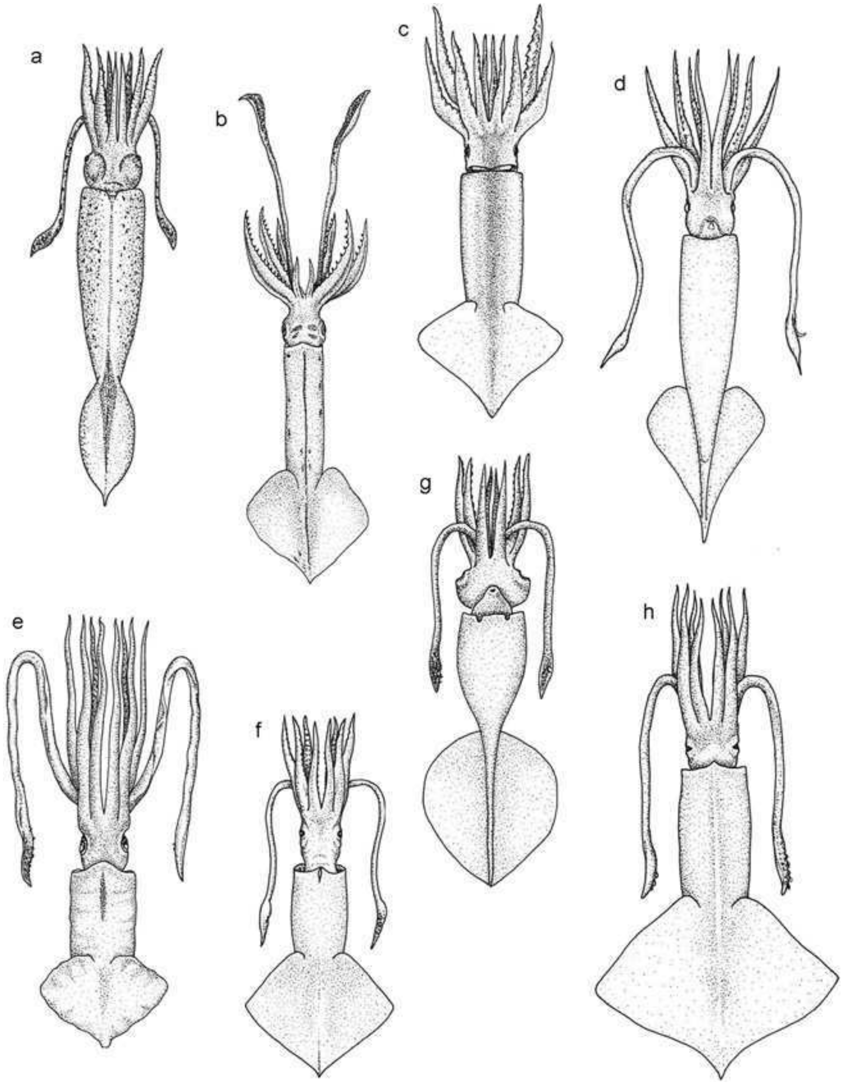

Figure 4 Southern Ocean squid fauna: (a) *Galiteuthis glacialis*, (b) *Slosarczykovia circumantarctica*, (c) *Martialia hyadesi*, (d) *Gonatus antarcticus*, (e) *Kondakovia longimana*, (f) *Psychroteuthis glacialis*, (g) *Mesonychoteuthis hamiltoni* and (h) *Moroteuthis knipovitchi*.

Table 2 Bathymetric and geographic distribution of Southern Ocean squid species

Family	Species	Geographic distribution	Sources
Onychoteuthidae	*Kondakovia longimana* Filippova, 1972	Circumpolar Antarctic	Filippova, 1972; Lu and Williams, 1994a,b; Vacchi *et al.*, 1994; Lynnes and Rodhouse, 2002
	Moroteuthis ingens (Smith, 1881)	Circumpolar sub-Antarctic	Massy, 1916; Filippova, 1972; Filippova and Yukhov, 1979; Alexeyev, 1994
	Moroteuthis knipovitchi Filippova, 1972	Circumpolar Antarctic	Filippova, 1972; Filippova and Yukhov, 1979; Rodhouse, 1989b; Rodhouse *et al.*, 1996; Piatkowski *et al.*, 1998
	Moroteuthis robsoni Adam, 1962	Occasional sub-Antarctic	Rodhouse, 1990b
	Notonykia atricanae Nesis *et al.*, 1998	Sub-Antarctic	Nesis *et al.*, 1998b
Gonatidae	*Gonatus antarcticus* Lönnberg, 1898	Circumpolar sub-Antarctic	Kubodera and Okutani, 1986; Rodhouse *et al.*, 1996; Nesis, 1999a; Anderson and Rodhouse, 2002
Histioteuthidae	*Histioteuthis atlantica* (Hoyle, 1885)	Sub-Antarctic	Kubodera, 1989; Alexeyev, 1994
	Histioteuthis eltaninae Voss, 1969	Circumpolar sub-Antarctic	Lu and Mangold, 1978; Alexeyev, 1994; Piatkowski *et al.*, 1994; Rodhouse *et al.*, 1996
Batoteuthidae	*Batoteuthis skolops* Young and Roper, 1968	Circumpolar Antarctic	Young, 1968; Filippova and Yukhov, 1979; Rodhouse *et al.*, 1992b; Rodhouse *et al.*, 1996; Anderson and Rodhouse, 2002; Collins *et al.*, 2004

(Continued)

Table 2 (Continued)

Family	Species	Geographic distribution	Sources
Psychroteuthidae	*Psychroteuthis glacialis* Thiele, 1920	Circumpolar Antarctic	Filippova, 1972; Filippova and Yukhov, 1979; Kubodera, 1989; Rodhouse, 1989b; Piatkowski *et al.*, 1990, 1994, 1998; Lu and Williams, 1994a; Anderson and Rodhouse, 2002; Collins *et al.*, 2004
Neoteuthidae	*Alluroteuthis antarcticus* Odhner, 1923	Circumpolar Antarctic	Odhner, 1923; Dell, 1959; Filippova and Yukhov, 1979; Filippova and Yukhov, 1982; Rodhouse, 1988; Kubodera, 1989; Anderson and Rodhouse, 2002
Bathyteuthidae	*Bathyteuthis abyssicola* Hoyle, 1885	Circumpolar Antarctic	Hoyle, 1886, 1912; Odhner, 1923; Roper, 1969; Lu and Mangold, 1978; Lu and Williams, 1994a; Rodhouse *et al.*, 1996
Brachioteuthidae	*Slosarczykovia circumantarctica* Lipinski, 2001	Circumpolar Antarctic	Kubodera, 1989; Rodhouse, 1989b, 1996; Piatkowski *et al.*, 1994; Lipinski, 2001; Anderson and Rodhouse, 2002; Collins *et al.*, 2004
	Brachioteuthis linkovski Lipinski, 2001	Occasional sub-Antarctic	Lipinski, 2001; Cherel *et al.*, 2004

Ommastrephidae	*Martialia hyadesi* Rochebrune and Mabille, 1887	Circumpolar sub-Antarctic	O'Sullivan *et al.*, 1983; Rodhouse and Yeatman, 1990; Rodhouse, 1991; Piatkowski *et al.*, 1991; Uozomi *et al.*, 1991; Alexeyev, 1994; Rodhouse *et al.*, 1996; Gonzalez and Rodhouse, 1998; Anderson and Rodhouse, 2001
	Todarodes filippovae Adam, 1975	Circumpolar sub-Antarctic	Piatkowski *et al.*, 1991; Dunning, 1993; Alexeyev, 1994
Chiroteuthidae	*Chiroteuthis veranyi* Ferussac, 1825	Occasional sub-Antarctic	Alexeyev, 1994; Rodhouse and Lu, 1998
Mastigoteuthidae	*Mastigoteuthis psychrophila* Nesis, 1977	Circumpolar Antarctic	Jackson and Lu, 1994; Lu and Williams, 1994a; Piatkowski *et al.*, 1994; Rodhouse *et al.*, 1996; Cherel *et al.*, 2004
Cranchiidae	*Galiteuthis glacialis* (Chun, 1906)	Circumpolar Antarctic	Chun, 1910; Dell, 1959; Filippova, 1972; Lu and Mangold, 1978; McSweeney, 1978; Kubodera and Okutani, 1986; Rodhouse and Clarke, 1986; Rodhouse, 1989b; Lu and Williams, 1994a; Piatkowski and Hagen, 1994; Rodhouse *et al.*, 1996; Nesis *et al.*, 1998a; Piatkowski *et al.*, 1998; Anderson and Rodhouse, 2002
	Taonius sp (cf *pavo*)	Occasional sub-Antarctic	Rodhouse, 1990b
	Mesonychoteuthis hamiltoni (Robson, 1925)	Circumpolar Antarctic	McSweeney, 1970; Filippova and Yukhov, 1979; Rodhouse and Clarke, 1985
Lepidoteuthidae	*Pholidoteuthis boschmai* (Adam, 1950)	Scotia Sea	Nemoto *et al.*, 1985; Offredo *et al.*, 1985

beaks may not be indicative of local species. For instance, wandering albatrosses undertake long foraging migrations that extend well outside the Southern Ocean but return regularly to feed chicks, often with squid captured a long way north of the polar front. Xavier *et al.* (2003b) combined satellite tracking of wandering and grey-headed albatross with diet studies on tracked birds to estimate the distribution of some of the prey species. By utilising fresh cephalopod remains rather than beaks, it is possible to determine what the albatross was feeding on during its recent foraging trip and use this to help determine the distribution of the prey species. Diets of fish species such as patagonian toothfish (Xavier *et al.*, 2002b) and deepwater sharks (Cherel and Duhamel, 2004) can also give an indication of the depth range of prey species.

3.2. Octopodids

The benthic cephalopod fauna is dominated by the incirrate octopodids but also includes species of cirrates such as *Opisthoteuthis hardyi, Cirroctopus glacialis* and *Cirroctopus mawsoni*. Two genera *Pareledone* and *Adelieledone* are abundant and widespread in shallow water, with other genera such as *Graneledone, Thaumeledone* and *Megaleledone* typically found deeper.

The genus *Pareledone* is the most speciose (13 species) and widespread cephalopod genus in shallow water in the Southern Ocean. Until recently all papillated specimens of *Pareledone* were attributed to *P. charcoti*, but a detailed examination of material from the Antarctic Peninsula region (Allcock, 2005) has revealed seven new species. Detailed studies in other areas may reveal similar diversity (Allcock, 2005). Records of *Pareledone* off the South American coast, however, appear to be misidentifications, with the genus restricted to the Southern Ocean (Allcock, 2005). *Pareledone charcoti* is limited to relatively shallow water (<400 m) around the Antarctic Peninsula, and records from the eastern Antarctic (e.g., Lu and Stranks, 1994) are not attributable to this species (Allcock, 2005). *P. turqueti*, which occurs at South Georgia, Shag Rocks and the South Shetlands, is probably the best studied species and appears to be widely distributed on the South Georgia shelf, where it is regularly taken in bottom trawls (Yau *et al.*, 2002). *Adelieledone* includes three species, with *A. polymorpha* and *A. adelieana* recently removed from *Pareledone,* and the newly described *A. piatkowski*. Three species of *Graneledone* (*G. antarctica, G. macrotyla* and *G. gonzalezi*) are known from the Southern Ocean, but Kubodera and Okutani (1994) found two other, undescribed, species off the Palmer Archipelago. Collins *et al.* (2004) caught specimens of *Graneledone* in deep water near South Georgia that differed slightly from descriptions of the aforementioned species, but too few specimens have been critically examined to distinguish intraspecific from interspecific variation.

Thaumeledone includes three Southern Ocean deepwater species. *Thaumeledone gunteri* is only found at South Georgia, where it is abundant at depths >300 m (Yau *et al.*, 2002; Allcock *et al.*, 2004; Collins *et al.*, 2004); previous records from other areas (e.g., Kuehl, 1988) have probably been misidentifications (Allcock *et al.*, 2004). *Thaumeledone rotunda* appears to be circum-Antarctic, whilst *T. peninsulae* was described from the Antarctic Peninsula (Allcock *et al.*, 2004). Specimens of *Thaumeledone brevis* (Hoyle, 1885) have been recorded in the Southern Ocean, but the work of Allcock *et al.* (2004) has shown them to be misidentified, with *T. brevis* known only from the type locality off Montevideo (Uruguay).

Two new genera have been described from Southern Ocean octopods. *Bathypurpurata profunda* is a pygmy deepwater species from the Antarctic Peninsula (Vecchione *et al.*, 2005), whilst the genus *Praealtus* was erected to accommodate *Praealtus paralbida* from deep water north of the South Shetland Islands (Allcock *et al.*, 2004). *Praealtus paralbida* is very similar to *Bentheledone albida* and may be conspecific, but until new material is found from near the type location, *B. albida* is considered *nomen dubium* (Allcock *et al.*, 2004). *Megaleledone setebos* (=*M. senoi*) is the largest Southern Ocean octopod, it is circum-Antarctic in distribution but does not extend as far north as the sub-Antarctic islands (Allcock *et al.*, 2003a). The genus *Benthoctopus* is represented by two Southern Ocean species, *Benthoctopus thielei* from Kerguelen and *Benthoctopus levis* from off Heard Island, although Piatkowski *et al.* (1998) found specimens similar to *B. levis* at the Antarctic Peninsula.

Seven species (four genera) of cirrate octopods are reported in the Southern Ocean. Three species of *Cirroctopus, C. glacialis, C. antarcticus* and *C. mawsoni*, are found in the Southern Ocean. *C. glacialis* was described from a single specimen trawled near Deception Island (Robson, 1930; Hardy, 1963) but has subsequently been found abundantly around the Antarctic Peninsula (Vecchione *et al.*, 1998). The status of *C. antarcticus*, which was described from 62 °S in the Pacific sector (Kubodera and Okutani, 1986), is unclear. O'Shea (1999) considered it a junior synonym of *C. glacialis*, but the description of the beaks differs from that of *C. glacialis* (Vecchione *et al.*, 1998). *Cirroctopus mawsoni* is recorded from the Indian Ocean sector (see O'Shea, 1999), and Voss (1988) mentioned, without describing, another *Cirroctopus* species from collections by FS *Walther Herwig* in the Scotia Sea. *Stauroteuthis gilchristi* has been reported from South Georgia (Collins and Henriques, 2000; Collins *et al.*, 2004) but has also been caught in other parts of the Atlantic sector (Collins, unpublished) and beaks from toothfish stomachs at Kerguelen have been attributed to this species (Cherel *et al.*, 2004). *Opisthoteuthis hardyi* is known only from the type specimen (Villanueva *et al.*, 2002), caught at South

Georgia. Specimens of the blind octopod *Cirrothauma murrayi* were caught at ~4,000 m in the Drake Passage (Roper and Brundage, 1972; Voss, 1988) and from the Scotia Sea (Collins, unpublished). This species has an apparent circumglobal distribution, but a critical review of existing specimens may reveal more than one species. Finally, the type specimen of the rare large *Cirrothauma magna* was caught between Prince Edward and Crozet Islands (Hoyle, 1886), on the edge of the Southern Ocean.

3.3. Decapods

The Southern Ocean squids are primarily pelagic species, which are often associated with particular water masses or frontal zones. Some species have been caught with bottom trawls at South Georgia (Collins *et al.*, 2004), but these catches are usually from deep water with very few squid taken in bottom trawls on the shelf. Species such as *G. glacialis* and *Psychroteuthis glacialis* are restricted to cold Antarctic waters, whilst others are associated with waters between the APF and the sub-Antarctic Front (SAF) (Figures 5–8).

The onychoteuthids are large, muscular pelagic squids, possessing hooked tentacles and, in the Southern Ocean, are represented by the genera *Moroteuthis* (three species), *Kondakovia* (1) and the recently described *Notanykia* (1). *Moroteuthis knipovitchi* was originally described from a specimen taken north of South Georgia (Filippova, 1972) and has subsequently been reported in the Scotia Sea (Rodhouse, 1989b; Rodhouse *et al.*, 1996), off South Georgia (Collins *et al.*, 2004), and in the diet of seabirds at Crozet (Cherel and Weimerskirch, 1999), and is probably circum-Antarctic, south of the APF (Nesis, 1987) (Figure 5). *M. ingens* is also circum-Antarctic, further north than *M. knipovitchi*, typically spanning the Antarctic Polar Frontal Zone (APFZ), and has been the subject of several studies around the Falkland Islands, New Zealand and Kerguelen Island (Jackson, 1993, 1997, 2001; Jackson and Mladenov, 1994; Jackson *et al.*, 1998a,b; Phillips *et al.*, 2001; Cherel and Duhamel, 2003). *Moroteuthis robsoni* has been recorded in the Scotia Sea (Rodhouse, 1990b) and elsewhere occurs off the southern tip of South Africa and to the south of Australasia (Roper *et al.*, 1984; Nesis, 1987). *Kondakovia longimana,* which reaches sizes in excess of 1 m ML (Lynnes and Rodhouse, 2002), was originally described from the Scotia Sea (Filippova, 1972), and although it is rarely caught in nets, evidence from predators (Clarke and Prince, 1981; Clarke *et al.*, 1981; Offredo *et al.*, 1985; Cooper *et al.*, 1992a; Green and Burton, 1993) and strandings (Lu and Williams, 1994b; Vacchi *et al.*, 1994; Lynnes and Rodhouse, 2002) indicates a widespread circumpolar distribution, occurring as far south as

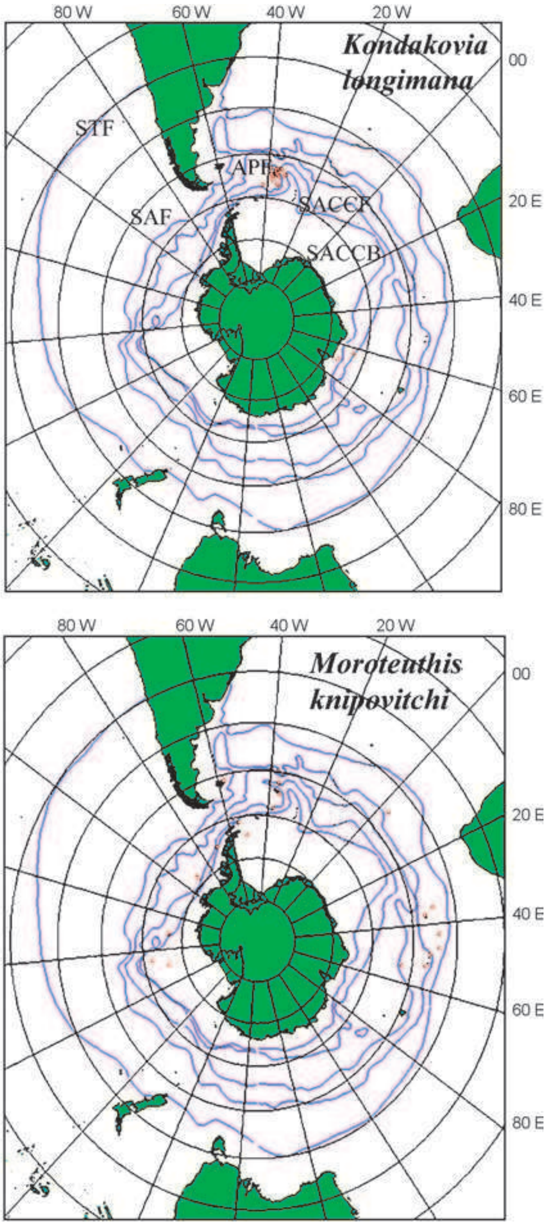

Figure 5 Distribution of *Kondakovia longimana* and *Moroteuthis knipovitchi* in relation to the main water masses and fronts. Figures were modified from web pages developed by Xavier *et al.* (1999). Red dots represent records of each species and relate to references in Table 2. STF: sub-tropical front, SAF: sub-Antarctic front, APF: Antarctic Polar Front, SACCF: Southern Antarctic Circumpolar Current Front, SACCB: Southern Antarctic Circumpolar Current Boundary.

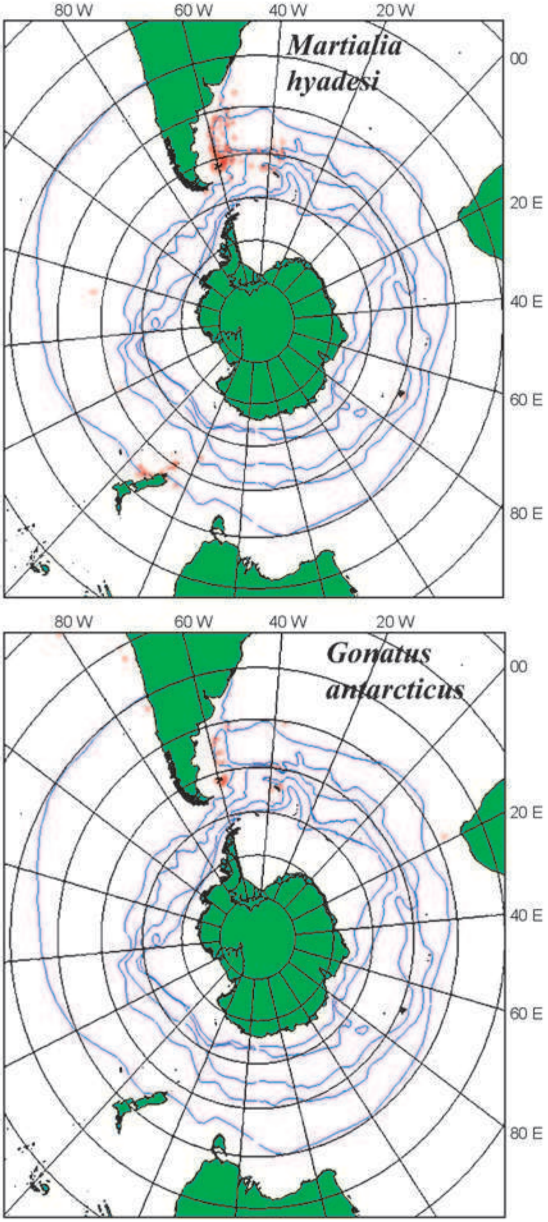

Figure 6 Distribution of *Martialia hyadesi* and *Gonatus antarcticus* in relation to the main water masses and fronts. Figures were modified from web pages developed by Xavier *et al.* (1999). Red dots represent records of each species and relate to references in Table 2.

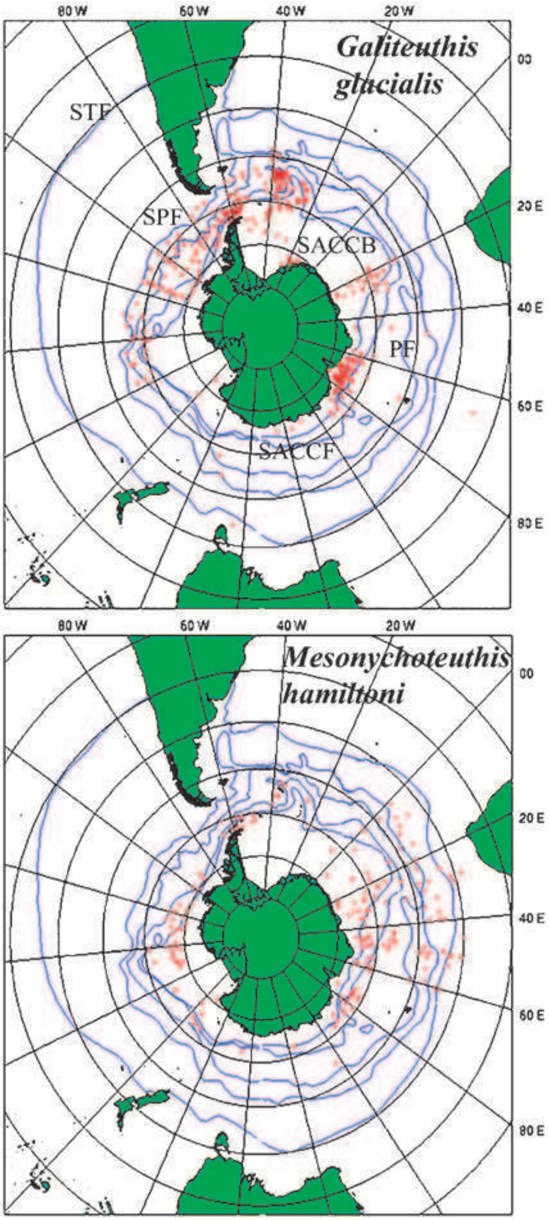

Figure 7 Distribution of *Galiteuthis glacialis* and *Mesonychoteuthis hamiltoni* in relation to the main water masses and fronts. Figures modified from web pages developed by Xavier *et al.* (1999). Red dots represent records of each species and relate to references in Table 2.

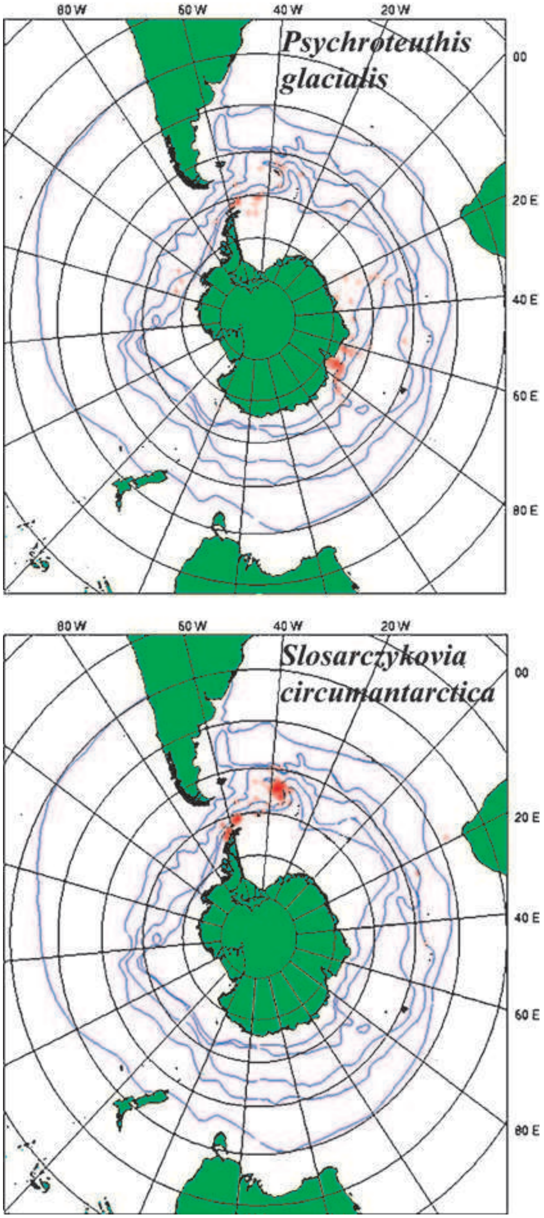

Figure 8 Distribution of *Psychroteuthis glacialis* and *Slosarczykovia circumantarctica* in relation to the main water masses and fronts. Figures were modified from web pages developed by Xavier *et al.* (1999). Red dots represent records of each species and relate to references in Table 2.

74 °S in the Ross Sea (Figure 5). The recently described *Notanykia africanae* (Nesis *et al.*, 1998b) occurs in the sub-Antarctic region and is probably circumpolar.

Two ommastrephid species *Megaleledone hyadesi* and *Todarodes filippovae* are more northerly species that are periodically caught south of the APF. As with other ommastrephids, they are muscular, reach relatively large size and have been considered potential fishery targets (Rodhouse, 1989a, 1998; Rodhouse *et al.*, 1993). *M. hyadesi* has a circum-Antarctic distribution typically associated with the APFZ (Figure 6) and is important in the diets of many predators, particularly grey-headed albatross, whilst *T. filippovae* is also circumpolar, usually between the APF and STF (Figure 6). The biology of *M. hyadesi* has been studied in more detail than most Antarctic cephalopods, with studies undertaken on adult distribution with respect to oceanography, age, growth and diet (Rodhouse, 1990, 1991; Rodhouse *et al.*, 1992a; Gonzalez *et al.*, 1997; Gonzalez and Rodhouse, 1998; Dickson *et al.*, 2004), but patterns of migration, spawning areas and paralarval distribution remain largely unknown. Xavier *et al.* (2002a) reported the presence of another ommastrephid squid, *Illex argentinus*, in the diets of grey-headed and black-browed albatross at South Georgia and considered that these were taken close to South Georgia. *I. argentinus* has been caught in small numbers near the APF (Rodhouse, 1991) but is also the bait used by toothfish long-liners at South Georgia, from which albatross frequently scavenge, and this may be the source of these specimens.

The gonatids are typically high-latitude, cold water, oceanic, pelagic squids and are represented in the Southern Ocean by *Gonatus antarcticus*. *G. antarcticus* is a circumpolar species, primarily occurring between the APF and the SAF, where it is locally abundant (Nesis, 1999a), but has been caught south of the APF in the western part of the Atlantic sector (Kubodera and Okutani, 1986; Rodhouse *et al.*, 1996). The absence of *G. antarcticus* from areas further south, such as Prydz Bay (Lu and Williams, 1994a), suggests that it is principally a sub-Antarctic species (Figure 6), although beaks have been found in predator stomachs from further south (e.g., Clarke and MacLeod, 1982a).

The cranchids (*Galiteuthis, Mesonychoteuthis* and *Taonius*) are generally considered sluggish planktonic squids, but *Mesonychoteuthis hamiltoni* is muscular, growing to extremely large size (Young, 2003). *G. glacialis* and *M. hamiltoni* are both circum-Antarctic in distribution (Figure 7), whilst *Taonius pavo* has only occasionally been found in the Southern Ocean. Like many other Southern Ocean squid, *M. hamiltoni* was first described from the remains in a predator stomach, in this case a sperm whale at the South Shetlands (Robson, 1925). Juveniles were subsequently described by McSweeney (1970) from collections in the Atlantic and Pacific sectors, with others taken in Prydz Bay (Indian Ocean Sector) (Lu and Williams, 1994a) and the Atlantic sector (Rodhouse and Clarke, 1985). A large 2.5 m ML specimen was captured at the surface in the Ross Sea, suggesting that they can reach sizes in excess of the true giant squid (*Architeuthis*) (Young, 2003). *G. glacialis* is one of the most abundant and widely distributed of the Antarctic squids, occurring only sporadically north of the APF (McSweeney, 1978; Rodhouse and Clarke, 1986; Nesis *et al.*, 1998a). A single specimen preliminarily identified as *Taonius pavo* was caught near South Georgia (Rodhouse, 1990), and beaks from this species have been reported in the diets of toothfish (Xavier *et al.*, 2002b) and grey-headed albatross (Rodhouse *et al.*, 1990) at South Georgia. Another species of *Taonius* has also been identified from predators at Crozet and Kerguelen (Cherel and Duhamel, 2004; Cherel *et al.*, 2004).

Brachioteuthids are probably the most abundant squid in the upper layers of pelagic waters of the Southern Ocean, where they are taken as by-catch in krill trawls (Filippova, 2002); however, the taxonomy of the family (Brachioteuthidae) is highly confused. Until recently, *Brachioteuthis* specimens from the Southern Ocean were referred to either as *B. ?picta* (Piatkowski *et al.*, 1994; Rodhouse *et al.*, 1996), *B. ?riisii* (Filippova, 1972) or simply *Brachioteuthis* sp., although evidence from predators indicated the presence of two species of Brachioteuthidae in the Southern Ocean (Cherel *et al.*, 2004). Lipinski (2001), albeit briefly, described two new species of brachioteuthid, *Slosarczykovia circumantarctica* and *Brachioteuthis linkovskyi*, and suggested that the former is widespread in the Southern Ocean. Subsequently Collins *et al.* (2004) found specimens of *S. circumantarctica* in waters around South Georgia and many previous records of brachioteuthids in the Southern Ocean may be attributable to this species (see Figure 7). Cherel *et al.* (2004) examined the beaks of the type specimens of Lipinski's new species and clarified previous identifications of *Brachioteuthis* beaks. The lower beak of *B. linkovskyi* possesses a distinct ridge, which is absent in the beak of *S. circumantarctica*. Beaks of *S. circumantarctica* were previously described as *Brachioteuthis ?picta* (Rodhouse *et al.*, 1990, 1992c, 1998; Reid, 1995; Reid and Arnould, 1996; Berrow and Croxall, 1999; Croxall *et al.*, 1999; Daneri *et al.*, 1999, 2000; Xavier *et al.*, 2002b, 2003c), *Brachioteuthis ?riisei* (Cherel *et al.*, 1996, 2002a,b,d; Catard *et al.*, 2000; Lea *et al.*, 2002) or *Brachioteuthis* sp. (Clarke and MacLeod, 1982b). Beaks of *B. linkovskyi* were identified as *Brachioteuthis* "B" (Xavier *et al.*, 2002b, 2003c) or *Brachioteuthis* sp. (Cherel *et al.*, 1996). However, a full review of previously collected material has yet to be undertaken and the family Brachioteuthidae remains in need of detailed revision.

P. glacialis (Psychroteuthidae) was originally described from fragments found in the stomach contents of Weddell seals and penguins (Thiele, 1920). Subsequently, Filippova (1972) provided a full description from intact specimens that were caught in the Scotia Sea. *P. glacialis* is circumpolar, extending to the Antarctic continent (Figure 8), with adults (max. reported size 380 mm ML (Gröger *et al.*, 2000) probably living near the bottom at the shelf break area (300–1000 m) (Lu and Williams, 1994a; Collins *et al.*, 2004). Data from predators (Offredo *et al.*, 1985; Lake *et al.*, 2003) suggest that *P. glacialis* is abundant in high Antarctic areas and extends as far north as South Georgia in the Atlantic sector, but not beyond the APF. Despite the importance of this species to predators (see later discussion), little is known about the biology.

Alluroteuthis antarcticus (Family Neoteuthidae) is also circumpolar, having been caught in the Atlantic (Rodhouse, 1988, 1989b; Anderson and Rodhouse, 2002), and the Indian Ocean (Kubodera, 1989; Filippova and Pakhomov, 1994; Lu and Williams, 1994a) sectors from the Antarctic continent to the APF. It grows to sizes in excess of 200 mm ML (Lu and Williams, 1994a), but the vast majority of captured specimens have been smaller than 50 mm. Beaks from larger specimens (lower rostral length up to 11 mm) have been found in predator stomachs (Xavier *et al.*, 2003c).

The family Batoteuthidae is monotypic, and *Batoteuthis skolops* is a mesopelagic or bathypelagic species that was first described from four specimens captured at RV *Eltanin* stations in the Pacific and Atlantic sectors (Young, 1968). Subsequently, a small number of additional specimens have been taken in midwater trawls in the Scotia Sea (Rodhouse *et al.*, 1996; Anderson and Rodhouse, 2002) and in bottom trawls at 700 m around South Georgia (Collins *et al.*, 2004).

The mastigoteuthids are bathypelagic squids. Lu and Williams (1994a) caught 41 specimens (77–129 mm ML) of *Mastigoteuthis psychrophila* in pelagic trawls in Prydz Bay and a small number have been caught in scientific midwater trawls near South Georgia (Rodhouse, 1990; Rodhouse and Piatkowski, 1995; Rodhouse *et al.*, 1996; Collins, unpublished). In both Prydz Bay and north of South Georgia, the majority of specimens have been taken at depths of 800–1000 m over deep water (Lu and Williams 1994a; Collins, unpublished).

The Histioteuthidae are mesopelagic and bathypelagic squids, found throughout the world's oceans, but only *Histioteuthis eltaninae* has been recorded south of the APF (Rodhouse and Piatkowski, 1995; Rodhouse *et al.*, 1996; Collins *et al.*, 2004), although *Histioteuthis atlantica* has been reported in the diets of predators (Cherel and Duhamel, 2004; Cherel *et al.*, 2004). Three species of apparently widespread bathypelagic squids are reported from the Southern Ocean. *Chiroteuthis veranyi* (Chiroteuthidae) has been caught in closing nets fished to 1000 m and 2000 m in the Scotia Sea (Rodhouse and Lu, 1998). Elsewhere, this species is found in the equatorial Atlantic and Mediterranean and the species may be present throughout the deep parts of the Southern Ocean. *Bathyteuthis abyssicola* occurs in the Atlantic, Pacific and Indian Oceans (Roper, 1969). In the Southern Ocean, it has been recorded in Prydz Bay (Lu and Williams, 1994a) and at the APF near South Georgia (Rodhouse *et al.*, 1996). *Pholidoteuthis boschmai* has been reported in the Scotia Sea (Nemoto *et al.*, 1985) and possibly in the diets of emperor penguins from Adelie Land (Offredo *et al.*, 1985).

3.4. Geographic migration patterns

Extensive migrations are common among the oceanic squids, particularly the families Ommastrephidae and Onychoteuthidae. Typically, a passive migration takes eggs and paralarvae downstream in ocean currents, and juveniles and adults may then migrate towards feeding grounds, with an upstream migration to the spawning area completing the life cycle. These migrations are linked to the major current systems and the success of a generation influenced by oceanographic variability (O'Dor, 1992; Anderson and Rodhouse, 2001). The migrations of *M. hyadesi* are not fully understood, and this species occasionally appears on the eastern edge of the Patagonian shelf (Gonzalez *et al.*, 1997; Anderson and Rodhouse, 2001) and has been taken at the APF (southwest Atlantic) and northwest of South Georgia (Rodhouse *et al.*, 1996). Xavier *et al.* (2003a,c) have shown interannual variability in the availability of *M. hyadesi* to predators at South Georgia, which may be a consequence of oceanographic variability influencing migration patterns. However, insufficient data have been collected on the seasonal distribution of any Antarctic species to determine or describe seasonal changes in distribution patterns.

3.5. Vertical migration patterns

Many temperate planktonic and nektonic animals, including cephalopods, are known to undertake daily, seasonal and ontogenetic vertical migrations. Diurnal vertical migration (DVM) usually involves animals migrating from deep water to the surface at night, although reverse migrants are known. Various hypotheses have been proposed to explain DVM, including avoidance of visual predators and the energetic advantage of being in cool water during the day. In the largely unstratified Southern Ocean, there will be little energetic advantage in vertically migrating, so predator avoidance is probably the principal reason for migrations (Robison, 2003). Studies with opening and closing nets have revealed distinct patterns of DVM in *Slosarczykovia circumantarctica*, which is generally deeper than 400 m by day and migrates towards surface at night (Piatkowski *et al.*, 1994). Juvenile and subadult *Gonatus antarcticus* also migrate between 525 and 1000 m by day to 60–200 m at night (Nesis, 1999a). Other species may also vertically migrate, but the data are too scarce for any patterns to emerge.

Ontogenetic shifts in bathymetric distribution are reported in many oceanic squid species (Clarke, 1966), typically with juveniles found in the surface waters and adults deeper, although mature females of some species migrate to the surface. Many Antarctic squids appear to follow this pattern, although data from nets are rather limited, as scientific nets tend only to catch the juveniles, with the adults able to avoid the nets, making inferences from opening and closing nets difficult to interpret. Russian data suggest that *Gonatus antarcticus* undergo an ontogenetic descent, with larvae and early juveniles in the surface 200 m layer, with growing squids gradually moving deeper (Nesis, 1999a) and with juveniles and adults undertaking diurnal vertical migrations. Mature squid are thought to be at 1000–2000 m (Nesis, 1999a). In *G. glacialis* (Rodhouse and Clarke, 1986) and *A. antarcticus* (Rodhouse, 1988), there is also clear evidence of ontogenetic descent. In *G. glacialis*, juveniles occur at depths of 200–400 m, with larger specimens found deeper, concentrated in the 800–1000 m layer, with some vertical spreading during the night. In other species, such as *M. hamiltoni*, there is no evidence of ontogenetic descent, but the size range of specimens caught is limited. *M. hamiltoni* juveniles (5–27 mm) were mostly caught between 20 and 500 m, concentrated in the warm deep water, directly below the Antarctic surface water (Rodhouse and Clarke, 1985). In Prydz Bay, juveniles of *P. glacialis* (5–17 mm ML) were found close to the surface, with adults generally deeper (Filippova and Pakhomov, 1994).

3.6. Mass strandings

Mass strandings of *M. hyadesi* have been reported in the Falkland Islands (Nolan *et al.*, 1998) and at Macquarie Island (O'Sullivan *et al.*, 1983). The cause of these strandings is not known, but other migratory oceanic squid are known to strand occasionally and Nolan *et al.* (1998) speculated that this was due to localised changes in oceanographic circulation trapping the squid close to land.

4. GROWTH

4.1. Methods of measuring growth

The main methods of assessing growth in cephalopods are by counting growth rings in statolith microstructure (squid only) (see Rodhouse and Hatfield, 1990a; Jereb *et al.*, 1991), analysis of length-frequency data (e.g., Collins *et al.*, 1999) and laboratory-rearing studies (e.g., Forsythe and Hanlon, 1989). However, all these methods are problematic and can be subject to biases. Statolith growth rings are now routinely used to age squid, but results must be treated with caution unless the daily periodicity of deposition has been validated, which is not the case for any Southern Ocean species. Furthermore, validation can only really be achieved by maintaining squid in laboratory tanks, which is notoriously difficult. Octopodid species, which cannot be aged using statoliths, can be kept in experimental tanks, but it is not known whether natural rates of growth are reproduced in a captive environment. Length-frequency analysis has been applied to many temperate and tropical species. In putative short-lived species, it requires regular sampling over the course of a year, which is not normally possible in the short Antarctic field season and is subject to a number of potential biases, particularly in migratory species (Caddy, 1991; Hatfield and Rodhouse, 1994).

4.2. Rates of growth

Low temperature is a major factor affecting metabolism and growth in polar organisms (Clarke, 1998; Somero, 1998), with, in general, Antarctic ectotherms showing considerably lower growth rates than warmer water counterparts and attaining larger final sizes. Most tropical and temperate species of cephalopod have short life cycles, with rapid growth and longevity, typically $\leq$1 yr, but this is unlikely to be the case in Southern Ocean species, with low temperatures and highly seasonal primary and secondary production. In the only study to have directly measured growth in an Antarctic cephalopod, Daly and Peck (2000) determined the captive growth of the octopod *P. charcoti* at 0 °C. Growth rates were extremely slow ($\sim$0.1% body weight d^{-1}), although growth efficiency was high. Similar results have been obtained for growth of Arctic octopodids such as *Bathypolypus arcticus* (O'Dor and Macalaster, 1983).

Whilst statolith growth increments have been used in many temperate and tropical species of squid (Rodhouse and Hatfield, 1990a), they have not been applied to any of the high Antarctic species, and of the sub-Antarctic species, only *M. hyadesi* and *M. ingens* have been studied in detail, and the growth of these species is likely to be faster than the high Antarctic squid. Ageing studies, based on the putative daily deposition of growth rings on *M. hyadesi* statoliths, suggest a 2-yr life cycle (including egg stage) for animals caught at South Georgia (Rodhouse *et al.*, 1994; Gonzalez *et al.*, 1997; Gonzalez and Rodhouse, 1998) compared with estimates of 1 yr for Falklands-caught squid (Rodhouse *et al.*, 1994; Arkhipkin and Silvanovich, 1997). Growth rates at the APF were 1.10 and 1.06 mm ML d^{-1} for males and females, respectively, compared with rates of 1.38 and 1.46 mm ML d^{-1} for Patagonian shelf animals. This may support the hypothesis that growth is slower in cold Antarctic waters, but given that *M. hyadesi* is migratory, they may have sampled the same population.

Growth of *M. ingens*, investigated in New Zealand waters, showed that females (2.11 mm ML d^{-1}) grew at twice the rate of males (1.13 mm ML d^{-1}), with mature females (maximum 5 Kg) reaching weights five times those of males (Jackson, 1997). This study indicated a life cycle of ~1 yr in New Zealand waters, assuming daily deposition of growth rings, but growth may be slower in cold Southern Ocean water. Jackson and Lu (1994) examined the statolith microstructure of seven species of squid from Prydz Bay and found clear increments, similar in appearance to daily increments in temperate and tropical species, in *K. longimana* (445 mm ML), *P. glacialis* (95–142 mm ML), *Brachioteuthis* sp. (242 mm ML), *M. psychrophila* (116–129 mm ML) and *G. glacialis* (185–355 mm ML). The number of specimens was small, but in all cases, the increment count was <300. However, the deposition may not be daily, particularly in the seasonal absence of diel light cues.

The presence of two to three size classes of *P. glacialis* in Prydz Bay (Lu and Williams, 1994a), the Weddell Sea (Piatkowski *et al.*, 1990) and in stomach contents from predators (e.g., Offredo *et al.*, 1985; Lake *et al.*, 2003) is indicative of an extended life cycle of 2 or perhaps 3 yr, with considerably slower growth than temperate and sub-Antarctic species. However, based on evidence from predators (emperor and adelie penguins), Offredo *et al.* (1985) suggested that the two size classes of beaks could be explained as spent animals and new recruits, with a life cycle of ~1 yr. Multiple size classes could also be explained by multiple spawning events within a year, but this appears less plausible in a highly seasonal system and with putative planktonic paralarvae. Two size classes are also frequently found in *G. glacialis* (Lu and Williams, 1994a; Rodhouse and Clarke, 1986).

Two species of Southern Ocean squid, *K. longimana* and *M. hamiltoni*, reach extremely large size (Lynnes and Rodhouse, 2002; Young, 2003) and are likely to live much longer than the 1 yr typical of temperate and tropical squid species. Gigantism is common among polar (and deepsea) animals and is typically associated with slow growth in cold oxygen-rich waters (Atkinson and Sibly, 1997; Chapelle and Peck, 1999).

5. REPRODUCTION

5.1. Life-cycle strategies

With the exception of *Nautilus*, all extant cephalopods are semelparous, with a single cycle of egg production, albeit with different strategies for releasing the eggs (Mangold, 1987). There has been considerable debate in recent cephalopod literature regarding spawning strategies of species (Villanueva, 1992; Boyle *et al.*, 1995; Rocha *et al.*, 2001), with attempts made to categorise the strategies of different species; however, this pigeonhole approach is probably not appropriate, with species occupying a continuum from a single burst of spawning to a continuous release of individual eggs (cirrates). There are limited data on reproduction in the high-latitude Antarctic cephalopods and only slightly more in the sub-Antarctic species such as *M. hyadesi* and *M. ingens*, but a certain amount of information can be inferred from closely related species about which more is known.

5.2. Fecundity, egg size and development

Fecundity and egg size are essentially inversely related, with large egg size necessitating reduced fecundity. Thorson (1950) suggested that, in general, lecithotrophic and direct developing eggs would be expected at the poles, with large eggs and extended development times, and this appears to be the case in the Southern Ocean cephalopod fauna (Table 3). Within the Southern Ocean octopods, the eggs are amongst the largest in the cephalopods and consequently fecundity is low (Kuehl, 1988; Lu and Stranks, 1994; Collins and Henriques, 2000). In the squids, eggs tend to be larger than confamilial species from lower latitudes, with, for instance, *M. hyadesi* (1.9 mm) having larger eggs than other ommastrephids. Eggs of *M. ingens* are ~2.1 mm. Little is known about egg size in the cranchiids, but Nesis *et al.* (1998a) found single mature eggs in the ovaries of two spent *G. glacialis* with lengths of ~3.2 mm, rather large for an oegopsid squid. Laptikhovsky and Arkhipkin (2003) caught a mature *G. glacialis* in deep water near the Falkland Islands, with similarly sized mature eggs and relatively few (3600) oocytes in the ovary, indicating relatively low fecundity. Nesis *et al.* (1998a) suggested that potential fecundity may be higher (40,000–80,000), but that a large portion of the oocytes may not develop. In the north Atlantic, *Gonatus fabricii* has large eggs (~5 mm) (Bjørke *et al.*, 1997), and egg size is probably similar in *G. antarcticus*.

The inverse relationship between environmental temperature and duration of embryonic development in marine poikilotherms is well established (Naef, 1928; Clarke, A., 1982). In cephalopods, the duration of the embryonic phase is related to both egg size and incubation temperature (Boletzky, 1994, 2003; Nesis, 1999b), with smaller eggs having shorter embryonic phases. The large size of Antarctic incirrate octopod eggs (8–19 mm) (Table 3) indicates an extremely long developmental time, probably in excess of a year if the data of Boletzky (1994: Figure 1) are extrapolated to temperatures of <2 °C. Based on egg size and temperature, and Nesis

Table 3 Egg size, fecundity and seasonality of reproduction in Southern Ocean cephalopods

	Egg size (mm)	Fecundity	Seasonality	Source
Martialia hyadesi	1.9	115,000–560,000	Winter	Laptikhovsky and Nigmatullin, 1999
Todarodes filippovae		1–1.5 million		Laptikhovsky and Nigmatullin, 1999
Moroteuthis ingens	2.1	84,000–287,000	Winter	Jackson and Mladenov, 1994; Jackson 2001
Galiteuthis glacialis	3.3	12,700–24,000[a]		Nesis *et al.*, 1998a
Pareledone turqueti	19	37[b]	Autumn?	Kuehl, 1988
Adelieledone polymorpha	14	34–65[b]	Autumn?	Kuehl, 1988
Adelieledone adelieana	8–9			Lu and Stranks, 1994
Pareledone sp.[c]	18	21–58[b]	Autumn?	Kuehl, 1988
Pareledone sp.[c]	11–14			Lu and Stranks, 1994
Pareledone harissoni	12–15		Not known	Lu and Stranks, 1994
Megaleledone setebos	18–19		Not known	Lu and Stranks, 1994
Stauroteuthis gilchristi	9.5	~750	Not known	Collins and Henriques, 2000
Cirroctopus glacialis	10 × 16		Not known	Vecchione *et al.*, 1998

[a] Minimum estimate.

[b] Kuehl (1988) only included maturing and mature ova.

[c] Recorded as *Pareledone charcoti.*

(1999b) suggested incubation times of ~30 and 41 mo for *C. glacialis* and *Megaleledone setebos*, respectively. All cirrate octopods (e.g., *Stauroteuthis gilchristi* and *Cirroctopus* spp.) have large eggs (9–16 mm), which are laid individually and protected in a tough chitinous coat, again indicating extremely long development. The squid generally have smaller eggs, although those of Southern Ocean squid tend to be larger than temperate counterparts, again suggesting a relatively extended development.

5.3. Maturation and spawning

In a strongly seasonal environment, such as the Antarctic, it might be expected that maturation and spawning would be highly seasonal, with hatching timed to coincide with the productive summer period, although this is not always the case in temperate species (e.g., *Illex argentinus* a winter spawner) (Rodhouse and Hatfield, 1990b). However, the extended development times at low temperatures, particularly in species with large eggs, will make it difficult to coordinate the timing of spawning with the brief summer season and many species of octopod appear to have extended spawning seasons or even spawn throughout the year (Kuehl, 1988; Allcock *et al.*, 2001; Yau *et al.*, 2002).

In the squids, with smaller eggs, spawning may be more seasonal, and the distinct size classes present in populations of *Psychroteuthis* and *Galiteuthis* (Rodhouse and Clarke, 1986; Piatkowski *et al.*, 1990; Lu and Williams, 1994a) are indicative of discrete spawning periods, as is the size frequency of eggs in the ovary of mature *G. glacialis* (Laptikhovsky and Arkhipkin, 2003). Back-calculation of hatching dates from statoliths of *M. hyadesi* suggests that spawning occurs in the winter in this species (Gonzalez *et al.*, 1997), although this would depend on the time taken to hatch.

In cephalopods, the females are generally larger than males, the main exception being the loliginid squids that are not present in the Southern Ocean. The larger size is probably achieved by faster growth rather than greater longevity (e.g., *M. ingens*) (Jackson, 1997). In many cephalopods, mating happens well ahead of spawning, with sperm transferred by a modified male arm (hectocotylus) and females using a range of methods to store either spermatophores or sperm. Among the Antarctic squids, *G. glacialis* females store spermatophores in the mantle wall (Nesis *et al.*, 1998a). The cirrate octopods lack a hectocotylus but transfer sperm packets, presumably through the funnel, to the female, which are believed to be stored in the oviducal gland (Aldred *et al.*, 1983).

In some squid species, the adults migrate deep and it is possible that spawning occurs in deep water, with either the egg masses rising to the surface or females migrating to the surface with them, perhaps brooding them until hatching. Female squid of the families Gonatidae (Seibel *et al.*, 2000), Onychoteuthidae (Bello, 1998) and Cranchidae (Nesis *et al.*, 1998a) are known to undergo muscle degeneration and become gelatinous following spawning. This gelatinous degeneration may be associated with an increase in buoyancy, particularly once the eggs are released, making spent stages available to surface (nondiving) seabird predators such as albatross (see Section 6.2).

6. TROPHIC ECOLOGY

Cephalopods clearly play an important role in the ecology of the Southern Ocean, having been identified as key species in the diets of many higher predators, including penguins, seals, albatross and cetaceans. Whilst Antarctic krill are considered a key species in Southern Ocean food webs (particularly in the Scotia Sea), linking phytoplankton to higher predators in short efficient food chains (Atkinson *et al.*, 2001), a food web involving planktivorous mesopelagic fish, cephalopods and higher predators provides an alternative and potentially highly significant pathway in the Antarctic Polar Frontal Zone (APF) (Rodhouse and White, 1995). Studies of predator diets and foraging have been a major source of information on cephalopods in the Southern Ocean; however, knowledge of the diets of squid and octopods in the Southern Ocean remains rather limited.

6.1. Role as predators

The conventional method of studying the diet of squid is from stomach contents analysis. However, because the prey of cephalopods is macerated before swallowing, the identification of prey is not always straightforward and is even more problematic in some octopus species where some digestion occurs before ingestion. In many cases, squid reject the head of fish prey, precluding identification from otoliths, and any soft-bodied prey are likely to be underestimated. Alternative methods of investigating the diets of cephalopods include serological methods (Grisley and Boyle, 1985; Kear, 1992) and the use of biomarkers (e.g., Phillips *et al.*, 2001, 2002, 2003a; Cherel and Hobson, 2005). Serological methods are labour intensive, requiring antisera to be developed for each putative prey species. The use of biomarkers, such as fatty acids and stable isotopes, may prove a useful tool in determining cephalopod diets. In a recent innovation, Cherel and Hobson (2005) have demonstrated that stable isotope signatures in cephalopod beaks can be used to investigate trophic ecology. Beaks of the same species show an increase in $\Delta^{15}N$ values with increased size, which agrees with a dietary shift from lower to higher trophic levels with growth. Differences in $\Delta^{15}N$ between species indicated that the cephalopod fauna of Kerguelen operates over three trophic levels, with large *M. hamiltoni* operating at a higher trophic level than all other species investigated. Differences in $\Delta^{13}C$ indicated that Kerguelen cephalopods grow in three marine ecosystems, with most species studied living in Kerguelen waters but with species migrating from both Antarctic and subtropical regions. The ability to gain insights in cephalopod trophic ecology from beaks represents a major advance, particularly with the difficulty in capturing squid in nets and the availability of beaks from a range of predators.

Data on Antarctic cephalopod diets are limited (Table 4), but in general the squid are pelagic feeders, whilst the octopods, with the probable exception of *Stauroteuthis gilchristi*, are benthic feeders (see also Rodhouse and Nigmatullin, 1996). In general, the squids are catholic opportunistic predators, feeding on a variety of fish, cephalopods and crustacea, with a general shift from crustacea to fish with increased size (Rodhouse and Nigmatullin, 1996).

Largely on the basis of work undertaken by the former Soviet Union, Filippova and Yukhov (1979) divided the squid into two trophic groups. The first group, including brachioteuthids, live near the surface and feed almost exclusively on crustaceans (krill, hyperiid amphipods and mysids). The second group includes the larger species such as adults of *Mesonychoteuthis* and *Kondakovia*, which are thought to inhabit the mesopelagic and bathypelagic zones and feed mostly on vertically migrating fish, such as myctophids and gonostomatids. These larger squid will feed on crustaceans during early life and changes in the allometry of the brachial crown during ontogenesis are associated with a shift in prey (Rodhouse and Piatkowski, 1995).

The only squids that have been the subject of detailed dietary studies are the sub-Antarctic squids *M. hyadesi* and *M. ingens* (Table 4) and the adults of both species feed on mesopelagic fish and invertebrates. The diet of *M. hyadesi* is dominated by the hyperiid amphipod *Themisto gaudichaudii* and myctophid fish (particularly *Protomyctophum choriodon, Electrona carlsbergi* and *Krefftichthys anderssoni*) (Rodhouse *et al.*, 1992a; Gonzalez *et al.*, 1997; Gonzalez and Rodhouse, 1998; Dickson *et al.*, 2004), although significant consumption of other cephalopods, including cannibalism, has been reported (Gonzalez and Rodhouse, 1998).

The diet of *M. ingens* has been studied at various locations in the Southern Ocean, to the north and south of the APF, and the diet is dominated by mesopelagic (particularly myctophid) fish (Jackson *et al.*, 1998b; Phillips *et al.*, 2001, 2003a,b,c; Cherel and Duhamel, 2003). In studies south of the APF, the main prey species are myctophids of the genera *Electrona, Gymnoscopelus* and *Krefftichthys* and the paralepid *Acrtozenus risso* (Cherel and Duhamel, 2003; Phillips *et al.*, 2003c). In common with many squid species, there is evidence of a gradual switch from crustacea to fish and squid with increasing size (Phillips *et al.*, 2003b).

Table 4 Diets of Southern Ocean squids

Species/location	Size range (mm)	Prey types	Main prey species	Source
Martialia hyadesi				
South Georgia	278–370	Myctophids, crustacea and cephalopods	*Krefftichthys anderssoni, Protomyctophum choriodon, P. bolini, Gymnoscopelus nicholsi, Euphausia superba, Gonatus antarcticus*	Gonzalez and Rodhouse, 1998
South Georgia	190–310 (n = 61)	Myctophids, euphausids, amphipods	*K. andersoni, Electrona carlsbergi E. superba*	Rodhouse *et al.*, 1992a
Falkland Islands	190–350 (n = 336)	Myctophids, euphausids, amphipods and cephalopods	*K. anderssoni, G. nicholsi, Themisto gaudichaudii, Martialia hyadesi*	Gonzalez *et al.*, 1997
Patagonian Shelf	220–370	Myctophids, euphausids, amphipods and cephalopods	*Protomyctophum tenisoni, G. nicholsi, M. hyadesi*	Ivanovic *et al.*, 1998
Scotia Sea	216–260 (n = 25)	Fish and cephalopods	*K. anderssoni, G. nicholsi, Electrona antarctica*	Kear, 1992
South Georgia	225–312 (n = 40)	Amphipods, myctophids and cephalopods	*T. gaudichaudii, K. anderssoni, P. choriodon*	Dickson *et al.*, 2004
Moroteuthis ingens				

(Continued)

Table 4 (Continued)

Species/location	Size range (mm)	Prey types	Main prey species	Source
New Zealand	264–445 (n = 37)	Principally fish >90%; 9% squid	*Stomias boa/Chauliodus sloani, Lampanyctodes hectoris*	Jackson *et al.*, 1998b
Macquarie and Heard	150–432 (n = 54)	96% Myctophids *Bathylagus*	*Electrona* spp., *Gymnoscopelus* spp., *P. bolini, K. andersoni*	Phillips *et al.*, 2001
New Zealand, Macquarie, Falklands	200–500 (n = 316)	Primarily myctophid fish	*L. hectoris, E. carlsbergi*	Phillips *et al.*, 2003a
Falklands	75–375 (n = 100)	Crustacea, myctophids and cephalopods	*G. nicholsi, Loligo gahi, Moroteuthis ingens*	Phillips *et al.*, 2003b
South Shetlands	(n = 1)	Krill	*E. superba*	Nemoto *et al.*, 1988
Kerguelen	112–286 (n = 72)	Principally fish, with squid & crustacea	*Arctozenus risso, Paradiplospinosus gracilis, M. ingens*	Cherel and Duhamel, 2003
Kondakovia longimana				
South Shetlands	60–360 (n = 121)	Macroplankton	*E. superba, T. gaudichaudii, T. macrura,* amphipods, chaetognaths, fish, squid	Nemoto *et al.*, 1985, 1988
Moroteuthis knipovitchi				
South Shetlands	140–360 (n = 23)	Krill, fish	Myctophids, *E. superba*	Nemoto *et al.*, 1985, 1988
South Georgia	212–321 (n = 8)	Krill, fish	*E. superba, G. nicholsi*	Collins *et al.*, 2004
Moroteuthis robsoni				
South Shetlands	60–100 (n = 5)	Euphausids	*E. superba*	Nemoto *et al.*, 1988

Alluroteuthis antarcticus				
South Shetlands	40–140 (n = 7)	Macroplankton	*E. superba, T. gaudichaudii*, fish, squid	Nemoto *et al.*, 1985, 1988
Scotia Sea	221 (n = 1)	Euphausids, fish	*E. superba*	Kear, 1992
Prydz Bay	(n = 2)	Squid, fish	*Psychrateuthis glacialis, Pleurogramma*	Lu and Willliams, 1994a
Galiteuthis glacialis				
South Shetlands	100–240 (n = 19)	Macroplankton	*E. superba, T. gaudichaudii*, chaetognaths	Nemoto *et al.*, 1985, 1988
		Macroplankton	Eupausids, amphipods, copepods and chaetognaths	McSweeney, 1978
Prydz Bay	74–493 (n = 3)	Crustacea, fish	*E. superba*	Lu and Williams, 1994a
Slosarczykovia circumantarctica				
South Shetlands	40–160 (n = 75)	Krill	*E. superba*	Nemoto *et al.*, 1985, 1988
Scotia Sea	67–113 (n = 3)	Crustacea		Kear, 1992
Gonatus antarcticus				
South Shetlands	40–160 (n = 48)	Krill	*E. superba*	Nemoto *et al.*, 1988
Scotia Sea	57–375 (n = 2)	Unidentified fish		Kear, 1992
Psychroteuthis glacialis				
Scotia Sea	114–360 (n = 13)	Euphausids, fish	*E. superba, Chionodraco, Chaenodraco*	Kear, 1992
Prydz Bay	121–201 (n = 53)	Krill & fish	*Pleuragramma, E. superba.*	Lu and Williams, 1994a
South Georgia	(n = 4)	Krill	*E. superba*	Collins *et al.*, 2004

Trophic links between Antarctic krill and squid are not well established. Krill are not a major component of the diet of sub-Antarctic species such as *M. ingens* or *Martialia*, but there are too few data on other species to consider the role of squid in a krill-independent food chain that was proposed by Rodhouse and White (1995) in the APF. Myctophid fish are abundant in the Southern Ocean, and like the squid, their role in the ecology of the ocean is poorly known. Nemoto *et al.* (1985, 1988) found krill to be a major component in the diet of a range of Antarctic squid species taken as by-catch in the Japanese krill fishery to the north of the South Shetland Islands (Table 4). However, the sample sizes were small, and most of the squid were small (so might be expected to be feeding on crustaceans; see Rodhouse and Nigmatullin, 1996) and the association with krill aggregations may give a biased view. Kear (1992) applied serological methods to determine the presence of krill in the diet of 12 species of Antarctic squid and obtained positive results for six (*P. glacialis, M. psychrophila, M. knipovitchi, M. robsoni, Slosarczykovia circumantarctica* and *M. hyadesi*). Collins *et al.* (2004) also found krill to be the major item in a small number of *P. glacialis* and *M. knipovitchi* stomachs from specimens caught at South Georgia. The significance of krill in squid diets is still not clear, but around South Georgia the availability of krill varies both seasonally and interannually (Murphy *et al.* 1998; Brierley *et al.*, 2002), and with squid generally being catholic opportunistic predators, krill are likely to be taken when abundantly available. Furthermore, at South Georgia, myctophids of the genus *Gymnoscopelus* feed extensively on krill (Collins, unpublished), so a food web involving squid and myctophids is unlikely to be entirely independent of krill south of the APF.

Cannibalism is well documented in squids, either with larger members of the cohort preying on smaller ones or with a larger cohort consuming animals from a smaller cohort (see Johnston, 2002). Cannibalism appears to be particularly important in the shoaling, muscular, migratory species such as the ommastrephids (O'Dor, 1983; Lipinski and Linkowski, 1988) where cannibalism may serve to fuel the migration during periods of poor food availability (O'Dor, 1992). Among the Southern Ocean squids, cannibalism has been recorded in *M. hyadesi* (Rodhouse *et al.*, 1992a; Gonzalez and Rodhouse, 1998; Dickson *et al.*, 2004), *M. ingens* (Phillips *et al.*, 2003a) and *P. glacialis* (Lu and Williams, 1994a).

The diet of Antarctic octopods is also poorly known, although the incirrate octopods are all benthic feeders (Table 5). In a preliminary study, Piatkowski *et al.* (2003) examined the diet of five incirrate species from the Antarctic Peninsula and found amphipods, polychaetes and ophiuroids to be the most common prey items. Differences in beak morphology between species such as *P. turqueti* and *Adelieledone polymorpha* (Figure 9) suggest differences in foraging and diet (Daly and Rodhouse, 1994), and Daly (1996)

Table 5 Diets of Southern Ocean Octopods

Species/location	Size range (mm)	Prey types	Source
Adelieledone polymorpha	n = 41	Crustacea and polychaetes	Daly, 1996
	n = 3	Amphipods, polychaetes	Piatkowski *et al.*, 2003
Pareledone turqueti	n = 84	Crustacea, gastropods, bivalves & polychaetes	Daly, 1996
		Amphipods, polychaetes, fish, octopod	Piatkowski *et al.*, 2003
Megaleledone setebos	n = 15	Ophiuroids, amphipods, fish	Piatkowski *et al.*, 2003
Pareledone charcoti	n = 33	Amphipods	Piatkowski *et al.*, 2003
Benthoctopus cf *levis*	n = 7	Amphipods, fish, ophiuroids, crustacea	Piatkowski *et al.*, 2003
Cirroctopus glacialis		Unidentifiable crustacean fragments	Vecchione *et al.*, 1998

examined the stomach and crop contents of these species at South Georgia and found the diet of both species dominated by crustacea and polychaetes, with bivalve and gastropod molluscs also taken by *P. turqueti*. Because of the macerated nature of the contents and limited knowledge of the benthic fauna, specific identifications were not possible, which is a common problem in octopod diet studies. Vecchione *et al.* (1998) examined the stomach contents of a small number of the cirrate octopod *C. glacialis* but only found unidentifiable crustacean fragments. Given the difficulty in identifying the prey of octopods, the use of biomarkers, such as fatty acids, may be useful in determining broad patterns in diet and possible niche separation.

6.2. Role as prey

Cephalopods play an important role in the diets of Southern Ocean higher predators, which have been estimated to consume in the region of 34 million tonnes of cephalopods per annum (Clarke, 1983). In the Scotia Sea alone, Croxall *et al.* (1985) estimated that predators take ~3.7 million tonnes of

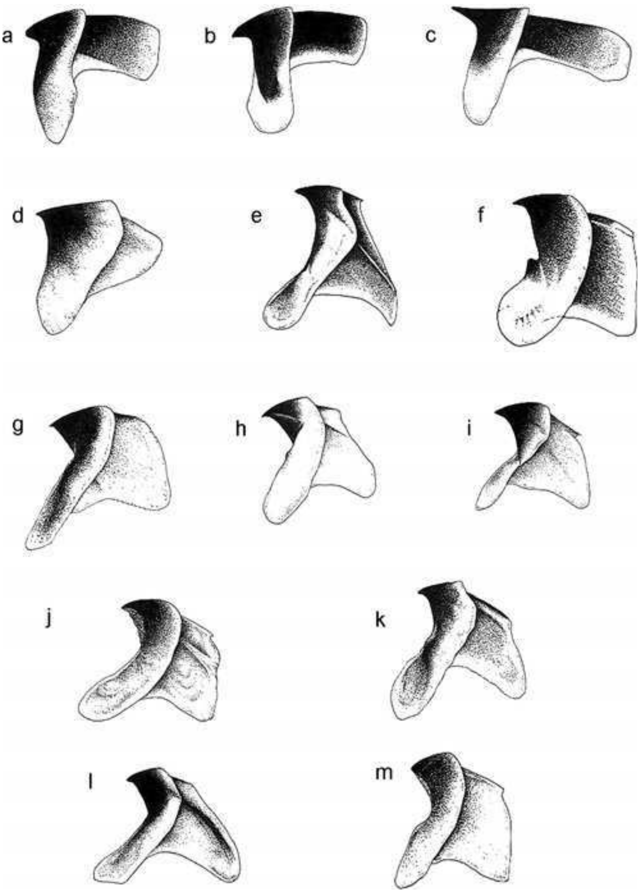

Figure 9 Lower beaks of some Southern Ocean cephalopod species (a) *Pareledone turqueti*, (b) *Thaumeledone gunteri*, (c) *Adelieledone polymorpha*, (d) *Stauroteuthis gilchristi*, (e) *Chiroteuthis veranyi*, (f) *Martialia hyadesi*, (g) *Alluroteuthis antarcticus*, (h) *Psychroteuthis glacialis*, (i) *Slosarczykovia circumantarctica*, (j) *Kondakovia longimana*, (k) *Moroteuthis knipovitchi*, (l) *Mastigoteuthis psychrophila* and (m) *Mesonychoteuthis hamiltoni*.

squid per annum. Four main methods have been used to determine the cephalopod component of the diet of Antarctic higher predators: stomach contents from dead animals; stomach flushing; regurgitations; and faeces (scats). All these methods are highly dependent on the identification of beaks, which was pioneered by Clarke (1962a,b, 1977, 1986). Beaks are the major indigestible parts of cephalopods and their identification to genus and in some cases species level (see Figure 9) has led to major advances in understanding the trophic ecology of cephalopods but is subject to certain biases. In particular, beaks are frequently retained in predator stomachs for considerable periods, potentially leading to an overestimation of the importance of cephalopod prey (Piatkowski and Pütz, 1994), and different sized beaks may be differentially retained. Piatkowski and Pütz (1994) showed that using only relatively undigested beaks, rather than all beaks, had a major impact on the assessment of the importance of cephalopods in emperor penguin diet. Furthermore, there has been considerable confusion in the literature regarding the correct identification of beaks, making comparisons between studies difficult (see Imber, 1992). Part of the problem is the lack of good reference collections of beaks from captured squid, particularly large squid. For instance, two types of *Psychroteuthis* beak have been described from predators, but the genus is considered monotypic (Imber, 1992). However, the two types of beak are different sizes and may simply represent different sizes of a single *Psychroteuthis* species (Rodhouse, 1989b). Despite these difficulties, the use of beaks has added greatly to our knowledge of Southern Ocean cephalopods and many Antarctic cephalopods are better known from dietary studies of predators than from captures in nets.

Biomarkers, such as fatty acids and stable isotopes, have been used to indicate diet and trophic level of many predators (e.g., Lea *et al.*, 2002). However, the majority of the lipid in cephalopods is found in the digestive gland, which is likely to be of dietary origin, and thus, the fatty acid signature of a cephalopod may simply reflect that of its prey, which could lead to an underestimate of the contribution of cephalopods (Phillips *et al.*, 2002).

Cephalopod predators can be divided into four main groups: seabirds, marine mammals, fish and other cephalopods. Different predators forage at different depths (Figure 10) and over different scales, taking a different range of species and sizes of cephalopods (Figure 11), not all of which will be Southern Ocean species. Tables 6–10 include data from studies that have identified cephalopods as prey, but for many species there are other studies that have not found a cephalopod component in the diet. The method of reporting the cephalopod contribution also varies between studies. Where percent mass is used, it is often based on the reconstructed mass, estimated from the size of all beaks, and may overestimate the relative amount of cephalopods taken.

6.2.1. Seabirds

Cephalopods are important in the diet of many seabird species and squid are the major prey of grey-headed, wandering and light-mantled sooty albatross (Table 6). In particular, *M. hyadesi* is the main prey of grey-headed albatross (Clarke and Prince, 1981; Rodhouse *et al.*, 1990; Xavier *et al.*, 2003a,b,c),

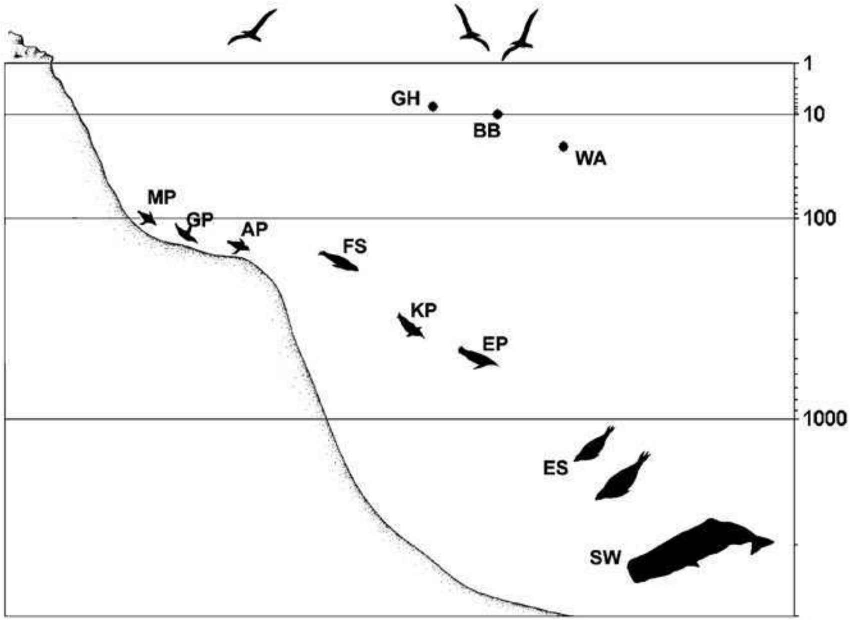

Figure 10 Foraging depths of Southern Ocean cephalopod predators. MP: macaroni penguin, GP: gentoo penguin, Ap: adelie penguin, GH: grey-headed albatross, BB: black-browed albatross, WA: wandering albatross, FS: fur seal, KP: king penguin, EP: emperor penguin, ES: elephant seal, SW: sperm whale. Depth in metres.

whilst *K. longimana* is the main prey of wandering albatross and light-mantled sooty albatross (Clarke *et al.*, 1981; Rodhouse *et al.*, 1987; Cooper *et al.*, 1992a; Hoff, 2001; Xavier *et al.*, 2003b). The foraging range of most albatross species extends outside of the Southern Ocean (e.g., wandering albatross; Xavier *et al.*, 2004), so some of the prey will be non–Southern Ocean species (Xavier *et al.*, 2003c); however, much of the diet work is undertaken during the chick-rearing period when foraging trips are shorter (Weimerskirch *et al.*, 1986).

Satellite tracking studies indicate that albatross frequently rest on the surface at night, and this may well be the time that they feed, but the question of when and how albatross feed remains largely unanswered (see Croxall and Prince, 1994). The size of beaks found in wandering albatross regurgitates (Figure 11) indicates that they are frequently taking very large squid, particularly *K. longimana, M. hamiltoni* and *M. knipovitchi.* Given that larger squid are generally found deeper and are capable of rapid movement, it seems unlikely that albatrosses are taking these large squid alive either by dip feeding or by diving in the surface layer (Croxall and Prince, 1994). Instead, the wandering albatross probably

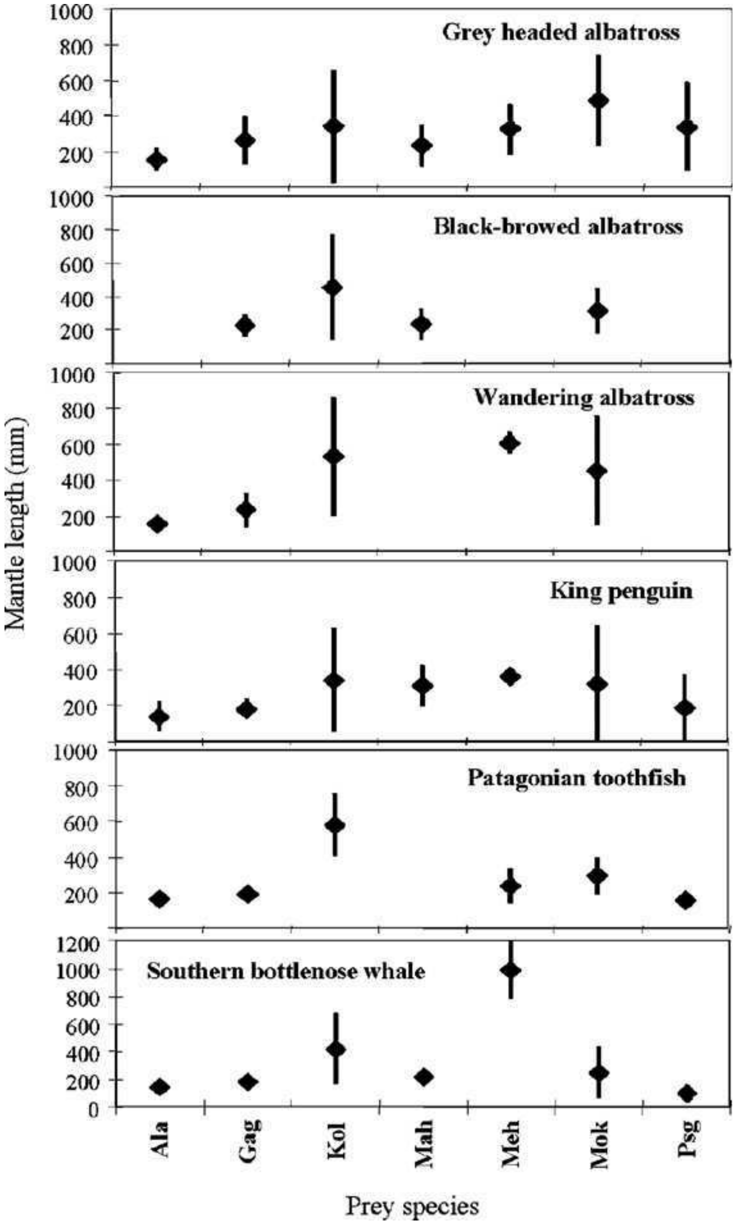

Figure 11 Size ranges (mean and range) of seven cephalopod species taken by different Southern Ocean predators. For abbreviations see key to Table 6.

Table 6 Cephalopod prey of Southern Ocean albatross

Predator	Location	% cephalopods in diet	Main cephalopod prey	Source
Wandering albatross (*Diomedea exulans*)	South Georgia	Not recorded	Kol, Mor, Hi, Tap, Tnd	Clarke *et al.*, 1981
	Circum-Antarctic	Major	Kol, Hia, Gag, Hie	Imber, 1992
	Marion Island	59% (mass)	Kol, Mok, Moi, Ala	Cooper *et al.*, 1992a
	Macquarie Island	100% (occurrence)	Moi, Msp, Aa, Pb	Hoff, 2001
	South Georgia	32% (mass)	Kol	Xavier *et al.*, 2003b
	South Georgia 1989–1989	Not available	Kol, Tap, Hi	Xavier *et al.*, 2003c
Royal albatross (*Diomedea epomophora*)	New Zealand	Major	Moi, Hia	Imber, 1999
Black-browed albatross (*Thalassarche melanophrys*)	South Georgia	21% (mass)	Mah*[1], Meh, *Ancistrocheirus*	Prince, 1980
	South Georgia	Not recorded	Mah*[1], Gag	Clarke and Prince, 1981
	South Georgia (Feb)	31% (mass)	Mah, Gag	Rodhouse and Prince, 1993
	South Georgia	23% (mass)	Mah, Gag	Croxall *et al.*, 1999
	South Georgia (1996–2000)	7–49% (mass)	Mah, Kol, Gag, Mok	Xavier *et al.*, 2003b
Grey-headed albatross (*Thalassarche chrysostoma*)	South Georgia	49% (mass)	Mah*[1], Meh	Prince, 1980
	South Georgia	Not recorded	Mah*[1], Gag	Clarke and Prince, 1981
	Marion Island	Not recorded	Mok, Mor, Kol	Brooke and Klages, 1986
	South Georgia	Not recorded	Mah, Psg, Kol, Gag	Rodhouse *et al.*, 1990
	South Georgia	37% (mass)	Mah, Kol, Gag	Croxall *et al.*, 1999
	South Georgia (1996–2000)	17–75% (mass)	Mah, Kol, Gag, Psg	Xavier *et al.*, 2003a
	South Georgia (2003)	40% (mass)	Mah, Gag, Goa	Catry *et al.*, 2004

Yellow-nosed albatross (*Thalassarche chlororynchos*)	Prince Edward Island	Not recorded	Mok, Mor, Kol	Brooke and Klages, 1986
Light-mantled sooty albatross (*Phoebetria palpebrata*)	Marion Island	Major	Kol, Mok, Hie	Berruti and Harcus, 1978
	Marion Island	Not recorded	Gag, Mok, Kol, Psg, Hie	Berruti, 1979
	Prince Edward Islands	Not recorded	Kol, Ala	Imber and Berruti, 1981
	South Georgia	46% (mass)	Mah, Gag , Psg, Goa	Thomas, 1982
	Macquarie Island	Not recorded	Kol, Psg, Mah, Ala, Gag	Imber, 1991
	Marion Island	34% mass (94% occurrence)	Kol, Mok, Mor, Ala	Cooper and Klages, 1995
	Macquarie Island		Kol, Ala, Gag, Mah	Green *et al*., 1998
	Heard Island	70–100% occurrence	Kol, Gag	Green *et al*., 1998
		Not recorded		
Sooty albatross (*Phoebetria fusca)*	Marion Island	Major	Kol, Mok, Hie,	Berruti and Harcus, 1978
	Marion Island	42% mass (100% occ)	Kol, Mor, Ch, Gag	Cooper and Klages, 1995

Key: Ala = *Alluroteuthis antarcticus*; Bas = *Batoteuthis skolops*; Ch = *Chiroteuthis* sp.; Gag = *Galiteuthis glacialis*; Goa = *Gonatus antarcticus*; Hi = *Histioteuthis* sp.; Hia = *Histioteuthis atlantica*; Hie = *Histioteuthis eltaninae*; Kol = *Kondakovia longimana*; Mah = *Martialia hyadesi*; Meh = *Mesonychoteuthis hamiltoni*; Msp = *Mastigoteuthis psychrophila*; Mo = *Moroteuthis* spp.; Mok = *Moroteuthis knipovitchi*; Moi = *Moroteuthis ingens*; Mor = *Moroteuthis robsoni*; Psg = *Psychroteuthis glacialis*; Pa = *Pareledone* sp.; Pac = *Pareledone charcoti*; Pat = *Pareledone turqueti*; Slc = *Slosarczykovia circumantarctica*; Tap = *Taonius pavo*; Tnd = *Taningia danae*; To = *Todarodes* sp.; Tof = *Todarodes filippovae.*

*[1] Recorded as *Todarodes.*

*[2] Recorded as *Brachioteuthis picta.*

*[3] Recorded as *Discoteuthis* sp.

*[4] Recorded as *Brachioteuthis ?riisei.*

scavenge much of their food, and although some prey may be obtained from discards from fishing vessels, this is unlikely to account for all prey. A more plausible scenario is that the birds feed on post-spawning animals that lose neutral buoyancy and rise to the surface (Lipinski and Jackson, 1989). In the gonatids, onychoteuthids and *G. glacialis*, the mature females become highly gelatinous after spawning, with the mantle muscle losing its structure (Lipinski and Jackson, 1989; Nesis *et al.*, 1998a). Spawning may occur in the upper part of the water column, and as the female squid releases the last of the egg mass, neutral buoyancy may be lost, causing it to float to the surface. These post-spawning females may occur in a seasonal and geographically predictable manner, allowing albatross to take advantage. Clarke *et al.* (1981) also suggested that some seabirds, particularly wandering albatross, scavenge from squid remains vomited by sperm whales. Sperm whales are reported to vomit during whaling activities, but also to periodically empty their stomachs of cephalopod beaks. This may be another method by which seabirds ingest beaks from large squid and would lead to an overestimation of the importance of cephalopods. Imber and Russ (1975) suggested that bioluminescent squid are preferentially preyed upon, but as Clarke *et al.* (1981) pointed out, most Southern Ocean squid lack bioluminescence, and when present, it is on the ventral surface, which is unlikely to increase their visibility from above.

Xavier *et al.* (2003b) combined satellite tracking of wandering and grey-headed albatross with diet studies to determine the distribution of some of the prey species. Such analyses may be valuable in tracing the distribution of species that cannot be caught in nets but will be subject to the biases outlined earlier in this chapter. However, by using only fresh material, indicative of recent feeding, Xavier *et al.* (2003b) provided important data on interannual variability of prey species such as *M. hyadesi.*

King, emperor, royal, gentoo, adelie, macaroni and rockhopper penguins all take cephalopods (Table 7), but it is only the deeper diving king and emperor penguins (Williams, 1995) (Figure 10) that take significant quantities in any location. The other penguins tend to forage closer to shore and dive less deep, typically favouring krill and inshore fish. Cherel *et al.* (1996) found that 65% of king penguin diet at Crozet was squid (mostly *M. ingens*), whilst Piatkowski and Pütz (1994) found 54% of the diet of emperors in the Weddell Sea area was squid (predominantly *K. longimana, P. glacialis* and *A. antarcticus*). At South Georgia, the king penguins' diet is dominated by mesopelagic fish, with only small amounts of squid recorded (Olsson and North, 1997; Rodhouse *et al.*, 1998). In general, penguins take smaller sized cephalopod prey than albatross (Figure 11).

Among the other flying seabirds, white-chinned petrel diet includes up to 25% squid at South Georgia (Croxall *et al.*, 1995; Berrow and Croxall, 1999), Marion Island (Cooper *et al.*, 1992b) and Crozet Island (Ridoux, 1994), with

Table 7 Cephalopod prey of Southern Ocean penguins (Key: see Table 6)

Predator	Location	% cephalopods in diet	Main cephalopod prey	Source
King penguin (*Aptenodytes patagonicus*)	Marion Island	17 % (mass)	Kol	Adams and Klages, 1987
	Crozet	65% (mass)	Moi, Mok, Mah	Cherel *et al*., 1996
	South Georgia (summer)	~3% (mass)	Not identified	Olsson and North, 1997
	South Georgia (summer)	~3% (mass)	Mah, Mok, Kol, Psg, Ala	Rodhouse Olsson and North, 1997, 1998
	Falklands	not recorded	Mah, Moi, Mok	Piatkowski *et al*., 1998
Emperor penguin (*Aptenodytes forsteri*)	Adelie Land	Minor	Psg, Goa, Kol	Offredo *et al*., 1985
	Adelie Land	1% (mass)	Psg, Goa, Kol	Offredo and Ridoux, 1986
	Weddell	90–97% (occurrence)	Kol, Psg, Ala	Piatkowski and Pütz, 1994
	Mawson Coast: Auster Colony	45% (mass)	Ala, Psg	Robertson *et al*., 1994
	Taylor Colony	69% (mass)	Ala, Psg	Robertson *et al*., 1994
	Ross Sea	~3% (mass)	Psg	Cherel and Kooyman, 1998

(Continued)

Table 7 (Continued)

Predator	Location	% cephalopods in diet	Main cephalopod prey	Source
Gentoo penguin (*Pygoscelis papua*)	South Georgia	1.2% (mass)	Slc^{*2}	Croxall *et al*., 1999
	Laurie Island	~5% (mass)	Psg	Coria *et al*., 2000
	Kerguelen	up to 13% (mass)	Kol, Goa, octopods	Lescroël *et al*., 2004
Adelie penguin (*Pygoscelis adeliae*)	Adelie Land	3% (mass)	Psg	Offredo *et al*., 1985
Rockhopper penguin (*Eudyptes chrysocome*)	Marion Island	5% (mass)	Kol, octopods	Brown and Klages, 1987
	Macquarie Island	2% (mass)	Mah, Mo	Hindell, 1988a
	Marion Island	19% (occurrence)	Kol, octopods	Adams and Klages, 1989
Royal penguin (*Eudyptes schlegeli*)	Macquarie Island	3% (mass)	Mo, Mah	Hindell, 1988b
Macaroni penguin (*Eudyptes chrysolophus*)	Marion Island	8–13% (mass)	Kol	Brown and Klages, 1987
	South Georgia	1% (mass)	Mah	Croxall *et al*., 1999

the main species taken being *Gonatus antarcticus, G. glacialis* and *M. hyadesi.* Squid constitute the bulk of the diet of petrels of the genus *Pterodroma* at the Prince Edward Islands (Schramm, 1986) and have been reported in small quantities in the diets of blue petrels, giant petrels, Cape petrels, Antarctic fulmars and blue-eyed shags (Table 8).

6.2.2. Seals

Of the seals, the southern elephant seal (*Mirounga leonina*) is probably the most significant predator of squid, with many dietary studies indicating that cephalopods are normally the preferred prey (Table 9); however, this is based on a small number of studies and may be biased by the retention of beaks in the stomach. Elephant seals typically forage at depths of between 200 and 700 m (Boyd and Arnbom, 1991) but are capable of diving to depths in excess of 1,000 m (Slip *et al.*, 1994). They take a range of cephalopod species and sizes (Table 9; Figure 11), particularly *K. longimana, M. hyadesi, M. knipovitchi* and *A. antarcticus*. Elephant seals also take benthic octopods, which indicates that they forage on the sea floor and on pelagic squid prey, and this is supported by studies of foraging ecology (e.g., McConnell *et al.*, 1992) (Table 10).

Antarctic fur seals take a small amount of squid, but krill and fish usually dominate the diet of this species (Reid, 1995; Reid and Arnould, 1996). In some areas, cephalopods form a major part of the diet of Weddell seals with *M. knipovitchi, P. glacialis* and *P. charcoti* the main prey species at the South Shetlands and South Orkney Islands (Clarke and MacLeod, 1982b; Casaux *et al.*, 1997) and *P. glacialis* and *Pareledone* spp. the main cephalopod prey at four sites in east Antarctica (Lake *et al.*, 2003). *P. glacialis* was the main prey item during spring on the Mawson Coast, with two distinct size classes taken (Lake *et al.*, 2003). From a small number of studies, cephalopods appear to be the main prey of Ross seals (Oritsland, 1977; Skinner and Klages, 1994), with *Psychroteuthis, Galiteuthis* and *Alluroteuthis* the main species taken. However, Skinner and Klages (1994) noticed differences in the prey spectrum between full stomachs and those containing just hard parts, with fish comprising a greater part of the diet in animals with full stomachs. Cephalopods have also been reported in the diets of crabeater and leopard seals but are usually a minor component of the diet (Table 9).

6.2.3. Cetaceans

Since the cessation of commercial whaling, dietary data on cetaceans have been limited to stranded specimens, but many toothed whales are thought to be major consumers of cephalopods (Clarke, 1996). Sperm whales, which are

Table 8 Cephalopod prey of Southern Ocean petrels, fulmars and shags (key: see Table 6)

Predator	Location	% cephalopods in diet	Main cephalopod prey	Source
Northern giant petrel	South Georgia	Not recorded	Mah, Gag, Kol	Hunter, 1983
(*Macronectes halli*)	Crozet	1% (mass)	Kol	Ridoux, 1994
Southern giant petrel	South Georgia	Not recorded	Mah, Gag, Kol	Hunter, 1983
(*Macronectes giganteus*)	Ross Sea	74% (mass)	Goa, Psg, Gag	Ainley *et al.*, 1984
White-chinned petrel	Marion	17% (mass)	Mah, Hi	Cooper *et al.*, 1992b
(*Procellaria aequinoctialis*)	Crozet	25% (mass)	Goa, Gag	Ridoux, 1994
	South Georgia	19% (mass)	Mah, Goa	Croxall *et al.*, 1995
	South Georgia	19–25% (mass)	Gag, Goa, Kol	Berrow and Croxall, 1999
	South Georgia	20% (mass)	Gag, Slc*[2]	Berrow *et al.*, 2000
	Crozet	12% (mass)	Slc*[4]	Catard *et al.*, 2000
Antarctic petrel	AAT	75% (mass)	Psg	Norman and Ward, 1992
(*Thalassoica antarctica*)	Weddell Sea	22% (mass)	Goa, Psg	Ainley *et al.*, 1992
	Ross Sea	86% (mass)	Goa	Ainley *et al.*, 1984
Blue petrel	South Georgia	0.7 (weight)	Psg	Prince, 1980
(*Halobaena caerulea*)		6.4 (occasional)		
	Kerguelen	2.1% (mass)	Kol	Cherel *et al.*, 2002c
Cape petrel (*Daption*	Ross Sea	97% (mass)	Not identified	Ainley *et al.*, 1984
capense)	Weddell Sea	19% (mass)	Goa, Gag	Ainley *et al.*, 1992
	King George Island	<1% (mass)	Not identified	Creet *et al.*, 1994
Antarctic prion (*Pachyptila*	South Georgia	0.6 (mass)	Ala	Prince, 1980
desolata)		8.9 (occasional)		
	Kerguelen	3% (mass)	Slc	Cherel *et al.*, 2002d

Grey petrel (*Procellaria cinerea*)	Crozet	70% (mass)	Moi, Goa	Ridoux, 1994
Mottled petrel (*Pterodroma inexpectata)*	Ross Sea	98% (mass)	Goa, Psg, Gag	Ainley *et al*., 1984
Snow petrel (*Pagodroma nivea*)	Ross Sea	35% (mass)	Goa, Psg, Gag	Ainley *et al*., 1984
Great-winged petrel (*Pterodroma macroptera*)	Prince Edward Islands	90% (mass)	Goa, Hi, Psg*[3]	Schramm, 1986
	Crozet	64% (mass)	Ta, Goa, Hi	Ridoux, 1994
Soft-plumaged petrel (*Pterodroma mollis*)	Prince Edward Islands	89% (mass)	Goa, Ch, Psg*[3]	Schramm, 1986
	Crozet	16% (mass)	Hie, Tap	Ridoux, 1994
Kerguelen petrel (*Pterodroma brevirostris)*	Prince Edward Islands	70% (mass)	Goa	Schramm, 1986
	Weddell Sea	24% (mass)	Gag	Ainley *et al*., 1992
	Crozet	6% (mass)	Kol	Ridoux, 1994
Antarctic fulmar (*Fulmarus glacialoides*)	Weddell Sea	53% (mass)	Psg, Goa	Ainley *et al*., 1992
	AAT	Not recorded	Goa	Norman and Ward, 1992
	Ross Sea	94% (mass)	Goa	Ainley *et al*., 1984
South polar skua (*Catharacta maccormicki*)	Ross Sea	72% (mass)	Psg, Goa, Gag	Ainley *et al*., 1992
Blue-eyed shag (*Phalacrocorax atriceps)*	Bransfield Strait	0.1% (mass)	Pa	Casaux and Barreraoro, 1993

Table 9 Cephalopod prey of Southern Ocean marine mammals (key: see Table 6)

Predator	Location	Cephalopods in diet	Main cephalopod prey	Source
Elephant seal (*Mirounga leonina*)	Signy Island	81% (occurrence)	Mok, Goa, Pa,	Clarke and MacLeod, 1982a
	South Georgia	90% (occurrence)	Mok, Kol, Psg, Mah, Ala, Goa,	Rodhouse *et al.*, 1992c
	Heard	86% (occurrence)	Slc*^{2} Ala, Mok, Moi	Green and Burton, 1993
	Macquarie	100% (occurrence)	Ala, Kol, Moi, Mok,	Green and Burton, 1993
	Heard	Major	Psg, Ala, Mok, Kol, Goa, Pac	Slip, 1995
	South Shetlands	72% (occurrence)	Psg, Ala, Kol, Moi, Mok, Tof	Daneri *et al.*, 2000
	King George Island	Major	Psg, Ala, Gag, Slc, Kol, Goa	Piatkowski *et al.*, 2002
	Vincennes Bay, East Antarctica	35% (occurrence)	Psg, Ala	Hoff *et al.*, 2003
Fur seal (*Artocephalus gazella*)	Heard (Sep–Feb)	<5% (occurrence)	Not identified	Green *et al.*, 1989
	Heard (winter)	49% (occurrence)	Msp	Green *et al.*, 1991
	Laurie Island (South Orkneys)	34% (occurrence)	Not identified	Daneri and Coria, 1992
	South Georgia (winter)	1.3% (occurrence)	Slc*^{2}, Pat	Reid, 1995
	South Georgia (Jan–Mar)	5% (occurrence)	Mok, Slc*^{2}, Ala, Pat	Reid and Arnould, 1996
	South Georgia	<1% (occurrence)	Mah	North, 1996
	South Orkney	34% (occurrence)	Psg, Slc*^{2}	Daneri *et al.*, 1999
	South Shetlands	15% (occurrence)	Psg, Slc*^{2}	Daneri *et al.*, 1999

Crabeater seals (*Lobodon carcinophagus*)	Scotia/Weddell Sea Pack Ice	2% (occurrence)	Goa	Oritsland, 1977
Weddell seal (*Leptonychotes weddellii*)	McMurdo	17% (occurrence)	Pa	Dearborn, 1965
	Scotia/Weddell Sea Pack Ice	11% (occurrence)	Not identified	Oritsland, 1977
	Deception	88% (occurrence)	Mok, Psg, Pa	Clarke and MacLeod, 1982b
	Weddell Sea	28% (occurrence)	Not identified	Plötz, 1986
	Davis	2% (mass)	Not identified	Green and Burton, 1987
	Mawson	21% (mass)	Not identified	Green and Burton, 1987
	McMurdo	0.7% (mass)	Not identified	Green and Burton, 1987
	Weddell Sea	8.5% (mass)	Psg, Pac	Plötz *et al.*, 1991
	South Shetlands (Jan–Feb)	66% (mass)	Pac, Psg	Casaux *et al.*, 1997
	Commonwealth Bay	36% (mass)	Pa	Lake *et al.*, 2003
	Laresemann Hills	14% (mass)	Pa, Psg	Lake *et al.*, 2003
	Mawson	82% (mass)	Psg, Pa	Lake *et al.*, 2003
	Vestfold Hills	18% (mass)	Pa, Psg	Lake *et al.*, 2003
Leopard seal (*Hydrurga leptonyx*)	Scotia/Weddell Sea Pack Ice	8% (occurrence)	Not identified	Oritsland, 1977
	Antarctic Peninsula	Up to 40%	Not identified	Siniff and Stone, 1985
Ross seal (*Omatophoca rossii*)	Scotia/Weddell Sea Pack Ice	79%	Not identified	Oritsland, 1977
	Pack ice zone	94% (occurrence)	Psg, Gag, Ala, Kol, Ch	Skinner and Klages, 1994
Southern bottlenose whale (*Hyperoodon planifrons*)	Tierra del Fuego	Not recorded	Mah, Kol, Goa, Hie, Tap	Clarke and Goodall, 1994
	Heard Island	Major	Kol, Psg, Goa, Gag, Mok, Ala,	Slip *et al.*, 1995

(Continued)

Table 9 (Continued)

Predator	Location	Cephalopods in diet	Main cephalopod prey	Source
Sperm whales (*Physeter macrocephalus*)	Antarctica	Major	Mor, Mok, Kol, Meh, Goa, Hi	Clarke, 1980
	New Zealand	Not recorded	Not identified	Clarke and Roeleveld, 1998
Pilot whale (*Globiocephala malaena*)	Tierra del Fuego	Not recorded	Hie, Moi	Clarke and Goodall, 1994
False killer whales (*Pseudorca crassidens*)	Tierra del Fuego	Not recorded	Mah, Moi	Alonso *et al*., 1999

Table 10 Cephalopod prey of Southern Ocean fish and cephalopods (key: see Table 6)

Predator	Location	% cephalopods in diet	Main cephalopod prey	Source
Patagonian toothfish (*Dissostichus eleginoides*)	Kerguelen	1% (occurrence)	Unidentified	Duhamel, 1981
	Crozet	8% (occurrence)	Unidentified	Duhamel and Pletikosic, 1983
	South Georgia <300 m	1% (occurrence)	Octopods	Garcia de la Rosa *et al.*, 1997
	South Georgia 1000–1500 m	15% (occurrence)	Kol	Garcia de la Rosa *et al.*, 1997
	Macquarie Island	35% (occurrence)	Goa, Msp, cirrates	Goldsworthy *et al.*, 2002
	South Georgia	7% (occurrence)	Kol, Mok, Goa, Pat, Ala, Chv	Xavier *et al.*, 2002b
	Kerguelen	Not stated	Kol, Chv, Goa, To	Cherel *et al.*, 2004
	Crozet	Not stated	Kol, Moi, Goa	Cherel *et al.*, 2004
Antarctic toothfish (*Dissostichus mawsoni*)	Ross Sea	14% (occurrence)	Not identified	Fenaughty *et al.*, 2003
Lanternshark (*Etmopterus* cf. *granulosus*)	Kerguelen	86% (occurrence)	Msp, Slc, Hia, Bas	Cherel and Duhamel, 2004
Porbeagle shark (*Lamna nasus*)	Kerguelen	92% (occurrence)	Hia, To, Kol	Cherel and Duhamel, 2004
Sleeper shark (*Somniosus* cf. *microcephalus*)	Kerguelen	100% (occurrence)	Meh, Kol, Tad	Cherel and Duhamel, 2004
Squid (*Martialia hyadesi*)	South Georgia	54% (occurrence)	Goa, Mah	Gonzalez and Rodhouse, 1998

capable of diving to depths in excess of 2000 m (Clarke, 1980), feed predominantly on cephalopods. Clarke (1980) identified the squid beaks obtained from 46 whales processed at South Georgia and a further 35 taken by the pelagic whaling fleet in the Antarctic and found the most important species to be *M. hamiltoni* (76% by weight) and *K. longimana* (17% by weight), both of which grow to large size. Beaked whales are also considered to be major cephalopod predators, but the diet of this group is poorly known (Goodall and Galeazzi, 1985). Cephalopods formed the main part of the stomach contents of a southern bottlenose whale stranded at Heard Island (Slip *et al.*, 1995). Other whales that are reported to take Antarctic cephalopods are the long-finned pilot whale (Clarke and Goodall, 1994) and the false killer whale (Alonso *et al.*, 1999), but the cephalopod component of the diet is relatively small.

6.2.4. Fish and other cephalopods

The shallow water Antarctic fish fauna is dominated by the notothenioids, the diets of which have been studied in reasonable detail around Kerguelen and the South Georgia/Scotia Sea area, but these rarely take cephalopod prey (see Kock, 1987, 1992). Deeper-living fish such as toothfish (*Dissostichus* spp.) and larger sharks such as the sleeper shark do take a significant quantity of cephalopods. Adult toothfish live at depths of 200–2000 m and take a range of cephalopod prey. At South Georgia, Xavier *et al.* (2002b) found that the diet of long-line and pot-caught adult Patagonian toothfish (*Dissostichus eleginoides*) included around 7% cephalopods (frequency). Octopods were the most frequently taken prey, but the squids *K. longimana, M. knipovitchi* and *G. antarcticus* contributed the bulk of the biomass consumed. Garcia de la Rosa *et al.* (1997) only found cephalopods in the larger (deeper) toothfish, with *K. longimana* the only species identified. At Macquarie Island, where cephalopods made up 32% (by mass) of the diet (Goldsworthy *et al.*, 2002), the main species taken was *G. antarcticus*. In the Ross Sea, Antarctic toothfish (*Dissostichus mawsoni*) also take cephalopods, but the cephalopod component has not been studied in detail (Fenaughty *et al.*, 2003).

Cherel and Duhamel (2004) investigated the cephalopod component of three shark species, taken as by-catch in commercial fishing operations at Kerguelen. All sleeper sharks (*Somniosus* sp.) examined (36) had cephalopod remains in the stomachs, with 18 species identified, the most important being *M. hamiltoni, Taningia danae, Kondakovia longimana* and *Architeuthis dux*. In porbeagle sharks (*Lamna nasus*) 20 out of 26 stomachs included cephalopod remains, with 15 species identified, the most important being *K. longimana* and *Todarodes* cf *angolensis*. Finally cephalopod remains were found in 12 out of 32 lantern shark (*Etmopterus* sp.) stomachs, with *M. psychrophila* the dominant species.

Squid frequently consume squid of their own (see earlier discussion) and other species. *Graneledone antarcticus* is a common component of the diet of *M. hyadesi* (Gonzalez and Rodhouse, 1998), with *P. glacialis* also taken.

7. PHYSIOLOGY

While the physiology of Antarctic fishes and other invertebrates has been studied in detail, the Antarctic cephalopods have received little attention, which probably reflects their low abundance, the difficulty of maintaining captive animals and poor capture rates. The only detailed physiological studies that have been conducted are on octopods of the genus *Pareledone* (Portner and Zielinski, 1998; Daly and Peck, 2000). Portner and Zielinski (1998) showed that the upper lethal temperature for *P. charcoti* is 10 °C, which is considerably higher than the ambient temperature.

Daly and Peck (2000) maintained *P. charcoti* in captivity, developed an energy budget and undertook comparative physiological studies with the northern octopus *Eledone cirrhosa*. The captive respiration rate of *P. charcoti* at 0 °C was low, but consistent with predictions based on *E. cirrhosa* respiration at 4.5 and 11 °C, and with no evidence of metabolic compensation for low temperature.

Bustamante *et al.* (1998) investigated the concentration of trace elements in *Benthoctopus thielei* and *Graneledone* sp. from Kerguelen and found elevated levels of cadmium, but low levels of zinc and copper. The source of the high levels of cadmium is not clear but appears to be derived from diet and the cadmium is likely to be transferred to higher predators, which also show elevated cadmium.

8. COMMERCIAL EXPLOITATION

As yet no Antarctic cephalopods have been subject to significant commercial exploitation. Squid fisheries usually target muscular species such as the ommastrephids (e.g., *Illex argentinus*) and loliginids (e.g., *Loligo gahi*), which support major fisheries on the Patagonian Shelf (Hatfield and Rodhouse, 1991; Waluda *et al.*, 2002). There are no loliginid squid in the Southern Ocean, but the two ommastrephid species, *M. hyadesi* and *Todarodes filippovae*, have been the subject of commercial interest.

Evidence from predators, particularly grey-headed albatross, suggests that *M. hyadesi* is abundant in the South Georgia and Scotia Sea area, but a series of short exploratory fisheries in the vicinity of South Georgia have produced mixed results. In February 1989 two Japanese jigging vessels undertook exploratory fishing near South Georgia, catching around 8 tonnes of *M. hyadesi* close to the APF, northwest of South Georgia (Rodhouse, 1991). Further fishing to the north and south of South Georgia and at Shag Rocks failed to catch any *Martialia.* In June 1996, 52 tonnes were taken along the shelf break north of South Georgia and Shag Rocks by the Korean jigger *Ihn Sung 101* (Gonzalez and Rodhouse, 1998), but the same vessel failed to catch any in January of the following year. In June 1997, 81 tonnes were taken, again on the shelf break north of South Georgia, whilst the most recent attempt in June 2001 caught just 2 tonnes (Dickson *et al.*, 2004), mostly in the area of the APF, but with some caught near Shag Rocks. Outside Antarctic waters, *Martialia* is taken in some years in the Falkland Islands jig fishery that targets *Illex argentinus* (Rodhouse, 1991). The appearance of *M. hyadesi* to the northeast of the Falklands appears to be related to the extent of the cold-water Falkland Current spreading over the shelf (Anderson and Rodhouse, 2001).

Given the abundance in predator stomachs, *M. hyadesi* is clearly seasonally abundant in the Southern Ocean, but to date the fishers have been less successful than the albatross at catching it. Should a fishery develop for *Martialia*, it would be overseen by CCAMLR and require careful management to avoid competition with the dependent predators (Rodhouse, 2005). Rodhouse (1997) estimated that higher predators take 245,000 tonnes of *M. hyadesi* in the Scotia Sea and proposed that any future fishery should have a limited season avoiding the sensitive chick-rearing period of the main predator, the grey-headed albatross.

Todarodes fillipovae is another muscular squid that may have fishery potential but that to date has not been subject to any directed fishing. Rodhouse (1998) appraised the potential for exploitation and considered the management implications. As with *M. hyadesi*, it would need to be carefully managed with full consideration of the impacts of dependent species.

9. DISCUSSION

The evidence from higher predators suggests that cephalopods play a significant role in the ecology of the Southern Ocean, linking macrozooplankton and fish with higher predators such as toothed whales, albatross and elephant seals. However, this review highlights the paucity of basic (distribution, ecology) data available for many species, and much of our knowledge of the cephalopods has come from predator studies. Pelagic cephalopods are notoriously difficult to catch, and as much of the sampling in the Southern Ocean has been undertaken with small scientific nets, catches have been small. The use of commercial-sized nets and jigs has been more successful in capturing mobile squid species, particularly the large adult forms.

The Southern Ocean cephalopod fauna is distinctive, with high levels of endemism, particularly in the octopods and with some of the main groups found in temperate and tropical areas absent. The squid typically occupy broad often circumpolar ranges, whilst the octopods show greater diversity, much of which is only now becoming apparent.

Problems still remain with the taxonomy of many of the groups, which require detailed systematic studies, most notably in the Brachioteuthidae. It has also been suggested that there is more than one *Psychroteuthis* species and that *Todarodes filippovae* may include more than one species. Considerable taxonomic confusion remains in the benthic octopods, although work (Allcock *et al.*, 2003a,b, 2004; Allcock, 2005) has started to resolve some important issues in the southwest Atlantic sector. As research extends into deeper water, it is likely that more new species will be captured.

The cephalopods are usually considered to have a "live fast and die young" semelparous life cycle, and while the Southern Ocean cephalopods conform to the basic semelparous pattern, the rather sparse data indicate that growth is considerably slower than equivalent temperate species. Even within the same species (*M. hyadesi*), there is some evidence of slower growth to the south of the APF than on the Patagonian Shelf. This slower growth, presumably accompanied by greater longevity, is a consequence of the low temperatures and the limited food supply outside of the productive but brief summer period. Despite the greater longevity, there is no evidence to suggest that Southern Ocean cephalopods are anything other than semelparous.

ACKNOWLEDGEMENTS

Thanks to Ian Rendall and Liz White for the illustrations in Figures 3, 4, 8 and 10; Peter Fretwell for producing Figure 1 and Jose Xavier for allowing the modification of his maps for Figures 5–8. Richard Phillips helped source information for the seabird predator section. Jose Xavier, Jon Watkins, Louise Allcock and an anonymous referee provided constructive comments on the manuscript. The photographs (Figure 2) were taken by Louise Allcock, Amanda Lynnes, Inigo Everson, Chris Gilbert and Paul Rodhouse.

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Effects of Shallow-Water Hydrothermal Venting on Biological Communities of Coastal Marine Ecosystems of the Western Pacific

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ADVANCES IN MARINE BIOLOGY VOL 50
0065-2881/06 $35.00
DOI: 10.1016/S0065-2881(05)50004-X

This review is based on integrated studies of the composition, structure and function of shallow-water ecosystems in the western Pacific that are influenced by underwater gas-hydrothermal activity. Most of the data were collected from 1985 to 1997 by the Institute of Marine Biology of the Far East Branch of the Russian Academy of Science during expeditions to zones of modern volcanism. Gas-hydrothermal activity of volcanoes has a great influence on the physico-chemical characteristics of the water column and plankton, and of bottom sediment and benthic communities. The abundance of nutrients (SiO_3^{2-}*,* PO_4^{3-}*,* NO_3^-*), gases (*CO_2*,* CH_4*,* H_2*,* H_2S*) and other reduced compounds (*C_nH_n*,* S_0*,* $S_2O_3^{2-}$*,* NH_4^+*) in zones of shallow-water hydrothermal vents provides conditions for the use of two energy sources for primary production: sunlight (photosynthesis) and the oxidation of reduced compounds (bacterial chemosynthesis). In areas of shallow-water volcanic activity, chemosynthesis occurs not only in the immediate vicinity of venting fluid release but also in the surface layer of the water column, where it occurs together with intense photosynthesis. This surface photosynthesis is found below the layer of chemosynthesis, which is related to the distribution of hydrothermal fluids at the water surface. The contribution of each of these processes to total primary production depends on the physical and chemical conditions created by the vents and on the range and adaptation potential of the organisms. On the seabed in zones of shallow-water venting, microorganisms form mats that consist of bacteria of various physiological groups, microalgae, the products of their metabolism and sedimentary particles. Oxygenic photosynthesis of benthic diatoms, bacterial photosynthesis (anoxygenic photosynthesis) and autotrophic chemosynthesis in algobacterial and bacterial mats generate organic matter additional to that produced in the water column. The high rates of primary production, abundance of organic matter in the water column and intense development of benthic microflora ensure the formation of an abundant benthic fauna. In Kraternaya Bight, Matupi Harbour and Bay of Plenty, the macrozoobenthos has low species diversity. The taxonomic composition of the populations is determined by geographical region (temperate or tropical), by the character of the seabed (hard or soft bottoms, rigid lava flows or hydrothermal structures), by the temperature of bottom sediments and of volcanic fluids and lastly by the chemical composition of the vent fluid (sulfide or nonsulfide). In most of the surveyed areas the fauna is derived from locally common species or from opportunistic species that can form high-density populations in eutrophic waters. The benthic communities of shallow-water venting areas have many characteristics in common with communities subject to anthropogenic impact (thermal, residential or industrial) or to changes resulting from a sharp deterioration of the marine environment. In contrast to the fauna of deeper water hydrothermal communities (i.e., those that exist below 200 m), shallow-water venting communities lack obligate hydrothermal species. The structure and function of the pelagic and benthic communities in* *areas of shallow-water venting can be regarded as transitional between those of deep-water vent communities and the normal communities of the coast.*

1. INTRODUCTION

The phenomenon of volcanism and related hydrothermal systems at the bottom of the deep sea has changed our traditional concept of the functioning of marine biological communities. There has been almost 30 years of research into zones of spreading, subduction and deepwater venting on the ocean floor. Investigations have been made on the biology, physiology and biochemistry of animal species and groups of bacteria-forming communities around the vents. The results of these studies concurrently with assessments of biogeochemical processes have been summarised in a number of reviews and monographs (Southward, 1987; Parson *et al.*, 1995; Van Dover, 1995; MacLeod *et al.*, 1996; Southward *et al.*, 1996; Tunnicliffe *et al.*, 1996; Van Dover, 2000; Van Dover *et al.*, 2002). It has been shown that in the absence of sunlight, bacterial chemosynthesis provides the base of the food chain in deep-sea hydrothermal communities, in communities at hydrocarbon and hydrogen sulfide seeps and more generally in reducing sediments.

Conversely, although volcanic activity was well known at shelf depths up to the middle 1880s, its influence on the marine biota was rarely mentioned (Zelenov, 1972; Kussakin, 1976; Gallardo *et al.*, 1977; Vidal *et al.*, 1978; Lukin, 1979; Stein, 1984). In 1985 shallow-water hydrothermal vents, together with bacterial mats and dense communities of benthic fauna, were found in Kraternaya Bight (Yankicha Island, Kurile Archipelago), located in the caldera of Ushishir Volcano (Tarasov *et al.*, 1985, 1986, 1988; Tarasov and Zhirmunsky, 1989). In subsequent years there has been a comprehensive study and analysis of the ecosystem of this bight (Tarasov *et al.*, 1990; Zhirmunsky and Tarasov, 1990, 1991; Tarasov, 1991a,b). Studies were extended to other volcanic areas of the Pacific: Matupi Harbour (New Britain Island, Papua New Guinea) and the Bay of Plenty (North Island, New Zealand) (Kamenev *et al.*, 1993; Tarasov *et al.*, 1993, 1998; Propp *et al.*, 1994, 1997; Miroshnichenko *et al.*, 1999; Tarasov, 1999).

Similar shallow-water hydrothermal venting has been found and studied off California (Kleinschmidt and Tschauder, 1985), New Zealand (Sarano *et al.*, 1989), off north Iceland (Fricke *et al.*, 1989; Olafsson *et al.*, 1991), in Kagoshima Bay (Kyushu Island, Japan) (Ossaka *et al.*, 1992; Hashimoto *et al.*, 1993; Miura *et al.*, 1997), in the Tyrrhenian and Aegean Seas (Abbiati *et al.*, 1994; Thiermann *et al.*, 1994, 1997; Dando *et al.*, 1995; Botz *et al.*, 1996; Fitzsimons *et al.*, 1997; Southward *et al.*, 1996, 1997; Cocito *et al.*, 2002), in the Bahia California Sur and on the Pacific coast of central Mexico

(Melwani and Forrest, 2003; Prol-Ledesma, 2003; Prol-Ledesma *et al.*, 2004), in Taiwan (Jeng *et al.*, 2004) and on the east coast of Papua New Guinea (Pichler and Dix, 1996; Pichler *et al.*, 1999a,b, 2000). In most of these studies the main attention was focused on the structure of the bottom communities and the distribution of benthos around the vents. The composition of vent fluids, the impact of volcanic venting on the marine environment, the production and breakdown of organic matter in hydrothermal zones have been described for the Mediterranean Sea (Dando *et al.*, 1999; Robinson, 2000).

The present contribution reviews the results of studies on the environment, microbiological and biogeochemical processes in the water column and bottom sediments, and the structure and distribution of biological communities in coastal ecosystems of the western part of the Pacific that are subject to hydrothermal impact. Original data were obtained during interdisciplinary expeditions to areas of present-day volcanism from 1985 to 1997 (Tarasov *et al.*, 1985, 1986, 1990, 1993, 1998, Borzenkov *et al.*, 1989; Kamenev, 1989, 1991a,b,c; Miroshnichenko *et al.*, 1989a,b, 1999; Shulkin, 1989, 1991, 1992a,b, 1995; Bonch-Osmolovskaya *et al.*, 1990, 1991, 1993; Bonch-Osmolovskaya, 1991; Namsaraev *et al.*, 1991; Namsaraev, 1992; Kamenev *et al.*, 1993, 2004; Sorokin *et al.*, 1993, 1998, 1994, 2003; Propp *et al.*, 1994, 1997; Kussakin and Kostina, 1996; Tarasov, 1999, 2002). Methods of measurement, sampling and analytical procedures have been published in special volumes (Tarasov, 1991a, b; Zhirmunsky and Tarasov, 1991; Gebruk, 2002). The aim of this review is to make these valuable contributions available to western scientists. (Editorial note: The author has compiled this review from a variety of Russian journals that appear to have different policies on the use of quantitative units. Some English-speaking workers may find gravimetric units unfamiliar, especially where they are mixed in one table with molar and volume units. It was felt that any rationalisation might introduce errors, so with one or two exceptions, the values are quoted here as originally published. The language used is U.K. English, except for substitution of sulfur and sulfide for sulphur and sulphide.)

The regions of current volcanic activity are related to convergent ocean margins, transitional regions between subduction zones and continents (Kennett, 1987; Selby, 1985). Active volcanic zones are found in island arcs where oceanic plates move under island chains. The greatest number of island arcs is located in the Pacific. Twenty-two island arcs form the Pacific "ring of fire," which contains three quarters of the total number of modern active volcanoes (Gushchenko, 1979; Marhinin, 1985). Two stages are usually distinguished in terrestrial and underwater volcanism: an active stage, with a plentiful output of solid products—pyroclastics and lavas—and post-volcanic processes, when volatile components transform rocks (Zelenov, 1972). At both stages the volcanic gas emissions, at temperatures from 50 to 800 °C, consist mostly of water vapour (88.0–99.6%); various gases such as H_2, HCl, HF, CO_2, CO, COS, N_2, NH_3, NH_4Cl, H_2S, SO_2, SO_3, CH_4 and C_nH_n, He, Ar, Xe form the remaining 0.4–12% (Naboko, 1959; White and Waring, 1961; Miyaki, 1969; Marhinin, 1985; Menyailov *et al.*, 1986). Along with the gases, Na, K, Fe, Al, Ca, Mg and Ti are found, as well as ore elements (including Fe, Cu, Zn, Cd, Ni, Pb, Ga, Sn) and elements of ultrabasic and basic magmas (Pt, Ni, Co, Mn), However, the ratios of water vapour/gases/metals by weight show the share of the last to be usually insignificant: 1,000:77:0.3 (Zelenov and Ivanenkov, 1982). In terrestrial volcanoes the volatile components are in part dissolved in the water vapour, in part adsorbed by explosive products, while a significant part disperses into the atmosphere. In underwater volcanoes practically all volatile components become dissolved in seawater (Zelenov, 1967, 1972).

The composition of gaseous emissions depends on the structure of the earth's crust, the stage of degassing of magma and its acidity. In gas jets, as the temperature decreases, the content of H_2, HCl and HF also falls, whereas the content of CO, CO_2, SO_2 and H_2S increases (Marhinin, 1985). Additionally, pressure and the proportion of vapour and liquid phases are important factors affecting the formation of gases and their ratio in the venting fluid. In subduction zones, the gas composition is also closely related to the products of metamorphism of sedimentary layers; the most common gases are CO_2, N_2, H_2S, NH_3, H_2 and CH_4.

The hydrothermal stage involves postvolcanic processes. It proceeds after eruption and the formation of breaks in the structure of the volcano. There are also thermal springs and steam-gas emissions that result from crustal rifting. The chemical composition of gas-hydrothermal fluids is determined by the depth of the volcanic core, the composition of the magma and sediments, by water filtration in the volcano and by the temperature of the gas phase. The most relevant factor affecting qualitative composition, content and properties of gas-hydrothermal vents is the origin of the water circulating in the volcanic structure. From the composition of oxygen and hydrogen isotopes, the water can be distinguished as juvenile, surface (atmospheric) or of marine origin. As a rule, juvenile water in fluids is an insignificant admixture (3–4%), and hydrothermal vents of terrestrial and shallow-water volcanism are mostly made up from water of surface and marine origin (Baskov and Surikov, 1975; Gavrilenko, 1997; Marhinin and Stratula, 1977). Penetrating into the volcanic core and intrusions, the water interacts with deeper emissions under conditions of high temperature and pressure. Boiling of the water and subsequent condensation of the steam phase results in differentiation of various elements and compounds and in enrichment of gas jets and the vent water (Krasnov and Sudarikov, 1990).

A hydrothermal system evolves over a long period. Its development can be divided into fumarole, solfatara and mofette stages (Zavarzin, 1984).

Fumaroles are characterised by high temperature (hundreds of degrees) and by emissions of dry gas. Solfataras are the sources of thermal solutions containing high concentrations of sulfur compounds. Mofettes, being the final stage of evolution of hydrothermal systems, are springs of low-temperature water saturated mostly with carbon dioxide.

Most hydrothermal vents range from thousands to tens of thousands of years in age, depending on the location of the magma intrusion in the upper layer of the crust. For example, a magma core 10 km^3 in size, lying in the top 10 km of the crust, heats up $\sim$100 km^3 of the crust to 200–400 °C. The lifetime of such a hydrothermal system is assessed as 10^5–10^6 years (Zavarzin *et al.*, 1989).

There are diverse classifications of hydrothermal vents, and various authors have chosen composition of gases, mineral composition and similarity of mineral associations, mineralisation, anion composition and relations between elements as criteria for their comparison (Naboko, 1970; Henley and Ellis, 1983; Kononov, 1983). The classification in which volcanic vents are characterised by composition of gases, anions and mineralisation is used most often. According to this classification shallow gas-hydrothermal vents of island arcs are united into one type: hydrogen sulfide-carbonic-chloride-magnesium-sodium (Kononov, 1983). In contrast, deep-water vents of the hydrogen sulfide-carbonic-chloride-magnesium-sodium type have a low content or complete absence of sulfate and magnesium, an acidic reaction, high concentrations of H_2, H_2S, CH_4 and enrichment of the fluid by alkali metals, alkaline-earth metals and heavy metals (Krasnov and Sudarikov, 1990). This classification defines the tendency of hydrothermal solutions to leaching and to formation of ore components.

According to a more simplified classification, terrestrial vents can be subdivided by composition of prevailing gases and temperature as follows: hydrogen; nitric-carbonic with high temperature; hydrogen sulfide-carbonic; and nitric and carbonic. The latter type prevails at the mofette stage of volcanism. Vents are also divided into acidic and neutral-alkaline. The acidic ones prevail at fumarole and at solfatara stages.

2. SHALLOW-WATER HYDROTHERMAL VENTS AND THE MARINE ENVIRONMENT

Shallow-water gas-hydrothermal vents emit gases and volcanic solutions at temperatures from 10 to 98 °C. They are formed in common volcanic centres as a result of interaction of seawater with underlying rocks of volcanic origin or with sedimentary deposits at high temperature (Figure 1). In the areas investigated, the duration of the gas-hydrothermal stage varies from 50 to

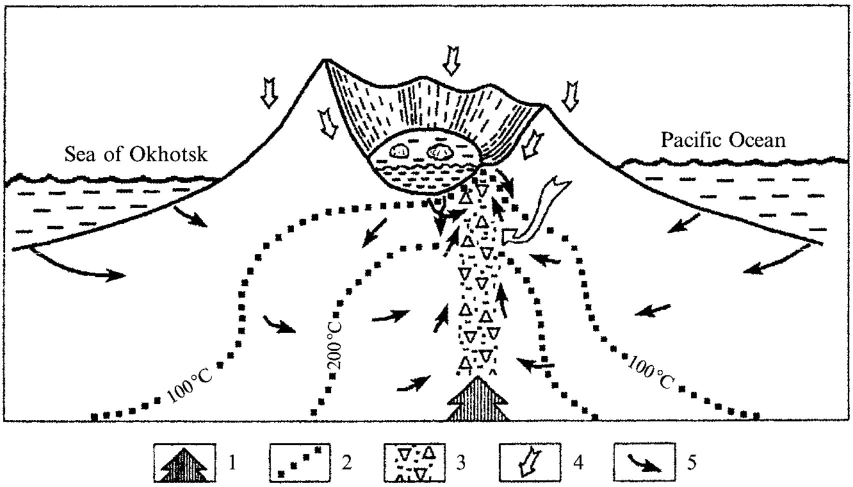

Figure 1 The hydrothermal system of Ushishir Volcano (Yankich Island, Ushishir Islands, Kurile Islands) (after Gavrilenko, 1997). (1) deep thermal fluid; (2) isotherms; (3) permeable beds; (4) atmospheric water; (5) infiltration of seawater into the volcanic structure.

10,000 years (Tarasov *et al.*, 1993; Gavrilenko, 1997). The vents contain a large quantity of gases (in free and dissolved forms: CO_2, N_2, Ar, H_2, H_2S, CH_4, C_nH_n), dissolved and particulate forms of metals and sulfur (Fe, Mn, Zn, Cu, Pb, Cd, Ni, Hg, S°), various anions and cations (Cl^-, F^-, HS^-, $S_2O_3^{2-}$, SO_4^{2-}, NO_3^-, PO_4^{3-}, SiO_3^{2-}, NH_4^+, Na^+, Ca^+, Mg^+) (Tarasov, 1991a, b; Tarasov *et al.*, 1993; Gavrilenko, 1997).

The vents can be divided into two basic groups: (1) those discharging hydrogen sulfide and (2) those that lack reduced sulfur compounds.

2.1. Hydrothermal venting in the flooded crater of a volcano and in a semi-enclosed bay

2.1.1. Kraternaya Bight

Kraternaya Bight is located in the crater of the active Ushishir Volcano, which is at the stage of gas-hydrothermal activity (Figure 2; Plate 1A). It has high and abrupt crater slopes and a narrow shallow inlet canal that protects it from the action of ocean waves and surf.

The diameter of the bight is <1 km; at the southern end, it is connected with the sea via a stony inlet that passes into a long, shallow and sandy channel. At low tide, this channel is only 30–40 cm deep and 50–70 m wide.

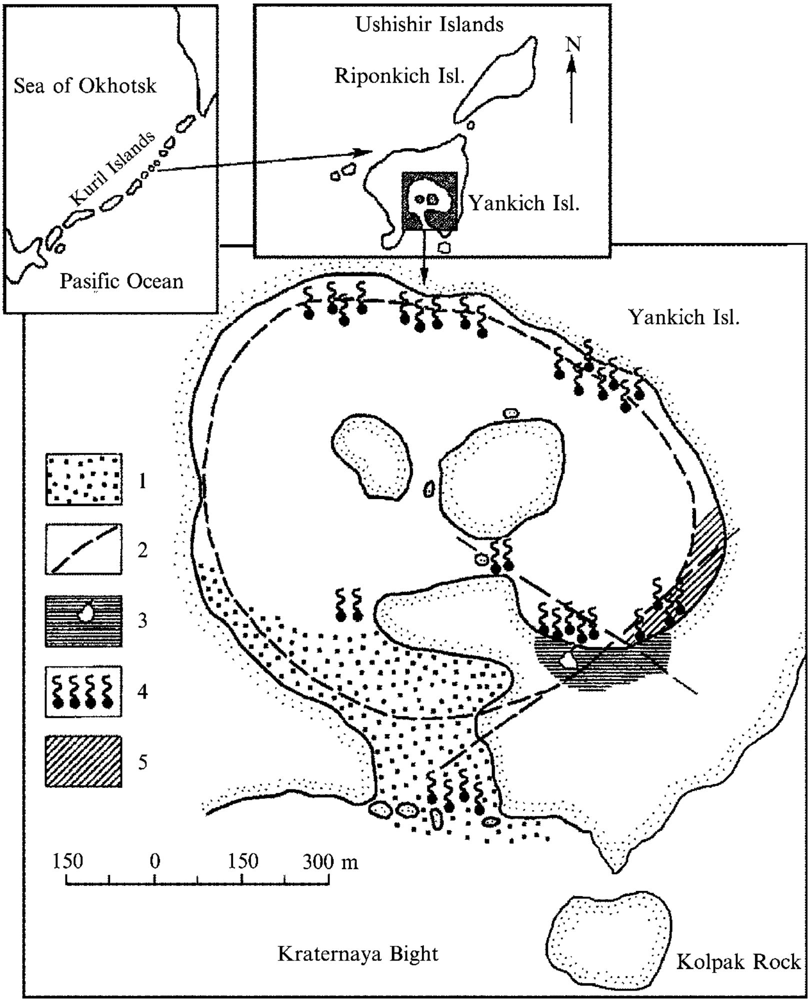

Figure 2 Kraternaya Bight (Yankich Island, Ushushur Islands, Kurile Islands). (1) sand bank and boulder in the channel to the bight; (2) circular and radial faults in the bight floor; (3) terrestrial hydrosolfatar field, fumaroles, boiling volcanic springs and volcanic brook; (4) areas of intertidal and sublittoral gas-hydrothermal vents; (5) areas of seeping volcanic fluid.

There are two islets in the middle of the bight that divide it into eastern and western basins, with maximum depths of 45 and 65 m, respectively. The channel opens to the south of the western basin (Figure 2). The average depth of the bight is 30 m.

The estimated date of formation of the bight in the volcanic crater is 7,000–9,500 years ago (Bondarenko, 1990, 1991). Present volcanic activity in the bay is related to ring and radial breaks, which exist under bottom deposits at the base of the volcanic structure (Bondarenko, 1986; Gavrilenko *et al.*, 1986, 1989, 1991). In 1987, Gavrilenko (1987, 1995, 1997) calculated the thermal capacity of the Ushishir Volcano as ~100 MWatt. The main portion of heat (90%) results from underwater volcanic activity. Calculations show that the output of underwater vents is $\sim 2 \times 10^4$ m^3 d^{-1}, while those on land emit $>1.7 \times 10^3$ m^3 d^{-1} (Gavrilenko, 1997).

Terrestrial volcanic activity is connected to a large solfatara field (150 × 100 m area) that consists of deep deposits of sulfur-cemented particles of clay, sand and metal oxides and spreads up the southeast slope of the caldera. The field surface is pierced by fumaroles (temperature >150 °C) and cracks, which emit gases and vapour. At the shore, the field ends in a steep wall of 1.5–2 m height and turns into a pebble beach. The beach surface and part of littoral zone are heated. In the southern part of the field, there is a pronounced depression, with some boiling "cauldrons" forming a small lake with temperatures of 96–98 °C. Hot water streams from the lake into the bight. The water temperature of this volcanic brook is 80–85 °C in its upper reaches and ~35 °C at its mouth. The flow rate of the brook varies from 5 to 20 $l.s^{-1}$ in different years.

There are also areas of gas-hydrothermal venting in the southern, southeast, eastern and northern parts of the bight and individual vents of volcanic solution or gas in the littoral zone (Marhinin and Stratula, 1977; Tarasov *et al.*, 1985, 1990; Gavrilenko *et al.*, 1986; Tarasov, 2002) (Figure 2). In the northern part, the littoral vents have temperatures of 5–8 °C, whereas in other parts of the bight, their temperature varies from 15 to 55 °C. The hot springs (40–55 °C) are characterised by low pH (3–4) and contain hydrogen sulfide and other reduced compounds of sulfur. Hydrogen sulfide has not been detected in the cold springs.

The sublittoral gas-hydrothermal vents in Kraternaya Bight can be divided into two types: (1) rather cold (5–15 °C), located in the southern and northeast parts of the channel, and in the northern part of the bight at depths of 3–15 m on the seabed that extend more than 100 m (Figure 2); (2) hot hydrogen sulfide vents and zones of seeping volcanic fluids (temperature 40–60 °C) in the south, southeast and eastern parts of the bight at depths of 0–23 m (Figure 2; Plates 1B, 3B, 9A).

The chemistry of the vent fluids and overlying water is shown in Tables 1–4. All vent fluids are characterised by lowered salinity (10–25) and a high concentration of dissolved forms of metals, including Mn, Fe, Zn, Cu, Ni, Cd and Pb (Shulkin, 1989). The vent fluid concentration of dissolved iron and manganese is 230–1500 times higher than in the seawater outside the bight, while the concentration of other metals is 2.5–25 times

Table 1 Chemistry of vent water fluids in Kraternaya Bight

			pH	PO_4^{3-}	NH_4^+	NO_2^-	NO_3^-	SiO_3^{2-}	H_2S	Fe^{2+}	SO_4^{2-}
Locality, object	T, °C	Salinity	µM								mM
Terrestrial solfatara field:											
Boiling spring	92–98	24.80	2.88	1.0	70.8	0	0	3060	42	ND	1.51
Mouth of brook	30	28.20	5.01	0.5–1.0	56.0	0–0.1	0–1.7	3060	0	9.3	2.31
Intertidal (=littoral) vents:											
Southeastern	40–45	19.50–29.69	3.45–5.86	1.0–3.0	9.7–38.1	ND	ND	785–2060	0.1–40	3.0–112.9	13.35–17.16
Eastern	12	22.00	6.20	0.6	1.2	0.14	2.1	550	4	ND	ND
Sublittoral vents (depth 5–10 m):											
Southeastern, 5 m	20	32.15	7.76	12.0	23.2	ND	ND	ND	89	ND	26.50
Southeastern, 10 m	15	33.10	5.45	10.0	38.0	ND	ND	ND	214	ND	24.10
Eastern, 3 m	30	ND	5.56	12.4	10.9	ND	ND	450	1722	0	30.21
Eastern, 5 m	20	ND	6.11	3.5	13.3	ND	ND	132	90	0	36.93
North, 10 m	7.5	33.08	5.81	0	11.9	ND	ND	144	0	18.3	25.09

ND – no determination; minimal and maximal values are given where available.
Data from Tarasov *et al.*, 1985, 1993; Propp *et al.*, 1989; Propp and Propp, 1991.

Table 2 Temperature and content of free gases (in % volume) in fumaroles and vents in Kraternaya Bight

Locality, object	T, °C	O_2	Ar	N_2	CO_2	H_2S	H_2	CH_4
Terrestrial fumaroles	100	0	0.12	4.7	85.10	5.8	4.60	0.02
Littoral vents:								
Southeastern	42	0	0.50	24.5	70.80	3.9	0.01	0.008
Eastern	37	4.3	0.33	29.2	64.00	0.9	0.008	0.01
North	20	3.5	0.90	62.5	32.90	0	0.0002	0.006
In strait of the bight:								
Left shore	22	0.8	0.11	9.5	89.10	0	0.53	0.003
Right shore	38	3.2	0.60	55.1	41.10	0	0.001	0.007
Sublittoral vents (depth 5–15 m):								
Southeastern, 5 m	35	0.2	0.07	7.3	92.00	0.9	0.02	0.02
Southeastern, 12 m	25	0.3	0.09	10.3	89.30	0	0.05	0.01
Eastern, 5 m	28	5.8	0.40	34.9	58.70	0.2	0.01	0.035
Northern, 10 m	15	0.4	0.20	46.3	35.00	0	0.001	0.008
Air in the bight	18	20.6	0.90	78.4	0.05	0	0.0005	0.0015

Data from Gavrilenko *et al.*, 1986, 1989, 1991; Tarasov *et al.*, 1993; Gavrilenko, 1997.

Table 3 Content of dissolved gases (ml l^{-1}) in terrestrial springs and vents in Kreternaya Bight

	O_2	Ar	N_2	CO_2[a]	H_2S	H_2	CH_4
Locality, object			ml l^{-1}			nl l^{-1}	
Terrestrial solfatara field:							
Boiling springs	0.1	0.4	9.4	3.24	6.5	300	100
Middle part of brook	3.0	ND	7.7	0.32	2.5	ND	30
Littoral vents:							
Southeastern	0.8	0.5	2.6	6.50	6.8	150	100
Eastern	0.4	0.5	2.4	6.00	0.1	100	200
North	0.4	0.7	4.5	3.50	0	20	50
Sublittoral vents (depth 5–15 m):							
Southeastern, 5 m	0.1	0.4	0.9	6.50	1.5	1.5	15
South-eastern, 12 m	0.8	0.3	0.8	7.50	1.8	1.0	250
Eastern, 5 m	0.1	0.5	0.7	8.20	2.2	1.0	200
Northern, 10 m	0.5	0.1	4.5	3.50	0	0.6	30
Seawater off Yankich Island (background level)	6.8	0.3	6.3	0.25	0	0.1	50

[a] Free CO_2.

ND, no determinations.

Data from Gavrilenko *et al.*, 1986, 1989, 1991; Tarasov *et al.*, 1993; Tarasov, 1999.

Table 4 Chemistry of water masses in Kraternaya Bight

Locality	T, °C	Salinity	pH	O_2, ml l^{-1}	PO_4^{3-}	NH_4^+	NO_2^-	NO_3^-	SiO_3^{2-}	H_2S	pCO_2[a], 10^{-6} mm Hg	CO_2^b	Alk	SO_4^{2-}, g l^{-1}	Chlorophyll *a*, mg m^{-3}
					μM							mM			
Seawater off Yankich Island (background level)	3	34.00	8.05	7.2	2.2	0	0.05	28.9	55	0	500 ± 40	2.26	2.34	2.53	0.4
Kraternaya Bight															
Southern basin:															
Surface layer	11	33.20	7.30	14.5	0.5	0.4	0.2	10.4	81	up to 40	1850 ± 960	2.08	2.36	2.52	22.4
Intermediate layer	5	33.85	7.80	5.5	2.5	4.5	0.5	25.0	90	0	475 ± 188	2.30	2.32	2.57	0.5
Near-bottom layer	3	33.60	7.40	3.0	4.2	12.0	0.8	32.0	118	0	2350 ± 876	2.41	2.34	2.48	0
Western basin:															
Surface layer	9	33.40	7.90	12.5	0.4	1.5	0.1	5.0	64	0	770 ± 240	2.03	2.33	2.53	21.4
Intermediate layer	3	34.00	7.75	6.0	2.3	7.0	0.2	23.2	74	0	750 ± 143	2.23	2.34	2.54	1.3
Near-bottom layer	2	33.60	7.32	3.3	3.5	22.5	0.3	40.0	100	0	2373 ± 673	2.25	2.40	2.53	0

[a] Partial pressure CO_2.

[b] Total stock of carbonic acid ($CO_2 + HCO_3^- + CO_3^{2-}$).

Alk, total alkalinity.

Source: Data from Tarasov *et al.*, 1985, 1993; Propp *et al.*, 1989; Propp and Propp, 1991.

higher (Shulkin, 1989, 1991). In addition, the fluids contain ammonium, phosphorus compounds and abundant silicate (up to 3000 μmol). In some groups of terrestrial vents, nitrates and nitrites have been detected.

Carbon dioxide (30–90%) and nitrogen (10–70%) dominate the gaseous and dissolved gas composition in terrestrial and sublittoral vents. Hydrogen sulfide, oxygen, hydrogen, methane and heavy hydrocarbons helium and argon are minor components (Tables 2 and 3). In the southeast and eastern parts of the bay, most of the vents are characterised by the presence of hydrogen sulfide and by higher concentrations of CO_2 and H_2, compared to the other areas of hydrothermal venting in the bay.

A distinct stratification of salinity, temperature, pH, gas content, nutrients, dissolved organic matter (DOM), chlorophyll, particulate and dissolved forms of metals has been observed in the water column of the bight (Tarasov *et al.*, 1985, 1986, 1990; Gavrilenko *et al.*, 1989, 1991; Propp *et al.*, 1989; Shulkin, 1989, 1991; Gavrilenko, 1995, 1997; Tarasov, 1999). The stratification is maintained by spreading of buoyant hydrothermal fluid over the water surface, by rising water heated at break zones and hot bottom sites and by incoming ambient seawater during high tides. Because the ambient seawater surrounding the island is colder (2–4 °C) and more saline than the water in the bight (8.0–12.5 °C), incoming tides penetrate as a wedge beneath the bight water. This phenomenon produces surface ripples during high tide.

Results of measurements of physical and chemical parameters of water in various seasons and for several years show that the water column in the bay can be divided into three main layers: surface, intermediate and bottom (Tarasov *et al.*, 1985, 1993; Propp *et al.*, 1989; Propp and Propp, 1991; Tarasov, 1999). Table 4 shows measurements of vent efflux.

The greatest changes connected to hydrothermal venting are observed in the surface layer (0–2 m) (Tarasov, 1999). Water in this layer is warmer and slightly fresher and contains high concentrations of oxygen, chlorophyll *a* (Figure 3), carbonic acid, dissolved and suspended organic matter, and dissolved and particulate forms of metals (Tarasov, 1999) (Figure 4). Maximum values of CO_2 and O_2 are found in the surface layer over littoral and sublittoral gas-hydrothermal venting (Figure 5). In the southeast part of the bight, there are small amounts of hydrogen sulfide (2–40 μM), other sulfur compounds (e.g., $S_2O_3^{2-}$ up to 110 μM), ammonium (up to 20 μM) and methane (Figure 6). High concentrations of silicon (up to 1000 μM) occur in the uppermost surface layer.

In the summer, the water is oversaturated with oxygen (200%) in the 0–1 m layer, and an oxygen content of up to 15 ml l^{-1} has been measured. A threefold decrease of oxygen concentration occurrs at 5 m depth (Tarasov *et al.*, 1985; Propp *et al.*, 1989; Propp and Propp, 1991; Tarasov, 1999) (Figures 3 and 5).

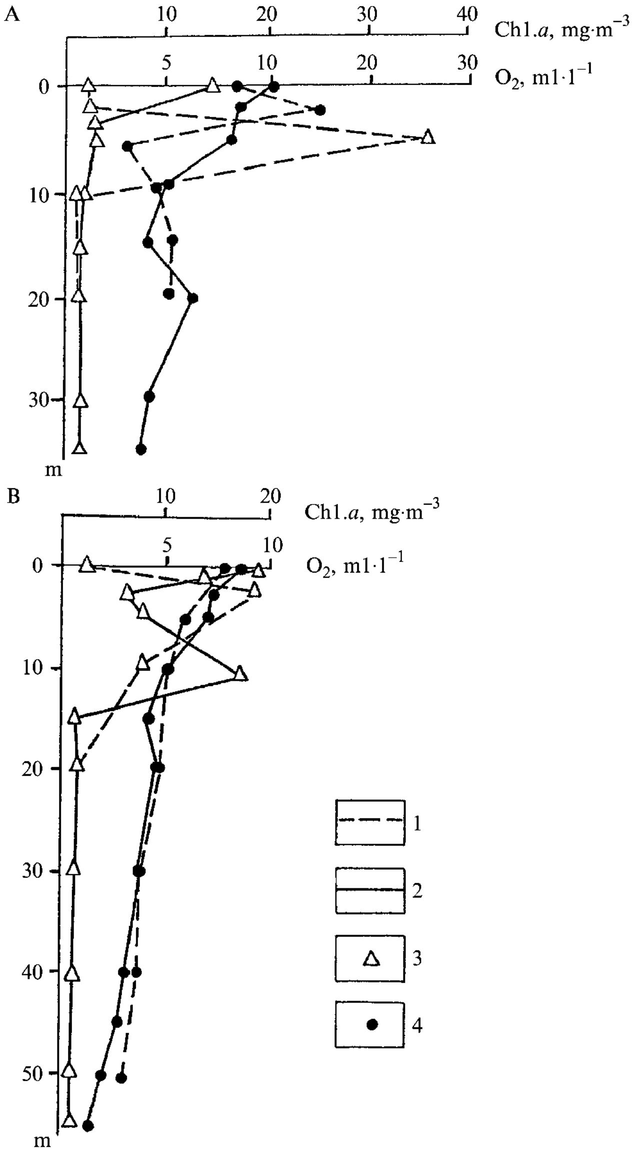

Figure 3 Chlorophyll *a* and oxygen in the water of Kraternaya Bight. (1) 1985; (2) 1986; (3) chlorophyll *a*; (4) dissolved oxygen. (A) eastern basin; (B) western basin.

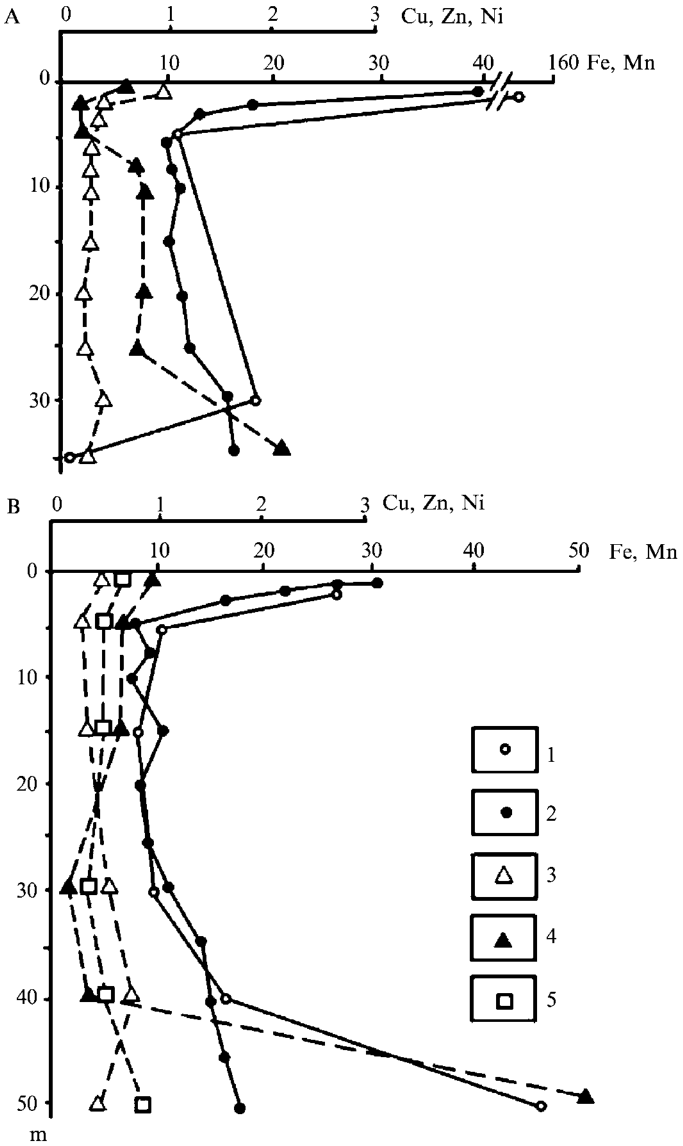

Figure 4 Dissolved metals (μg l^{-1}) in the water column of Kraternaya Bight. (1) iron; (2) manganese; (3) copper; (4) zinc; (5) nickel. (A) eastern basin; (B) western basin (after Shulkin, 1991).

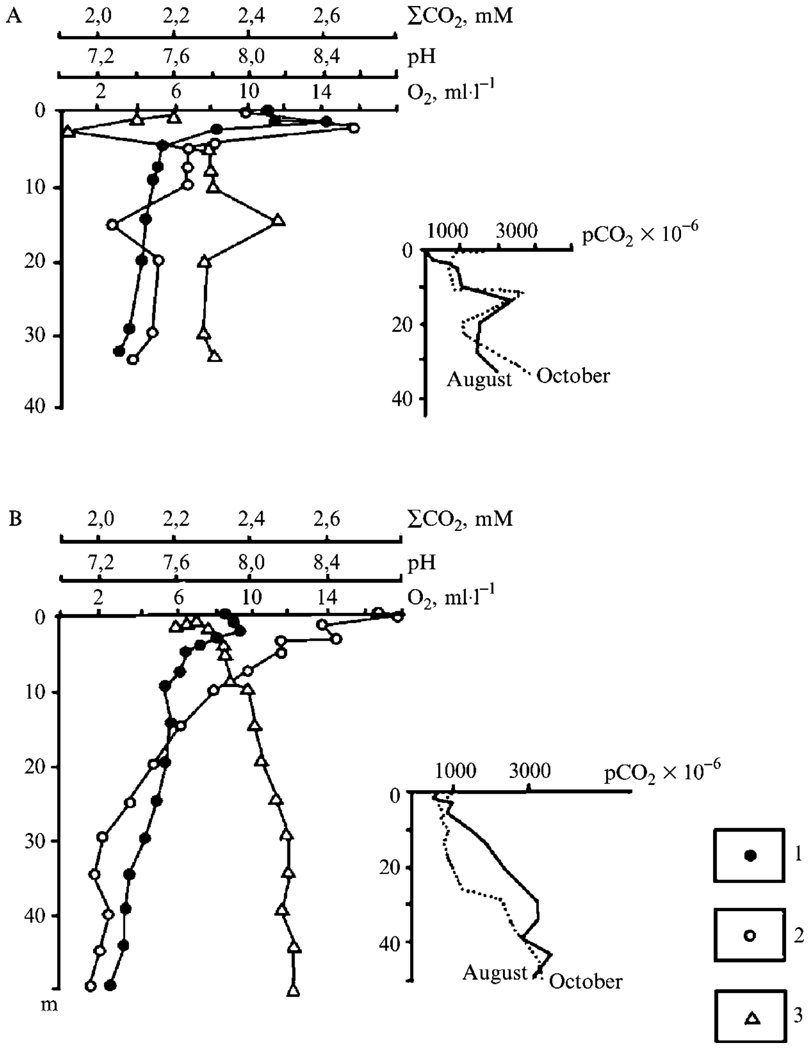

Figure 5 Oxygen concentration (1); pH (2); total alkalinity (3) and partial pressure of CO_2 (inset) in the water column of Kraternaya Bight. (A) eastern basin; (B) western basin.

Appreciable acidity is a characteristic of the bight water, as compared with ambient seawater. The acidity is related to high concentrations of carbonic acid emitted from the vents. Acidification of the water and high partial pressure of CO_2 are most pronounced in the 0–3 m layer of the eastern basin at 15 m (Figure 5). Coincident with lowered pH, hydrogen sulfide is

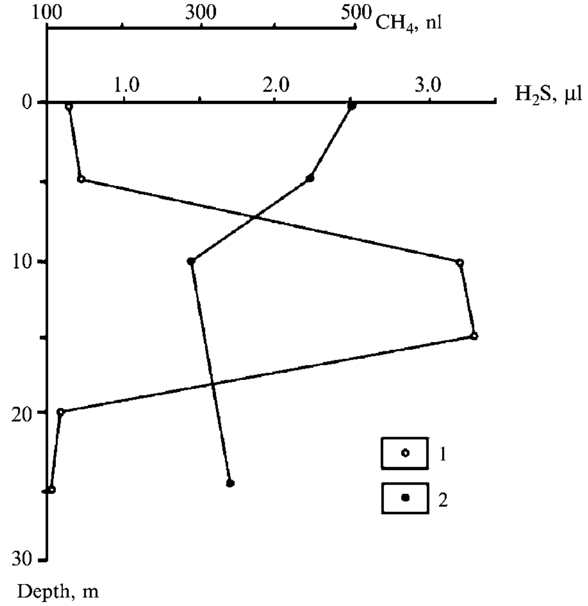

Figure 6 Concentration of hydrogen sulfide (1) and dissolved methane (2) in the water above sublittoral vents in the southeastern part of Kraternaya Bight.

present at concentrations of 0.05–0.41 μM in the surface layer and in layers <15 m. This is related to the input of volcanogenic carbon dioxide and hydrogen sulfide emitted from highly active vents located in the southeast part of the bay at depths of 15–22 m.

The boundary between the surface and the intermediate layers is at 3–5 m depth, following a temperature gradient of 2 °C/m^{-1}. The intermediate layer is located at 4–40 m. During high tides, ambient seawater spreads from the outer vicinity of Yankicha Island (Kondrashov and Danchenkov, 1991).

The increase of CO_2 concentration in near-bottom layers of the bay is determined by consumption of oxygen during breakdown of organic matter and metabolism of the bottom communities. Nutrient concentrations remain continuously high in the deeper layers, at least in summer and autumn.

The bottom sediments are mostly silt and silty-sand. The redox potential of the sediment surface varies from +57 to −128 mV at different sites, where there is a high content of organic matter (>4% of dry weight of the sediments) and high activity of sulfate reducing bacteria (up to 22 mM d^{-1}) (Karnachuk *et al.*, 1989, Namsaraev *et al.*, 1989, 1991; Namsaraev, 1992). However, hydrogen sulfide has not been recorded in near-bottom water or in the surface layer of the sediments (0–3 cm) (Propp and Propp, 1991; Tarasov, 1999), which are both oxygenated. Over the entire bay, the oxidising properties of sediments at the benthic boundary layer are affected by precipitating particulate matter containing high concentrations of metal oxides and hydroxides (e.g., Fe^{3+} was up to 220 $\mu g\ g^{-1}$ of dry weight of particulate matter) and by biogeochemical processes of transformation of various forms of metals with variable valency in the bottom sediments (Shulkin, 1989, 1991, 1992a, 1995; Tarasov, 1999).

2.1.2. Matupi Harbour

Matupi Harbour is in the northeast part of the ancient Rabaul Caldera, which is located on the north side of New Britain Island, Papua New Guinea (Figure 7). On the perimeter of the caldera walls, there are several extinct andesite-basalt volcanic structures together with three active volcanoes. Rabalanakaia and Tavurvur Volcanoes are at the fumarole stage, whilst active fissures are found at Sulfur Creek (Figure 7).

Matupi Harbour is a semi-enclosed basin of $\sim$4 km^2 area and 2 km diameter. Rabalanakaia and Tavurvur Volcanos are on the north and east coasts. On the south side, the bay is connected to Blanche Bay by a 1.5-km wide channel. Along the western part of this channel, there is large volcanic bank of 3 m depth, whilst the depth in the east part of the strait reaches 24 m (Figure 8). The average depth in the bay is 25 m, with a maximum of 65 m. Matupi Harbour is peculiar, being formed from two volcanoes, the eruptions of one them (Tavurvur Volcano) having occurred almost annually from 1937 to 1943. The last catastrophic eruption of Tavurvur Volcano, in September 1994, covered Rabaul City with ashes, and houses were destroyed by the accompanying earthquake. In the southwest part of the bay, in the channel, the shallow bank is a centre of intensive volcanic activity, and since 1973 the seabed has risen 14–17 cm yr^{-1} (McKee *et al.*, 1985; Greene *et al.*, 1986). Currents in the bay occur during low tide, with minor daily variations of water level (0.3–0.4 cm). A permanent current is absent.

Intense venting occurs along the eastern and northern coast of the bay. Up to 1990 only groups of terrestrial and occasional littoral vents were known (Ferguson and Lambert, 1972). The littoral and sublittoral vents of the harbour were surveyed in 1990 (Shulkin, 1992b; Tarasov *et al.*, 1993, 1999; Propp *et al.*, 1997; Tarasov, 1999).

There are emissions of gases and thermal fluids from the littoral and sublittoral zones down to 27 m deep in three areas of the bay, two of them close to Tavurvur and the other close to Rabalanakaia Volcano (Figures 7 and 8). Solitary vents occur, but more often emissions of gas bubbles and/or hot volcanic solutions arise from stiffened lava formations or bottom sediments.

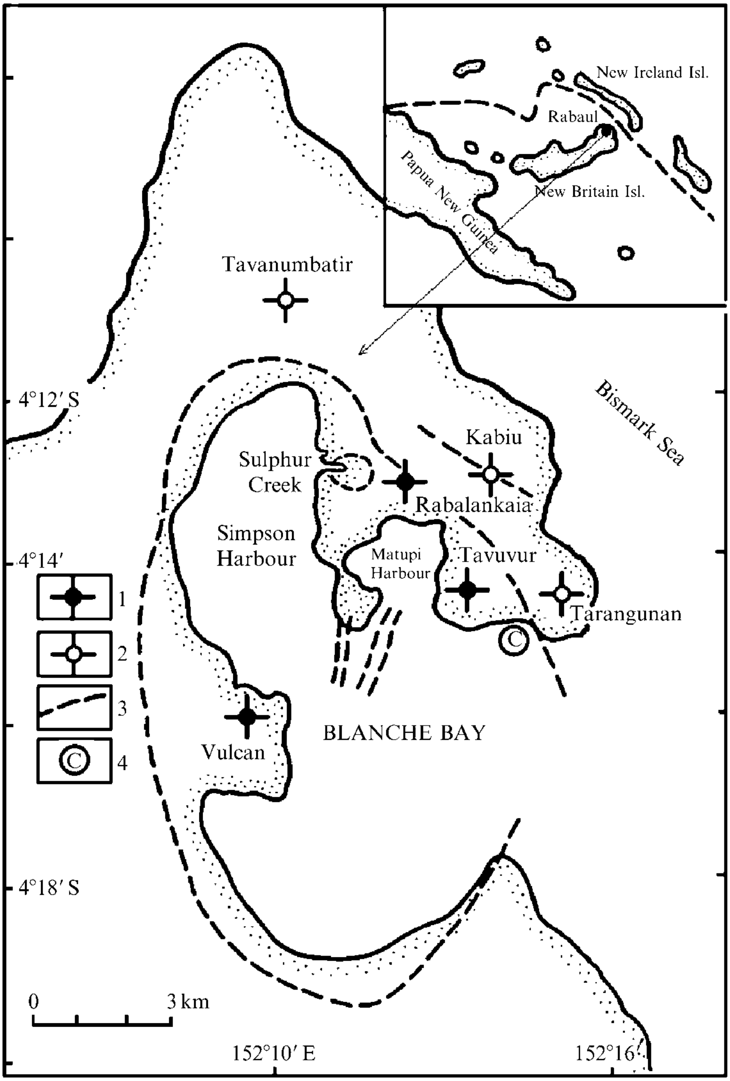

Figure 7 The caldera in Blanche Bay, Matupi Harbour, Papua New Guinea, and adjacent volcanoes. (1) active volcanoes; (2) inactive volcanoes; (3) volcanic faults; (4) control station where samples of gas, water, sediments, marine organisms were taken in 1990 (after Tarasov *et al.*, 1999).

At the eastern end of the bay, there are two areas of venting and sites of hot seabed covering 300–500 m^2, named Tavurvur I and II venting areas (Figure 8). Vents occur in littoral and sublittoral zones down to 10–12 m

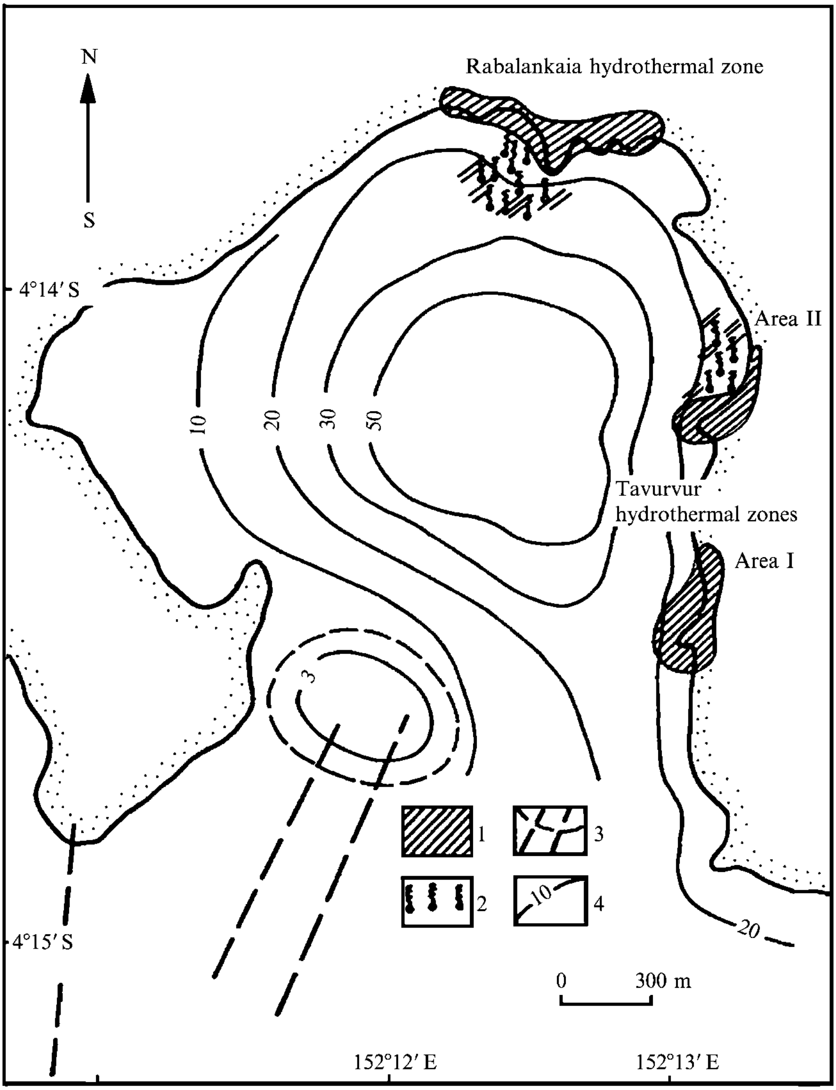

Figure 8 Areas of volcanic activity and hydrothermal venting in Matupi Harbour (Blanche Bay). (1) zones of hydrothermal activity and hot sediment; (2) sublittoral hydrothermal vents; (3) faults; (4) isobaths.

deep, with temperatures varying from 50 to 96 °C. Bottom gas emissions have not been found in Area I.

In the northern part of the bay, vigorous hot springs (temperature ~90 °C) extend over an area exceeding 1000 m^2, spreading from the upper intertidal zone (Plate 2A) to a depth of 27 m. This area, named Rabalanakaia venting area, is shown as Area III in Figure 8. Concurrently with gas-hydrothermal vents, sites of heated seabed (temperature 80–90 °C) can be found in all sublittoral zones.

Gases emitted from terrestrial, littoral and sublittoral vents consist mostly of carbon dioxide (70–94%) and nitrogen (2–30%), with hydrogen sulfide in some vents (Table 5). The gas has a comparatively high hydrogen content (up to 1%) and hydrogen sulfide content (up to 28%) (Obzhirov, 1992; Tarasov *et al.*, 1993; Tarasov, 1999). Methane did not exceed 0.05%, whilst heavy hydrocarbon gas levels were only 0.01–0.001% (Obzhirov, 1992).

Venting areas can differ significantly in metal content. In Area I the fluids were the most mineralised, acidic and enriched with metals, hydrogen sulfide and silicon. The metal concentration in the fluid forms a series: Mn → Fe → Zn → Cu → Pb → Cd, which is usual for acid hydrothermal solutions of andesite volcanism (Shulkin, 1992b). The peculiar trait in Matupi Harbour is dominance of manganese over iron, which makes the fluid composition similar to that of the vents in Kraternaya Bight. Because of the low pH in the vents, all metals enter the marine environment in dissolved form (Shulkin, 1992b). The hydrothermal fluids also contain abundant H_2S (up to 756 μM), NH_4 (42.5 μM), silicate and other nutrients (Table 6).

In Area II, vents are less acid and contain considerably lower concentrations of metals than in Area I. Nevertheless, enrichment of thermal fluids by metals was high and exceeded by two to three orders of magnitude the content of metals in Blanche Bay (ambient seawater). The increase of pH values in some vents causes hydrolysis of iron compounds; so only 27% of iron discharged into the bay is in dissolved form, the remainder being particulate (Shulkin, 1992b). Other metals are in the dissolved form. The H_2S content was 2–2.5 times lower in the littoral vents than in the vents of Area I. However, in assays collected from jets of sublittoral vents at 3–5 m depth, the H_2S content reached values of 756 μM. The silicon and ammonia content in thermal fluids of this area was also reduced (Table 6), but concentrations of phosphates and, to a lesser degree, nitrates (Propp *et al.*, 1997; Tarasov, 1999) were higher. The vents had low salinity, apparently caused by dilution of volcanic fluids with atmospheric water.

In the northern part of the bay, the pH values of vents close to Rabalanakaia are nearly neutral (6.8–7.2). The same series of metals occurs in these fluids as in other hydrothermal areas of the bay. The maximum concentrations of dissolved and suspended forms of metals occur in the surface and bottom layers (Figure 9). From their metal concentration, Rabalanakaia vents are at an intermediate position between Areas I and II of Tavurvur (Shulkin, 1992a). These vents are characterised by low concentrations of hydrogen

Table 5 Temperature and content of free gases (in % volume) in terrestrial, littoral and sublittoral gas-hydrothermal vents in Matupi Harbour

Locality, object	T, °C	O_2	N_2	CO_2	H_2	CH_4	C_2H_6	H_2S
Tavurvur zones:								
Terrestrial fumaroles 1	98	2.6	9.9	59.6	0.80	0.002	0.00040	27.9
Terrestrial fumaroles 2	98	1.6	6.6	91.3	0.20	0.022	0	ND
Littoral vents								
Area I	96	1.5	4.9	93.5	1.000	0.003	0	8.3
Area II	80	1.9	11.3	72.6	0.030	0.004	0.00001	14.2
Sublittoral vents Area II, depth:								
2 m	50	1.8	9.5	88.4	0.0020	0.008	0.00007	0
7 m	55	2.7	28.8	62.3	0.0006	0.010	0	6.0
9 m	60	2.8	17.7	72.4	0.0340	0.007	0	7.0
Rabalanakaia zone:								
Terrestrial fumaroles 1	96	1.6	2.9	93.6	0.20	0.040	0	5.9
Terrestrial fumaroles 2	101	0.5	2.2	91.3	0.90	0.020	0.00001	5.0
Littoral vents	90	1.4	8.2	90.3	0.001	0.008	0	0
Sublittoral vents, depth:								
7 m	90	2.9	14.1	82.7	0.1430	0.045	0	0
27 m	90	1.5	11.7	86.5	0.1543	0.040	0	0

ND, no determination.

Source: From Tarasov *et al.*, 1999.

Table 6 Temperature and chemistry of littoral and sublittoral vents in Matupi Harbour

				PO_4^{3-}	NH_4^+	NO_3^-	SiO_3^{2-}	H_2S		
Locality	T, °C	Salinity, ‰	pH	μM					SO_4^{2-}, g l^{-1}	pCO_2,[a] mm Hg
Tavurvur zone, Area I:										
Littoral	76	27.62	3.13	1.3	42.5	0.1	1940	127	5.01	ND
Littoral	55	34.54	3.56	0.5	13.2	0.3	925	0	ND	0.333868
Tavurvur zone, Area II:										
Littoral	41	32.01	6.02	12.3	26.2	5.1	608	51	2.89	0.109036
Sublittoral, depth:										
0.5–1.0 m	40	34.08	6.48	0.2	4.3	0.6	62	ND	2.89	0.027664
4.0 m	45	34.17	6.09	ND	ND	ND	ND	756	2.87	0.082156
Rabalanakaia zone:										
Littoral	90	31.80	6.23	1.6	26.5	1.3	1176	0	ND	0.279674
Littoral	56	30.85	6.17	2.5	23.8	1.7	1092	0	2.64	0.146200
Sublittoral, depth:										
25 m	42	34.53	6.60	3.1	2.7	2.9	587	0	2.87	0.024409
27 m	42	34.53	7.18	3.1	6.2	1.8	613	0	ND	0.005977

[a] Partial pressure CO_2.

ND, no determination.

Source: From Tarasov *et al.*, 1999.

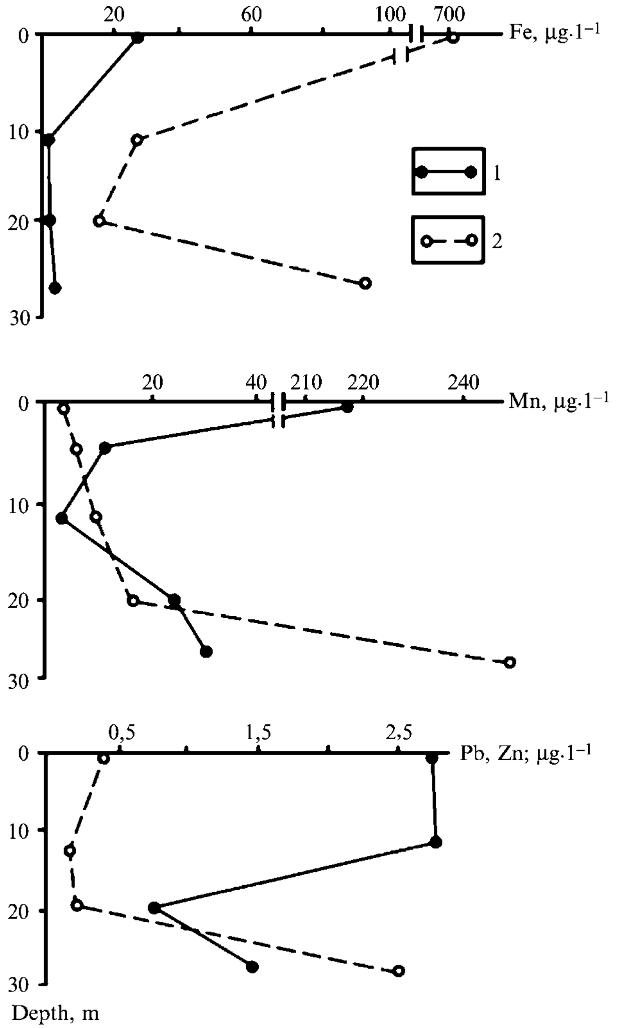

Figure 9 Concentration of dissolved (1) and suspended (2) forms of metals in the water column of the Rabalanakaia vents zone of Matupi Harbour (after Shulkin, 1992b).

sulfide or its absence but still contain abundant silicate (up to 1.2 mmol) and high levels of other algal nutrients (Propp *et al.*, 1997; Tarasov, 1999).

In contrast to ambient seawater in Blanche Bay, the water column in the volcanic areas was very acidic because of a high concentration of free carbonic acid, which resulted in an increase of partial pressure of CO_2 above equilibrium pressure (Tarasov, 1990).

Matupi Harbour is physically similar to Kraternaya Bight. Both have the same semi-enclosed form with steep underwater slopes and an average depth of 25 m. However, Matupi Harbour is not a volcano crater. Venting occurs in zones of local breaks at the bases of the Tavurvur and Rabalanakaia Volcanoes. Because of the weakly pronounced temperature gradient in the water column, especially in the western and central parts of Matupi Harbour, the relatively small tidal range and the significant depth of the channel (20–25 m), water exchange with outside waters occurs in practically all layers of the water column, except for the top layer 0–1 m. Judging from the width of the channel (1.5 km) and from gas-chemical measurements in the water mass at the entrance to the Bay, the volcanic fluids are continuously carried out from the bay in the surface layer, independently of tide cycles.

The littoral and sublittoral vents show maximum gas content near the seabed. High amounts of hydrogen and hydrocarbons are found in the surface (0–1 m) and bottom layers inside the bay (Table 7).

Enrichment of the waters of Matupi Harbour by volcanic gases is of the same order of magnitude as in Kraternaya Bay. Hot fluids entering the waters of Matupi Harbour from the numerous vents are mostly derived from seawater circulating in the volcanic structures. They contain abundant metals and nutrients (Obzhirov, 1992; Shulkin, 1992a; Propp *et al.*, 1997; Tarasov *et al.*, 1999). As a result of the distribution of warm waters, the water column of the bay is stratified. The highest concentration of dissolved and suspended forms of metals, 3–1,000 times exceeding the background, is found in the surface layer along the east and north coasts of the bay (Tarasov, 1999).

The impact of volcanic venting is most pronounced in the hydrochemical parameters measured at the east and northern parts of the bight, near the outlets of the vents and in the surface layer (Tarasov, 1999; Tarasov *et al.*, 1999). This can be recognised from the low pH values and from increased levels of carbon dioxide, sulfates, silicate and algal nutrients. The central part is characterised by very low concentrations of phosphorus and nitrogen compounds. The nutrient levels (PO_4^{3-}, SiO_3^{2-}, NH_4^+, NO_3^-) in the surface layers are influenced by the non-uniform distribution of thermal fluids and by their poor mixing with waters of the bay. Hydrogen sulfide in the water column was recorded only in Tavurvur hydrothermal fields. Levels of chlorophyll *a* were low and comparable to those in typical mesotrophic waters (Table 8).

In contrast to Kraternaya Bight, and because of the effect of vigorous hydrothermal venting, two types of hydrothermal formations can be recognised in volcanic areas of Matupi Harbour: ferriferous crusts, depleted in manganese and especially zinc, copper and other metals; and ferri-manganese-silicon ring structures (Tarasov *et al.*, 1999), containing also a lot of lead and zinc (Table 9). In these areas the bottom deposits are enriched with

Table 7 Dissolved gases in water masses and bottom sediments in Matupi Harbour

		O_2	CO_2	N_2	H_2	CH_4	C_2H_6
Locality, object	Depth, M	ml l^{-1}			nl l^{-1}		
Matupi Harbor Central part:							
Surface layer	0–1	4.0	0.21	8.2	158	200	ND
Near-bottom layer	55	3.0 ± 0.2	0.19	9.6 ± 0.5	34	508 ± 170	50 ± 10
Sediments, 0–10 cm layer	50	ND	5.5	ND	115,000	3162	522
Eastern part:							
Surface layer	0.2	3.9 ± 0.3	2.8 ± 1.5	10.0 ± 0.5	168 ± 45	340 ± 41	118 ± 17
Near-bottom layer	8	4.3	0.24	9.9	130	222	230
North part:							
Surface layer	0.2	3.1	5.6	9.0	312	800	30
Near-bottom layer	27	4.4	0.2	10.5	80	200	185
Blanche Bay							
Control area	0–2	4.4	0.16	10.5	80	65	47

ND, no determination.

Source: From Tarasov *et al.*, 1999.

Table 8 Chemistry of water masses in Matupi Harbour

					PO_4^{3-}	NH_4^+	NO_2^-	NO_3^-	SiO_3^{2-}	H_2S		CO_2[b]	Alk		
Locality	T, °C	Salinity, ‰	pH	O_2 ml l^{-1}	μM						pCO_2,[a] 10^{-6} mm	mM		SO_4^{2-}, g l^{-1}	Chlorophyll A, mg l^{-1}
Matupi Harbour, Central part:															
Surface layer	30.2	34.2	7.8	4.5	0.03	0.7	ND	0.1	23.9	0	551	2.07	2.30	2.67	0.8
Near-bottom layer, 56 m	29.0	34.7	8.0	2.4	0.8	0.7	ND	5.1	26.0	0	609	2.30	2.30	2.74	0
Eastern part:															
Surface layer	30–50	34.2	6.5	3.2	0.8–3.8	5.7–13.0	ND	0.2–2.2	219	4.4	3000	2.40	2.38	2.87	0.6
Near-bottom layer	35	34.3	7.8	4.3	0.2–0.9	0.5–3.3	0.2	0.8–1.0	30–130	1.2	988	2.27	2.14	2.95	0.3
Northern part:															
Surface layer	40–50	34.3	7.4	4.0	0.1	0	0	0	153	0	3300	2.27	2.38	2.70	0.4
Near-bottom layer, 27 m	32	34.5	7.5	3.8	0.4	2.7	0.2	2.0	30	0	1030	2.18	2.30	2.66	0.2
Blanche Bay, Control area:															
Surface layer	28.7	34.7	8.2	4.5	0.1	0.5	0	1.1	1.8	0	339	2.02	2.34	2.67	0

[a] Partial pressure CO_2.

[b] Total stock of carbonic acid ($CO_2 + HCO_3^- + CO_3^{2-}$).

Alk=total alkalinity

ND, no determination; minimal and maximal values are given where available.

Source: From Tarasov *et al.*, 1999.

Table 9 Metal content of suspended matter and bottom sediments in Matupi Harbour

			Mn	Zn	Cu	Pb
Locality, object	Metal form	Fe, %	$\mu g\ g^{-1}$			
Central part of the bight:						
Suspension in water column						
	1	2.05	0.51	238	35	8
	2	1.80	0.54	57	6	20
	3	5.65	0.08	108	31	36
	4	9.50	1.13	403	72	64
Bottom sediments, silt (0–5 cm)						
	1	1.15	0.79	105	7	6
	2	0.95	0.05	42	3	3
	3	9.31	0.15	166	43	20
	4	11.31	1.00	300	53	29
Tavurvur zone:						
Fe crust on the bottom	1	0.11	0.01	17	0.3	1
	2	0.63	0.01	11	0.6	0.1
	3	44.58	0.34	66	10	5
	4	45.32	0.36	94	11	6
Rabalanakaia zone:						
Fe-Mn ring-structures on the bottom						
a. Inner part ring-structure	1	0.04	0.10	17	2	0.1
	2	0.12	0.39	10	2	0.1
	3	13.11	0.07	177	22	242.0
	4	13.27	0.56	204	26	242.2
b. Outer part ring-structure	1	0.01	1.00	462	2	6
	2	0.62	50.36	758	10	29
	3	14.14	0.53	208	52	466
	4	14.76	51.89	1458	64	501

1 – highly mobile form, 2 – reduced form (bound with amorphous hydroxides and organomineral), 3 – lithogenous form, 4 – total of all forms.
Source: From Tarasov *et al.*, 1999.

lithogenic forms of Fe and Mn, apparently related to the breakdown and mechanical transport of particles containing metals from hydrothermal structures and their sedimentation to the seabed. Outside the zones of the direct effect of gas-hydrothermal vents, the enrichment of bottom sediments by metals appears to result principally from settlement of suspended matter out of the water column (Figure 9). Relative to Blanche Bay sediments, the Fe, Mn and Zn levels in bottom sediments of Matupi Harbour are 2–3 times higher, while levels of Pb and Cu are 1.5–2.0 times higher. The sediments can be classified as metalliferous (Shulkin, 1992c).

The bottom sediments of Matupi Harbour are notable for a high content of trivalent iron in the interstitial (pore) water and in the solid phase (Propp *et al.*, 1997). This, together with other physical, chemical and biological processes, determines their high redox potential and the absence of hydrogen sulfide in all layers of the bottom sediments from 0 to 36 cm (Tarasov, 1999). Different forms of manganese have an important role in the biogeochemical processes at Matupi Harbour. However, the role of Fe^{3+}, Fe^{2+}, Mn^{4+} and Mn^{2+} in the volcanic sediments and the pore water has yet to be studied.

2.2. Hydrothermal venting in open coastal areas

Open coast venting occurs in the Bay of Plenty (North Island, New Zealand). Volcanic activity in North Island and at two small volcanic islands in the Bay of Plenty (Whale and White Islands) has been known from the time of first settlement by Europeans in New Zealand. The Bay of Plenty is one of the largest bays (>200 km^2) in the northeast part of New Zealand and more than a half of its area is open to the ocean. The bottom of the bay is covered mostly with silty-sand and silt (Kohn and Glasby, 1978). Hydroacoustic surveys of the seabed of the Bay of Plenty at various depths between Whale and White Islands discovered several venting zones related to tectonic activity of the Rotorua-Taupo graben, which spreads through the central part of North Island and the Bay of Plenty in a northeast direction (Duncan and Pantin, 1969; Glasby, 1971; Lyon *et al.*, 1977; Hodkinson *et al.*, 1986; Sarano *et al.*, 1989; Menyailov *et al.*, 1991) (Figure 10; Plate 2B).

Whale Island is a volcano of Quaternary age. Hydrothermal activity has continued for >9000 years (Lloyd, 1974). On the south coast of the island, there are two small open bays, Sulfur Bight to the southwest and MacEwans Bight to the southeast (Figure 11). Both bights are widely cut into the coast of the island. The area of each is 0.5 km^2. The average depth is 5 m.

In Sulfur Bight underwater vents are found only in an area off the west cape at depths of 12–15 m. They are solitary gas vents of low flow rate protruding from the seabed, which is covered with coarse-grained sandy sediments and boulders. The temperature of the bottom sediments and vent water was 18 °C and did not differ from ambient seawater temperature. Hydrothermal vents were not found (Tarasov, 1999).

In MacEwans Bight, numerous gas-hydrothermal vents occur in its central part at depths from 3 to 12 m (Figure 11). The vents are located on fine-grained silty-sand, at densities of 15–20/m^2 of seabed. The temperature of the bottom sediments reaches 55 °C.

The largest centres of volcanic activity in the shallow-water area of Whale Island are ~1–2 km south of the coast, at depths from 20 to 45 m (Figure 11). There are two volcanic circular depressions (volcanic craters) in silty-sand

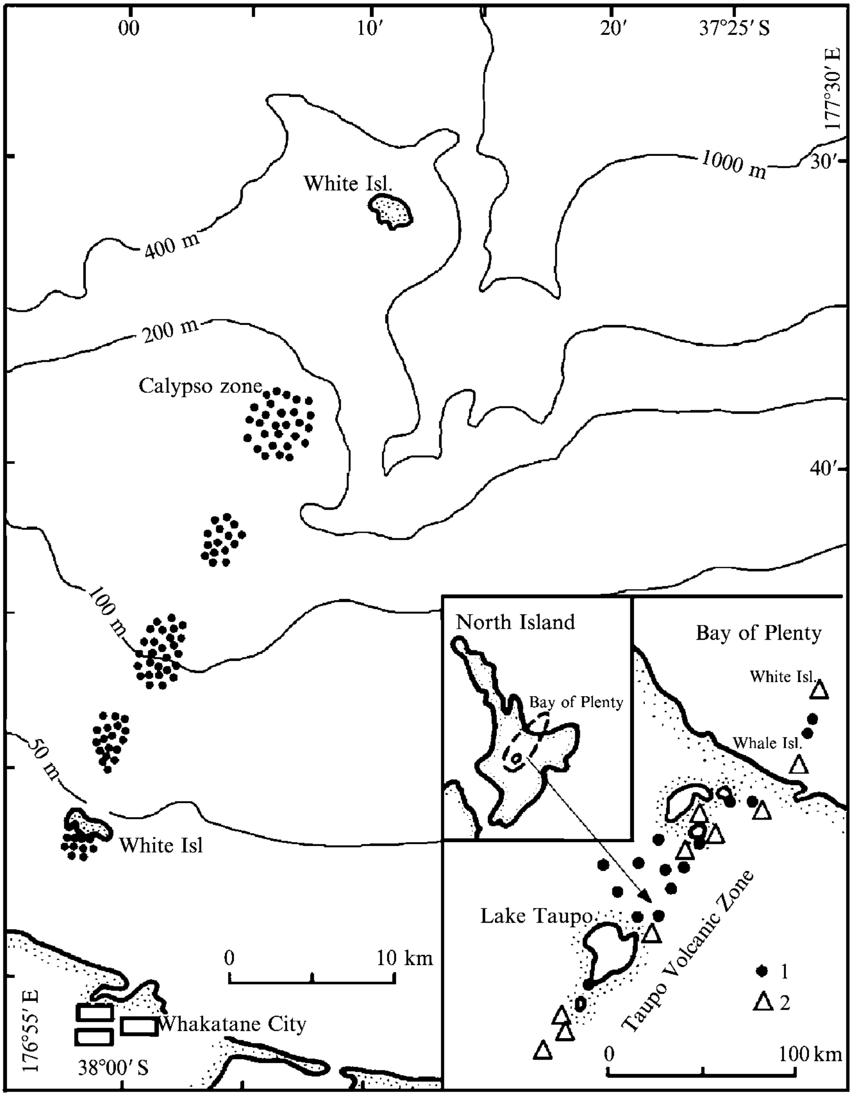

Figure 10 Areas of volcanic activity and underwater gas-hydrothermal vents in the Bay of Plenty, North Island, New Zealand. (1) vents, (2) volcanoes.

sediments, <1 km apart. The west crater is 500–600 m in diameter and its depth below the surrounding seabed is 25–30 m. The east crater, which has more vigorous volcanic activity, is ~1 km in diameter with a depth of 15–20 m. The bottom of the crater deepens gradually from its margin towards

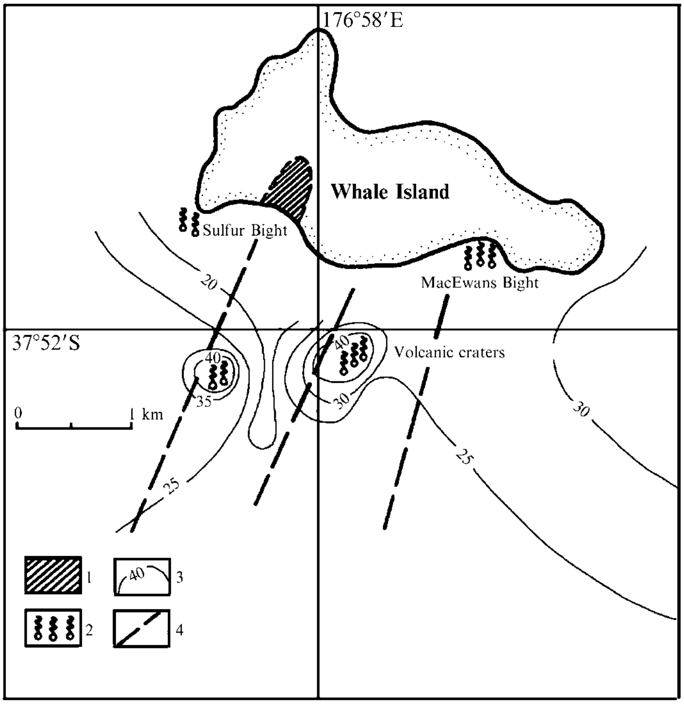

Figure 11 Areas of gas-hydrothermal venting in coastal water at Whale Island, Bay of Plenty. (1) terrestrial hydrosolfatar field and volcanic springs, (2) areas of underwater gas-hydrothermal vents, (3) isobaths in metres, (4) volcanic faults.

the centre, but close to the centre the depth drops sharply forming almost vertical walls. The craters have high sediment temperatures (up to 86 °C) and abundant gas emissions, in which carbon dioxide, nitrogen and methane dominate (Lyon *et al.*, 1977; Menyailov *et al.*, 1991; Tarasov *et al.*, 1993).

Hydrothermal venting in the Whale Island area is linked to several fractures, which run in basement rocks under seabed deposits and cross the island in a northeast direction (Kibblewhite, 1966; Duncan and Pantin, 1969; Glasby, 1971; Menyailov *et al.*, 1991) (Figure 11).

Between Whale and White Islands, there are four other areas of volcanic activity at depths from 50 to 200 m (Duncan and Pantin, 1969; Glasby, 1971; Sarano *et al.*, 1989; Menyailov *et al.*, 1991), the most extensive of which is located 15 km southwest from White Island at depths of 150–170 m; its position is 37 °38.06′S and 177 °05.92′E. This area is called Calypso after the French research vessel of the same name, from which F. Sarano *et al.* (1989) conducted seabed research in a manned submersible. On a silty bottom at 167 m depth, these workers observed many gas emissions. There was a

Table 10 Temperature and content of free gases (in % volume) in terrestrial and sublittoral gas-hydrothermal vents in volcanic areas of Whale Island

Locality	T, °C	O_2	Ar	N_2	CO_2	H_2	CH_4	C_2H_6
Terrestrial fumarole	97	0.20	0.04	4.55	88.79	1.370	4.99	0.05
Terrestrial fumarole	96	0.81	0.07	7.15	88.52	0.47	2.94	0.05
Sublittoral vents:								
Sulfur Bight	18	ND	ND	53.90	21.60	0.003	8.50	0
MacEwans Bight	35	ND	ND	7.10	81.70	0.020	9.20	0.09
Volcanic crater	81	ND	ND	5.30	83.40	0.030	9.40	0.81

ND, no determinations.
Source: From Tarasov *et al.*, 1999.

gypsum dome of 10 m diameter towering 6–8 m above the bottom, which emitted hot volcanic fluid (temperature was not measured), and gas. The dome was inhabited by numerous sponges, hydroids, anemones, corals and starfishes (Sarano *et al.*, 1989).

Analysis of gases emitted from terrestrial and littoral gas-hydrothermal vents at Whale Island shows that they are mostly carbon dioxide, with appreciable amounts of methane and hydrogen; there is only slight variation in gas composition between vents (Table 10). Comparison of recent and older measurements shows that the composition of gas from terrestrial vents has hardly changed from 1974 to 1990 (Lyon *et al.*, 1977; Giggenbach and Glasby, 1977; Menyailov *et al.*, 1991; Propp *et al.*, 1992; Tarasov *et al.*, 1993).

Free gases in sublittoral vents, which rise as bubbles to the surface, include significant amounts of hydrocarbon components along with carbon dioxide (Table 10). This may result from transformation of organic matter in thermocatalytic reactions in deep hot bottom deposits or from microbiological processes in the shallower and cooler layers of the bottom sediments. The thermocatalytic transformation of organic matter is corroborated by high values of the CH_4:H_2 ratio and by the large quantities of ethane and other heavy hydrocarbons emitted from the vents (Propp *et al.*, 1992).

In MacEwans Bight, volcanic products affect the entire water column, because the venting area and flow rate are both high. This was manifested in the enrichment of the water by hydrocarbons, metals and, to a lesser degree, algal nutrients (mostly silicate and ammonium) (Tables 11–13). Hydrogen sulfide is found in low concentrations (up to 1.3 and 26 μM, respectively; Tables 13 and 14) only in some vent fluids at depths of 12 m and in pore waters of deep sediments (3–12 cm layer).

The basic traits of shallow-water gas-hydrothermal vents at Whale Island are high hydrocarbon content, high hydrogen content and high concentrations of

Table 11 Temperature, pH and content of some metals and compounds in vents and seawater in areas gas-hydrothermal activity of Whale Island, Calypso zone and outside of areas of volcanic activity of Bay of Plenty

			Fe	Mn	Zn	Pb	Cd	Cu	Ni	H_2S	NH_4	Si
Locality, object	T, °C	pH	$\mu g\ l^{-1}$									
MacEwans Bight:												
Sublittoral vents	30	1.6	49,000	1000	480	900	10	150	100	3.0	20	1360
Surface layer	20	8.0	$\frac{0.5}{4.7}$	$\frac{0.9}{0.4}$	0.4	$\frac{0.6}{0.1}$	0.06	ND	ND	1.3	0	ND
Near-bottom layer	28	7.9	$\frac{0.5}{12.3}$	$\frac{0.9}{0.6}$	0.4	$\frac{0.8}{0.6}$	0.04	ND	ND	ND	17	39
Calypso zone:												
Near-bottom layer	14	ND	$\frac{0.5}{0.1}$	$\frac{0.4}{0.1}$	0.6	$\frac{0.4}{0.1}$	0.07	ND	ND	0	ND	ND
Bay of Plenty:												
Outside of areas of volcanic activity	12	ND	$\frac{0.2}{0.1}$	$\frac{0.2}{0.1}$	$\frac{0.1}{0}$	$\frac{0.01}{0}$	$\frac{0.02}{0}$	ND	ND	0	0–0.5	4–6

Note: In numerator, dissolved form of metal; in denominator, suspended form. ND, no determination.

Source: From Tarasov, 1999.

Table 12 Content of dissolved gases in water masses and bottom sediments in areas of gas-hydrothermal activity of Bay of Plenty and for comparison in region of Challenger platform, Tasman Sea

		O_2	CO_2	N_2	H_2	CH_4	C_2H_6
Locality, object	Depth, m	ml l^{-1}			nl l^{-1}		
MacEwans Bight:							
Surface layer	0.5	ND	0.2	8.4	0	1950	80
Near-bottom layer	6	4.2 ± 0.1	0.2	10.2 ± 2.5	HO	2065 ± 114	85 ± 2
Volcanic crater:							
Near-bottom layer	30	4.2 ± 0.1	0.3 ± 0.1	10.0 ± 0.1	2500 ± 1100	30,680 ± 4700	4600 ± 432
Near-bottom layer	35	ND	0.3	9.6	5000	41,000	2000
Bottom sediments, silt, layer 0–10 cm	35	ND	174.0	ND	2000	100,000	1000
Calypso zone:	160	3.9 ± 0.2	0.2	10.4 ± 0.7	68 ± 21	1800 ± 114	32 ± 3
Challenger platform, Tasman Sea	400	4.1 ± 0.1	1.1 ± 0.6	10.6 ± 0.2	80 ± 40	33 ± 4	4 ± 1

ND, no determination.

Source: From Tarasov *et al.*, 1999. As mean and standard deviation.

Table 13 Chemistry of seawater and pore water in bottom sediments in areas of gas-hydrothermal activity of Whale Island, Calypso zone, and for comparison in the region of the Challenger platform, Tasman Sea

Locality, object	Depth, m	T, °C	Salinity, ‰	O_2, ml l^{-1}	pH	PO_4^{3-}	NH_4	NO_3^-	SiO_3^{2-}	H_2S	pCO_2[a] 10^{-6} mm Hg
						µM					
MacEwans Bight:											
Near-bottom layer	12	20	30	7.5	7.9	0.7	19.7	0.9 ± 0.1	118	1.3	543
Pore water	10	34.7	ND	ND	6.9	5.6	125 ± 29	8.5 ± 3.0	136 + 36	16.3 ± 5.5	10,400 ± 1300
Volcanic crater:											
Near-bottom layer	35	19	35.4	4.4	7.3	0.6	1.1 ± 0.4	3.4 ± 0.8	9.5 ± 2.3	0	1262 ± 320
Pore water	40	40–80	ND	ND	7.6	6.8 ± 0.4	155 ± 16	1.7	537 ± 23	ND	2690 ± 1200
Calypso zone:											
Near-bottom layer	160	10	35.1	4.3	8.04	0.6	0.5	12.5	5.9	ND	344
Challenger platform, Tasman Sea	20	18	35.4	4.0	8.0	0.1	0.5 ± 0.2	0	2.1	0	500 ± 40

[a] Partial pressure CO_2.

ND, no determinations.

Source: From Tarasov *et al.*, 1999. As mean and standard deviation.

Table 14 Some physicochemical characteristics of pore water in bottom sediments in areas of gas-hydrothermal activity of Whale Island

			Alk	PO_4^{3-}	NO_2^-	NO_3^-	NH_4^+	SiO_3^{2-}	H_2S			
Locality and depth	Eh, mV	pH	mM	µM						SO_4^{2-}, g l	$C_{org.}$, %	$\frac{Fe^{3+}}{Fe^{2+}}$
MacEwans Bight, depth 7 m												
Sediment depth (cm):												
0–3	+295	7.07	2.9	3.0	4.6	4.0	17	39	0	2.19	0.14	3.7
3–6	ND	6.70	4.0	4.6	3.2	4.0	79	77	0	2.71	0.07	2.4
6–9	+302	7.19	5.5	5.7	3.2	4.1	100	95	0	2.62	0.04	1.6
9–12	+358	6.62	6.2	7.4	2.3	3.9	125	109	0	2.62	0.05	1.0
MacEwans Bight, depth 12 m												
Sediment depth (cm):												
0–3	+249	6.99	2.8	3.0	3.3	13.8	46	46	0	2.71	0.24	6.7
3–6	+289	6.88	3.9	4.3	2.2	7.9	117	112	16	2.87	0.13	0.1
6–9	ND	6.90	4.1	4.5	2.2	3.8	158	186	7	2.75	0.13	0.6
9–12	+180	6.93	4.4	4.8	3.0	0.6	179	200	26	2.67	ND	ND
Volcanic crater, depth 35 m												
Sediment depth (cm):												
0–4	−59	7.71	3.2	3.1	1.7	1.7	95	553	0	2.67	0.94	0.2
4–8	ND	7.56	3.4	3.3	1.1	1.7	140	492	ND	ND	0.78	0.4
8–12	ND	7.27	4.6	4.7	1.1	ND	211	566	0	ND	0.75	0.4
12–16	−64	7.17	4.6	4.8	2.0	ND	250	635	ND	ND	0.57	0.3
16–20	−38	7.06	4.0	4 2	1.5	ND	306	635	0	ND	0.66	0.3
20–24	−20	6.62	3.5	4 1	1.6	ND	393	799	ND	ND	0.83	0.2
24–28	−12	7.13	5.2	5.4	0.6	ND	445	922	ND	ND	0.96	0.2
32–36	ND	6.47	4.6	5.9	1.6	1.2	451	922	ND	ND	0.96	0.3

ND, no determinations; Alk, total alkalinity.
Source: Data from Propp *et al.*, 1994.

heavy metals. This is apparently related to closeness of the magma core and the significant thickness of sedimentary deposits, through which the volcanic fluid seeps. The vents of Whale Island are considerably enriched with metals when compared to the gas-hydrothermal vents of Kraternaya Bight. The iron content is higher by two to three orders of magnitude, and zinc, lead and copper are two orders higher. The values are quite similar to those of the vents of Tavurvur Area I (Matupi Harbour). It might be assumed that local hydrothermal fluids could affect the gas-, geo- and hydrochemical composition of the seawater and bottom sediments over a large area. However, the data show that the effect of vents on the composition of seawater and bottom sediments in the coastal zone of Whale Island and in the Calypso area is localised to coastal shoals (MacEwans Bight) and small areas of the bottom layer (Tarasov, 1999). At these sites temperatures were high (up to 86 °C), and there was enrichment of water and bottom sediments by gases (CO_2, H_2, CH_4 and C_2H_4), and to a lesser extent, by nutrients and by some metals (mostly mobile forms of Fe and Mn) (Figure 12).

In the deeper and open areas of the Bay of Plenty (Volcanic Crater and Calypso Area), hydrogen and methane vary only in the near-bottom layer (Tarasov, 1999). This is especially notable in the bottom layer of Volcanic Crater, where methane and hydrogen reach very high concentrations (31 μl l^{-1} and 2.5 ml l^{-1}, respectively) (Propp *et al.*, 1992). Hydrogen sulfide was not detected.

The impact of venting on bottom sediments in the Bay of Plenty is shown by the high temperatures of the sediments (up to 86 °C), by gas bubbling out of the sediments and by precipitation of heavy metals (Table 15). These factors change the physical and chemical properties of the bottom sediments. Compared with the sediments of venting areas in Kraternaya Bight, the bottom sediments of Volcanic Crater have a carbon dioxide content two to three orders of magnitude higher, and hydrocarbon gas content several orders of magnitude higher. At the same time, the sediments have a low content of organic matter, with a maximum in the surface and deeper layers of the bottom sediments (Table 14).

Aleurite-pelitic sediments of Volcanic Crater show reducing conditions. Deeper in the sediment, Eh values increase from -59 up to -12 mV (Propp *et al.*, 1994). It is assumed that the redox potential depends on the available form of metals with variable valency (Fe^{3+}/Fe^{2+} and Mn^{4+}/Mn^{2+}) in pore water and solid phases of bottom sediments and is determined by flow rate, metal concentration in the hydrothermal fluids and by the transformation rates of the various forms of metals that undergo chemical and microbiological change. Hydrogen sulfide appears to be absent in the sediments (Table 14).

According to Sarano *et al.* (1989), the bottom sediments in the Calypso Area have a high content of carbon (up to 10% of dry weight of sediment)

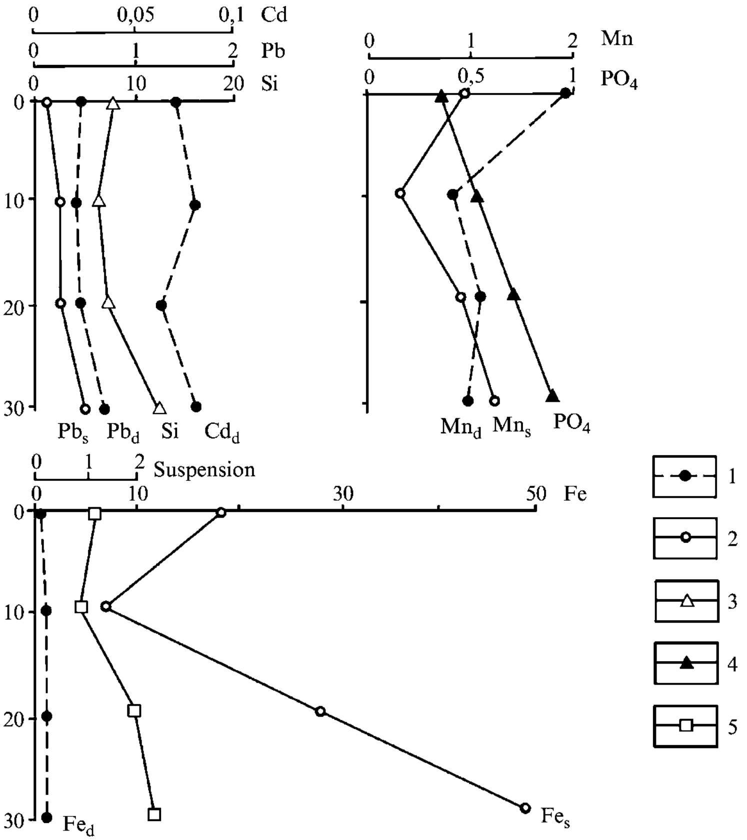

Figure 12 Vertical distribution of dissolved forms of metals (1, μg l^{-1}) and mobile forms of metals in suspension (2, μg g^{-1}) and silicon (μM l^{-1}), orthophosphate (μM l^{-1}) and suspension (mg l^{-1}) in the water column of Volcanic Crater, Whale Island. (1) dissolved forms of metals; (2) mobile forms of metals; (3) silicon, (4) phosphate, (5) suspension (after Shulkin, 1995).

and iron (5–7%), and high concentrations of arsenic (530 μg kg^{-1} of dry weight of sediment), antimony (150 μg kg^{-1}), mercury (90 μg kg^{-1}), uranium (138 μg kg^{-1}) and molybdenum (1,000 μg kg^{-1}). These abnormally high values appear to result from the proximity of the geothermal core to thick sediments and the very high temperature.

However, despite the intensive flow rates of gases and volcanic fluids, the impact of venting on the marine environment is quite local in character, related to hydrological conditions. The Bay of Plenty is crossed from north-east to south by a permanent current, whose speed can reach 3–4 km h^{-1} in the region of volcanic craters off Whale Island. During spring tides, the

Table 15 Metal content of bottom sediments in venting areas of Whale Island

Locality, object	n	Fe, %	Mn	Zn	Cu	Ni	Cr
			μg g^{-1}				
MacEwans Bight, silty-sand bottom	12	2.6 ± 0.4	789 ± 126	58 ± 5	8 ± 2	15 ± 1	25 ± 4
Volcanic crater, clay-silt bottom	6	3.3 ± 0.1	333 ± 36	69 ± 2	21 ± 1	24 ± 1	26 ± 2
Bay of Plenty	—	2.1	324	62	16	34	26

Source: Data for Bay of Plenty from Giggenbach and Glasby, 1977; the other two sites from Propp *et al.*, 1994.

speed of the current in the bay can reach 12 km h^{-1}. Wind waves and oceanic surf also affect water exchange.

2.3. Summary

In shallow-water gas-hydrothermal venting areas, the degree of enrichment of seawater by products of volcanic activity is determined by the gas content and chemical composition of the volcanic fluids, by the proportions of different gases, elements and their compounds in the vents, and by the flow rate, density, occupied area, and degree of openness or isolation of the water area, its depth and water dynamics.

The greatest impact of volcanic activity on the marine environment is seen in semi-enclosed bays such as Kraternaya Bight and Matupi Harbour, which have low water exchange with the open sea. Immediately adjacent to zones of venting, the seawater is enriched by products of volcanism, including gases, heavy metals, sulfur compounds, nitrogen, silicon, phosphorus and other elements. The concentration of such elements and compounds is hundreds or thousands of times greater than in normal marine basins.

Semi-enclosed bays become stratified because of tidal water exchange and differences in the physical and chemical properties of the surface and the underlying water layers. Water exchange with ambient seawater occurs mostly at intermediate and bottom levels of the water column. The distribution of seawater in bays depends on the strength of the tidal cycle and on the physical structure of the bays. In the bottom layer, physical and chemical conditions change under the impact of volcanic activity, precipitation of hydrothermal particles and digenetic transformations of organic matter in the sediments.

In open water areas (Volcanic Crater and Calypso Area, Bay of Plenty) with stronger currents, venting also has an impact on the bottom water layer and bottom sediments. In open shoal areas (MacEwans Bight), products of volcanic activity can be observed up to the water surface, as a result of the numerous vents and their high flow rate.

Carbon dioxide dominates the gas composition of vents and dissolves in the water to form carbonic acid. The water over the zone of venting contains so much carbon dioxide that some is released to the atmosphere as gas. High levels of hydrogen sulfide, hydrogen, methane and other hydrocarbon gases emitted in the vents cause increases in their concentration in the water column and sediments. A similar effect is observed for metals and compounds of volcanic origin. It is worth noting that in semienclosed waters where sulfide is venting, especially in Kraternaya Bight, part of the hydrogen sulfide is oxidised by chemical reactions at the surface, where there is a high concentration of oxygen (up to 200% saturation). However, the flow of hydrothermal fluids is so high that there is still some hydrogen sulfide remaining in the oxygen-saturated water at the surface.

The overlying water is enriched in algal nutrients by the hydrothermal fluids and their distribution in surface waters. In addition to this direct input from vents, there are three other sources of mineral substances for surface waters, related to volcanism and the physical form of the bays: (1) bottom regeneration of nutrients and their upwelling to surface layers of the water column, by vertical convective diffusion created by the heat of the volcanic core; (2) introduction of nutrients in ambient seawater during the rising tide; and (3) terrigenous input from the volcano slopes during and after rain.

Hydrothermal venting changes the conditions and properties of bottom sediments. The main bottom sediments in bays have hydrothermal or volcanic (periods of pyroclastic eruptions) origins. In open areas, the physical and chemical characteristics of soft bottoms change, resulting from the flow of gases and hydrothermal fluids through them. Key factors that determine the observed changes are temperature, gas bubbling through bottom sediments and biogeochemical redistribution of various forms of metals of variable valency.

The dissolved forms of metals released by vents in a neutral or alkaline environment are transformed to oxides and deposited with other particulates on the seabed. In zones of shallow water volcanic activity, there is a high content of metallic oxides and hydroxides both in suspension and in the surface layers of the sediments. The iron content (Fe^{3+}) in bottom sediments of the bights reaches exploitable ore concentration (>10% dry weight of the sediment); in zones of active venting it can reach 45% (Shulkin, 1989, 1991; Sazonov, 1991; Gavrilenko, 1997).

Redox conditions in the near-bottom and bottom layers are related to the flow of metals from vents, the availability of oxidised forms of iron and manganese (whose levels were much higher than those of other metals) in pore water and solid phases of bottom sediments and the biogeochemical transformations of metal species.

Shallow-water areas of hydrothermal activity provide chemical and ecological conditions that differ greatly from the relatively stable conditions of the chemical environment outside the venting areas.

3. PELAGIC COMMUNITIES

3.1. Phytoplankton

3.1.1. Kraternaya Bight

In Kraternaya Bight, the diatom *Thalassiosira anguste-lineata* dominates the phytoplankton. In the east part of the bight, where there is maximum impact of venting, the population density of *T. anguste-lineata* in some water layers can be 1.0–1.6 10^6 ind l^{-1}, with a biomass up to 40 g m^3 (Kharlamenko and Medvedev, 1991). In the centre of the east basin, the total biomass of this diatom in the entire water column has been calculated as 320 g m^{-2} in June 1990 (Sorokin *et al.*, 1993, 2003). These are record high values for marine ecosystems.

In summer-autumn, *T. anguste-lineata* is found at maximum density in the 3–5 m layer (Tarasov, 1999). Diatom cells accumulate at that depth predominantly under the pycnocline. In the uppermost layer (0–1 m), which is the layer most warmed and enriched by volcanic products, the density of microalgae is lower by one order of magnitude. At depths exceeding 10 m the density and biomass of phytoplankton sharply decreases.

In addition to diatoms, there is a planktonic ciliate *Mesodinium rubrum*, which contains endosymbiotic microalgae belonging to the cryptophyte genus *Chroomonas*, and this is a strong phototrophic component of the pelagic community of Kraternaya Bight (Tarasov *et al.*, 1985, 1986, 1993; Tarasov, 1999). This species of ciliate can be considered a primary producer (Sorokin and Kogelshatz, 1979). In the southeast part of the bight, in summer, the population density of *Mesodinium* can reach $1.6 \cdot 10^6$ cell l^{-1} at 2 m depth in the day (Nor, 1991), and the biomass may exceed 100 g m^{-2}.

The greatest aggregations of the ciliates occur at the end of July and in August. Their daily vertical migrations (Figure 13) produce "red tides" at the water surface (Tarasov, 1999). This phenomenon begins in the second half of the day, when red stripes appear on the water surface, which quickly (within 1 hour) merge into a single whole, with all the water surface becoming red-brown. "Red tides" caused by *Mesodinium* are known from zones of upwelling and in eutrophic shallow waters (Smith and Barber, 1979; Sorokin and Kogelschatz, 1979; Ratkova *et al.*, 1980; Lindholm, 1985; Orlova *et al.*,

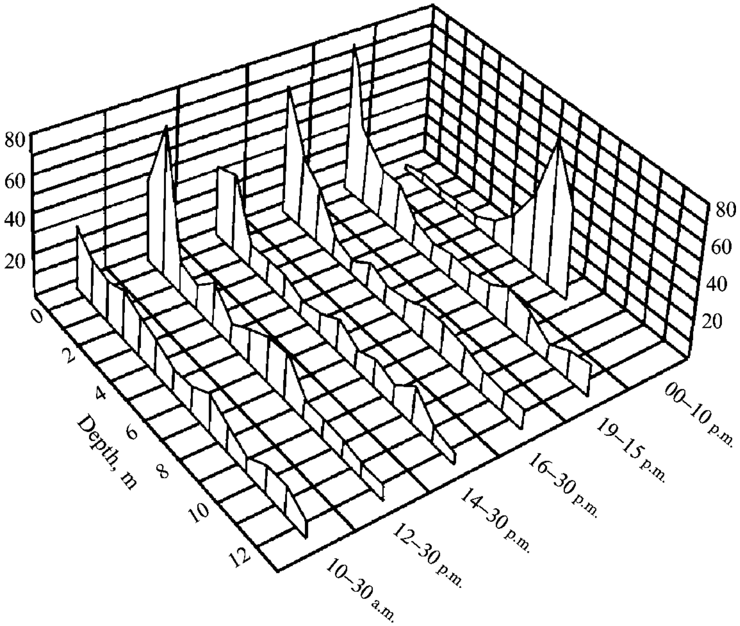

Figure 13 Daily vertical migration of the symbiotic ciliate *Mesodinium rubrum* (N 10^4 ind · l^{-1}) in the eastern basin of Kraternaya Bight; ordinates – number (N) of ciliates (after Tarasov, 1999).

1985; Tumantseva, 1985). For the first time, in 1985, this phenomenon was recorded in the zones of hydrothermal activity in Kraternaya Bight. In subsequent years, it was regularly observed during the summer (Tarasov *et al.*, 1985, 1986, 1990, 1993; Tarasov, 1999).

3.1.2. Matupi Harbour

In Matupi Harbour, the diatom *Chaetoceros vancheurckii* is abundant in the phytoplankton. In addition, there are cyanobacteria and small flagellates in appreciable quantities. The main population of these organisms is distributed below the surface layer at the boundary of the pycnocline and the mixing of hydrothermal fluids with waters of the bay. The highest population density of cyanobacteria and flagellates occurs in the bottom layers of the water column, close to venting: up to 24 thousand and 5 million cells l^{-1}, respectively, were recorded (Table 16). The total biomass reaches 30–60 mg m^{-3}, of which flagellates make up to 80–85% in some areas.

Table 16 Density and biomass (B, mg m^{-3}) of major groups of microplankton in Matupi Harbour

Depth, m	Nanophytoplankton				Total biomass of nanophytoplankton, mg m^{-3}	Bacterioplankton		Planktonic protozoa				Total biomass of protozoa, mg m^{-3}
	Cyanobacteria		Phytoflagellates					Zooflagellates and amoebas		Nonsymbiotic ciliates		
	N, 10^6 cell l^{-1}	B	N, 10^3 cell l^{-1}	B		N, 10^3 cell l^{-1}	B	N, 10^3 cell l^{-1}	B	N, cell l^{-1}	B	
Central part of the bay												
0	3.3	13	640	22	35	1425	413	480	8	500	10	18
5	4.2	13	1700	50	63	792	134	80	2	400	3	5
10	4	25	ND	ND	ND	864	163	100	4	400	4	8
20	ND	ND	1760	31	ND	580	230	100	2	400	5	7
30	ND	ND	ND	ND	ND	353	92	131[a]	7	ND	ND	ND
50	0	0	1200	18	ND	613	190	148[a]	6	250	5	11
Tavurvur vent field, Area I												
0	16.6	10	830	18	28	1156	347	140	4	770	6	10
14	24	12	2500	30	42	930	242	80	3	770	6	9
19	ND	ND	ND	ND	ND	837	176	80	3	350	3	6
Tavurvur vent field, Area II												
0	ND	ND	3300	33	ND	1512	635	430[a]	12	ND	ND	ND
15	ND	ND	ND	ND	ND	794	151	ND	ND	ND	ND	ND
21	13	9	830	16	25	980	235	100[a]	11	2300	13	24
Rabalanakaia vent field												
0	ND	ND	ND	ND	ND	485	107	ND	ND	ND	ND	ND
8	ND	ND	5030	49	ND	778	202	70	2	2300	14	16
14	1.7	7	800	25	32	856	231	60	2	250	3	5
18	ND	ND	ND	ND	ND	362	72	ND	ND	ND	ND	ND
23	ND	ND	ND	ND	ND	366	73	ND	ND	ND	ND	ND
Blanche Bay (control area)												
5	0	0	3800	37	37	427	84	160	5	300	8	13

N, number of cells.

ND, no data.

3.1.3. Bay of Plenty

In the Bay of Plenty diatoms dominate the water masses over the venting zone. They occur mostly in the surface layer. The population density of small phytoflagellates found in the surface layer varies from 10^3 up to 3×10^3 cells l^{-1} and biomass from 15 to 47 mg m^{-3}. In MacEwans Bight, phytoflagellates have not been recorded (Sorokin *et al.*, 1994).

3.2. Bacterioplankton

3.2.1. Kraternaya Bight

High population densities and biomasses of bacterioplankton (Table 17) occur in Kraternaya Bight. The bacterial cells are large (0.20–0.25 μm), twice the volume of bacterioplankton cells (0.13 μm) of the normal waters near the island. The maximum values of bacterial biomass occur in the east basin in the zone of venting. Their population density and biomass reaches record high values for marine and freshwater ecosystems at $4.73 \cdot 10^6$ cells l^{-1} and 1.13 g m^{-3}, respectively (Sorokin *et al.*, 1993, 2003).

The bacterioplankton number and biomass have similar values in the east and west basins and vary little with depth. In the uppermost layer, the density is $1.8–2.9 \cdot 10^6$ cells l^{-1}, with a biomass of 400–800 mg m^{-3}. At 50 m deep the corresponding values were $1.3 \cdot 10^6$ cells l^{-1} and ~300 mg m^{-3}, respectively (Table 17), which corresponds to the extremely high levels of bacterioplankton biomass found in certain eutrophic coastal seas.

The high values of bacterial biomass in Kraternaya Bight exceed the biomass of bacterioplankton recorded in outside waters by an order of magnitude. This high biomass is related to the presence of abundant dissolved organic matter (DOM) in the water column, especially near the surface. This DOM appears to be derived from the high densities of phytoplankton, the productive soft bottom communities (including sea grasses), and bacterial mats that develop near the vents. Additional DOM input may come from atmospheric and subsoil waters that flow down the slopes of the crater into the bight.

3.2.2. Matupi Harbour

In Matupi Harbour, the bacterial biomass is three to seven times greater than the biomass in coastal waters of Blanche Bay (Sorokin *et al.*, 1994). The population density of bacteria in Blanche Bay varies from $3.5 \cdot 10^5$ to $1.5 \cdot 10^6$ cells l^{-1}, with the maximum mainly in the surface layer, except for

Table 17 Density (N, cell l^{-1}) and biomass (B, mg m^{-3}) of major groups of microplankton, bacterial production and chemosynthesis (mg wet mass m^{-3} d^{-1}) in Kraternaya Bight

	Major groups of microplankton							Bacterial production per day			
	Bacterioplankton		Zooflagellates		Nonsymbiotic ciliates						
Depth, m	N, 10^6	B	N, 10^3	B	N, 10^3	B	Total biomass microheterotrophs, mg m^{-3}	Total	Heterotrophic	Chemosynthetic	Share of chemosynthesis in total bacterial production, %
Centre of the eastern basin											
0	2.90	760	140	7	3	20	787	285	276	9	3
7	2.87	746	100	4	14	210	960	306	306	0	0
12	2.81	731	50	3	6	72	806	238	238	0	0
18	2.88	580	30	2	16	100	696	151	151	0	0
25	1.48	237	20	1	2	15	253	122	122	0	0
Southeastern vent fields											
1	3.92	900	30	2	10	80	982	394	330	64	16
2	4.73	1130	100	4	12	130	1264	254	209	45	18

Area of mouth of volcanic brook											
0	2.84	540	100	2	4	30	572	204	138	66	32
2	2.70	513	80	1	4	30	544	ND	ND	ND	ND
4	2.77	500	<20	<0.5	6	40	540	ND	ND	ND	ND
7	2.75	496	<20	<0.5	<1	<5	500	308	204	104	34
12	2.51	450	<20	<0.05	3	20	470	235	84	151	64
18	2.12	317	<20	<0.05	<1	<5	318	194	56	98	51
25	1.47	176	<20	<0.05	<1	<5	177	198	120	78	39
1	2	3	4	5	6	7	8	9	10	11	12
Centre of the western basin											
0	1.82	387	700	24	26	250	661	134	134	0	0
10	2.20	507	60	2	15	120	629	208	192	16	8
20	1.76	335	80	3	3	24	362	78	78	0	0
30	1.45	290	210	7	4	24	321	13	13	0	0
40	1.28	240	50	2	14	10	252	8	8	0	0
50	1.29	258	400	16	6	35	309	9	9	0	0
Seawater near Yankich Island (background)											
0	0.51	67	80	2	1	12	80	16	16	0	0
8	0.49	64	60	2	2	10	76	28	28	0	0
25	0.52	68	60	2	2	10	70	14	14	0	0

the northern part of the bight (Rabalanakaia venting area), where most bacterial cells are at depths of 8–14 m (Table 16).

The highest abundance of bacterioplankton occurs in Tavurvur Area II, where biomass reaches 635 mg m^{-3}. Sorokin *et al.* (1994) have suggested that this is related to favourable environmental conditions for development of specific microflora, especially of sulfur bacteria in the presence of hydrogen sulfide as well as oxygen.

In Tavurvur Area I, as in the central part of Kraternaya Bight, the bacterial biomass is less but still high relative to normal coastal waters in the tropics, exceeding 300 mg l^{-1} in the top 3 m. The northern part differed from other areas of the bight by having lower values of bacterioplankton biomass, especially in the bottom and the surface layers (Table 16).

The bacterioplankton of Matupi Harbour, as in Kraternaya Bight, has larger than normal microbial cells, some two to three times larger than those developing in typical coastal tropical waters (Sorokin *et al.*, 1994). This may be related to the hydrogen sulfide enrichment of the surface layers, allowing greater development of sulfur bacteria. It has been noted that chemoautotrophic bacteria are often vacuolated, with the vacuole holding a reservoir of nitrate (Nelson and Fisher, 1995).

3.2.3. Bay of Plenty

In open volcanic water areas around Whale Island (Bay of Plenty), the number and biomass of bacterioplankton varies little with depth. In the Calypso area, the values increase slightly in the surface layer (Tables 18 and 19). Over shallow areas (up to 40 m), the bacterial biomass reaches 200–300 mg m^{-3} in various layers of the water column. In MacEwans Bight, the bacterial biomass reaches 860 mg^{-3}, an extraordinarily high value for temperate coastal waters (Sorokin *et al.*, 1994).

3.3. Photosynthesis and chemosynthesis at shallow-water hydrothermal vents

3.3.1. Kraternaya Bight

Using the oxygen bottle technique, Nor (1991) has shown that primary production can reach high values of 13.0 l O_2 m^{-2} d^{-1} (recalculated into carbon units: 7.3 g C m^{-2} d^{-1}) in the southeast part of Kraternaya Bight in July/August, when the peak of the algal bloom occurs. Following the succession of photoautotrophic plankton in September–October, production is reduced approximately two times (Table 20).

Table 18 Density (N, 10^6 cell l^{-1}) and biomass (B, mg m^{-3}) of bacterioplankton, bacterial production, chemosynthesis and photosynthetic production in the zone of venting at Whale Island

Locality	Depth, m	Bacterial plankton				Share of chemosynthesis in total bacterial production, %	Photosynthetic production, mgC m^{-3} d^{-1}
		N	B	Chemosynthesis	Total production mgC m^{-3} d^{-1}		
MacEwans Bight							
	0	1.61	360	4.0	40.2	10	425
	4	1.57	860	12.9	43.1	30	ND
	6	0.94	180	14.8	59.0	25	ND
(near bottom)	7	1.23	370	34.0	40.5	84	ND
Volcanic crater							
	0	1.00	250	0	40.4	0	381
	10	0.74	186	7.8	14.7	53	ND
	20	1.30	315	17.1	30.4	56	ND
(near bottom)	30	1.39	380	26.7	31.9	89	ND

ND, no determinations.

Source: Data from Tarasov *et al.*, 1993; Sorokin *et al.*, 1994.

Table 19 Density (N, 10^6 cell l^{-1}) and biomass (B, mg m^{-3}) of bacterioplankton, bacterial production, chemosynthesis and photosynthetic production in Calypso zone and Bay of Plenty (background)

Locality	Depth, m	N	B	Bacterial plankton		Share of chemosynthesis in total bacterial production, %	Photosynthetic production, mgC m^{-3} d^{-1}
				Chemosynthesis	Total production		
				mgC m^{-3} d^{-1}			
Calypso zone:							
37°38.1′ S	0	650	140	21.7	50.3	43	208
177°06.0′ E	60	510	110	12.0	25.8	42	ND
	100	475	105	20.3	35.9	57	ND
	150	321	72	41.9	62.9	67	ND
37°38.2′ S	0	680	89	5.9	45.8	13	231
177°07.2′ E	70	480	60	12.4	40.6	31	ND
	120	490	59	15.4	32.7	47	ND
	170	469	75	24.1	50.5	48	ND
Outside of Calypso zone (Bay of Plenty)							
37°38.2′ S	0	735	95	0	22.8	0	149
76°51.5′ E	60	832	115	4.9	20.5	21	ND
	100	365	58	2.1	22.2	7	ND

ND, no determinations.

Source: Data from Tarasov *et al.*, 1993; Sorokin *et al.*, 1994.

Table 20 Values of net and gross oxygen production of microplankton and oxygen consumption (l O_2 m^{-2} day^{-1}) in water column (0–10 m) of eastern basin of Kraternaya Bight

Date	Oxygen production		Oxygen consumption
	Net	Gross	
28.08.87	8.31	10.95	7.52
15.09.87	2.19	7.80	7.59
8.10.87	0.90	6.35	12.49
6.07.88	5.36	12.99	7.63

Source: From Nor, 1991.

Concurrently with primary production, a high consumption of oxygen (community respiration), varying from 7.5 to 12.5 l O_2 m^{-2} d^{-1}, has been recorded, with a maximum in July (Table 20).

In June 1990, Sorokin *et al.* (1993, 2003) determined that photosynthetic production in the east part of the Kraternaya Bight at a depth 2–3 m (Table 21) reached the highest recorded rate yet known for marine and freshwater ecosystems: 3.2 g C m^{-3} d^{-1}. They based their analysis on modified algalogical and radiocarbon methods and showed the effect of inhibitors on photosynthesis, chemosynthesis and heterotrophic assimilation of CO_2 in the populations of phytoplankton, protozoa and microplankton (Sorokin *et al.*, 1993, 2003). The rate of production reaches a maximum of 9.8 g C m^{-2} d^{-1} in the east basin at a depth of 2 m. Note that the layer of maximum photosynthesis in the bight is thin and occurs between 7 and 10 m depth. At greater depths, the photosynthesis of microalgae is limited by lack of light. In the period of the phytoplankton bloom, light penetrates only to 10 m depth, and below this, the light intensity is zero (Figure 14).

In the southeast venting area and in the mouth of the volcanic brook, photosynthetic production is reduced to 235 mg C m^{-2} d^{-1} in the surface layer, despite the high population density of diatoms (Table 22). This lower production has not been observed in the north venting area. Apparently, in the southeast part of the bight, volcanic products impede photosynthesis in the upper water layer.

In the waters outside Yankich Island, the layer of maximum photosynthesis occurs at 40 m, but the value of primary production is 20 times lower than in Kraternaya Bight, at only 300–500 mg C m^{-2} d^{-1}. Typically, the maximum production in the bight occurs at low production/biomass ratio (P/B coefficient) of 0.6–1.0, while in the outside water the P/B coefficient is 1.7 (Sorokin *et al.*, 1994, 2003).

Table 21 Pelagic photosynthetic production in Kraternaya Bight

			Photosynthetic production per day		
			mg C m^{-3}		
Locality	Date	Depth of photosynthesis maximum, m	At the surface layer	At the depth of photosynthesis maximum	In the water column, g C m^{-2}
Area of mouth of volcanic brook	20.06.90	3	235	2715	6.67
Area of mouth of volcanic brook	22.06.90	2	678	2170	7.08
Centre of the eastern basin	21.06.90	2	1370	3180	9.80
Northern vents field	21.06.90	2	1530	1710	6.60
Centre of the west basin	21.06.90	3	489	1490	7.07
Southwestern part of the west basin (near of the strait)	21.06.90	3	1300	2150	5.56
Outside Yankich Island (background)	21.06.90	5	15	19	0.27

Source: From Sorokin *et al.*, 1993, 2003.

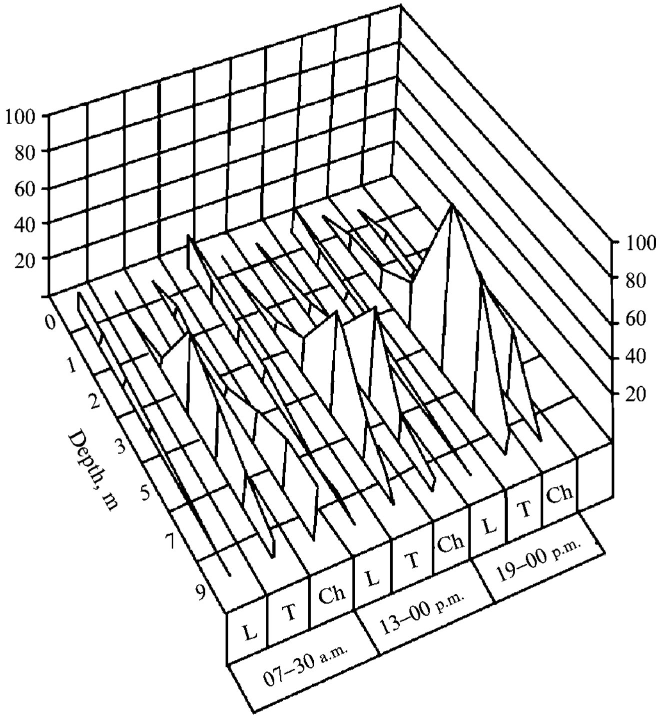

Figure 14 Daily changes of irradiance (L, 10^3 lux), the diatom *Thalassiosira anguste-lineata* (T, 10^4 cells l^{-1}) and chlorophyll *a* (Ch, mg m^{-3}) in the eastern basin of Kraternaya Bight; ordinates: irradiance values, diatoms and chlorophyll *a* (from Tarasov, 1999).

In Kraternaya Bight the share of bacterial chemosynthesis in total primary production of the pelagic zone is <1%. In the east basin, high rates of chemosynthesis (6–30 mg C m^{-3} d^{-1}) were recorded at the mouth of the volcanic brook and in zones of strong littoral and sublittoral gas-hydrothermal vents (Sorokin *et al.*, 1993, 2003). According to the microbiologists (Nesterov *et al.*, 1991), sulfur (10^4 cell ml^{-1}), ammonia-oxidising (10^5 cell ml^{-1}) and methane-oxidising (10^2 cell ml^{-1}) microorganisms were widespread, but the contribution of chemosynthesis to primary production of organic matter was only 4–6%. Activity of groups of chemosynthesising bacteria in this part of the bight varies with depth. The highest activity of autotrophic thionic bacteria was observed at depth of 12 m. Hydrogen-oxidising bacteria dominated the bottom layer, whilst methane-oxidising bacteria were found throughout the entire water column. However, the rate of methane oxidation was rather insignificant, 5.3 μg CH_4 m^{-3} d^{-1} (Nesterov *et al.*, 1991).

Table 22 Density (N, 10^3 cell l^{-1}) and wet biomass (B, mg m^{-3}) of major groups of phototrophic plankton in Kraternaya Bight

Depth, m	Phytoplankton						Total biomass of phytoplankton	*Mesodinium rubrum*		Total biomass of phototropic plankton
	Diatoms		Nanophytoflagellates		Dinoflagellates					
	N	B	N	B	N	B		N	B	
Centre of the eastern basin										
0	3300	26,000	—	—	—	—	26,000	3	150	26,150
2	2400	19,000	1600	260	25	200	19,500	190	9500	28,960
4	2830	12,830	5000	800	24	240	13,870	123	6150	20,020
7	2720	7920	3000	500	—	—	8420	72	3600	12,020
12	900	3550	1700	270	—	—	3820	33	1650	5470
18	600	1270	610	40	—	—	1310	7	50	1360
25	600	1270	50	3	—	—	1270	3	150	1420
Southern vents field										
1	5300	25,130	1660	270	12	100	25,500	225	11,000	36,500
2	300	2800	3500	530	9	70	3400	60	3000	6400
Centre of the western basin										
0	6600	35,130	5000	670	—	—	35,800	0	0	35,800
5	1320	11,000	830	150	—	—	11,150	50	2500	13,650
10	450	3500	420	70	11	90	3660	26	1300	4960
20	200	1200	520	40	—	—	1240	3	150	1390
30	—	—	850	70	—	—	—	—	—	70
50	—	—	420	33	—	—	—	—	—	30
Outside Yankich Island (background)										
0	30	70	160	6	—	—	76	2	90	170
8	40	100	—	—	—	—	100	1	35	140

(—), not found in samples.

Source: From Sorokin *et al.*, 1993, 2003.

3.3.2. Matupi Harbour

In some areas of Matupi Harbour phytoplankton activity is impeded by spreading of hot (up to 90 °C) volcanic fluids in the surface layer (Tarasov *et al.*, 1993; Sorokin *et al.*, 1994; Tarasov, 1999). These fluids also contain large quantities of particulate matter, which reduces light penetration in the water column. However, at a distance from those areas, the temperature and quantity of suspended matter decreases, and a steady stream of nutrients and trace elements from vents stimulates phytoplankton activity, where production in surface layers in the central part of the bay is ~100 mg C m^{-3} d^{-1} (Table 23). Such rates of photosynthesis are comparatively high for tropical latitudes. In mesotrophic neritic waters over coral reefs, photosynthetic rates are usually only 10–40 mg C m^{-3} d^{-1} (Sorokin, 1990b).

In the eastern and northern parts of Matupi Harbour, where the influence of venting on chemical composition of water was rather high, the rate of photosynthesis is low (32–33 mg C m^{-3} d^{-1}), but there is a high rate of bacterial chemosynthesis (from 3.0 to 83.9 mg m^{-3} d^{-1}, wet bacterial biomass or 0.6–17.9 mg C m^{-3} day) (Sorokin *et al.*, 1994, 1998).

Chemosynthesis was recorded throughout the entire water column with maxima in the middle and near-bottom layers in Tavurvur Area I and in Rabalanakaia venting area (up to 18.0 and 8.0 mg C m^{-3} d^{-1}, respectively (Figures 15 and 16). In Tavurvur venting Area II, where water is enriched with hydrogen sulfide, the highest intensity of chemosynthesis was observed in the surface layer, rising to 8.1 mg C m^{-3} d^{-1}. Bacterial chemosynthesis was also found in the deeper water part of the bay (Table 23; Figure 17), with a maximum in the near-bottom layer.

3.3.3. Bay of Plenty

Compared with the cool temperate waters of Kraternaya Bight, the rate of primary photosynthetic production in the venting areas of the Bay of Plenty is less by almost one order of magnitude (Tarasov, 1999). At the same time, relatively high rates of photosynthesis (300–425 mg C m^{-3} d^{-1}) were recorded in MacEwans Bight (average depth of the bight is 5 m) and in areas of the Volcanic Craters, alongside Whale Island (Sorokin *et al.*, 1994), compared with 149 mg C m^{-3} d^{-1} in the waters of the Bay of Plenty away from the venting areas (Tables 18 and 19).

Bacterial chemosynthesis was also found in the deep-water part of the bay (Calypso zone), with maximum in the near-bottom layer (Table 19). At the same time, chemosynthesis was not observed in that part of the bay (outside of Calypso zone), from the surface layer down to a depth of 20–30 m.

Table 23 Primary production of phytoplankton, total production of bacterioplankton and bacterial chemosynthesis in Matupi Harbour

Depth, m	Daily production of photosynthesis		Daily production of bacterioplankton		Share of chemosynthesis in total bacterial production, %	$P_{b.}/B_{b.}$
	mgC m^{-3} d^{-1}	gC m^{-2} d^{-1}	Total	Chemosynthesis		
			mgC m^{-3} d^{-1} (wet biomass)			
1	2	3	4	5	6	7
Central part of the bight						
0	98	1.63	67.8	0	0	0.2
10	70	ND	52.8	0	0	0.3
20	23	ND	35.5	4.9	14	0.2
30	9	ND	43.1	13.1	30	0.5
40	1.5	ND	52.6	19.6	40	0.4
50	0	ND	56	25.3	45	0.3
Tavurvur vent field. Area I						
0	33.1	0.31	90.5	18.1	20	0.3
14	0	ND	216.3	89.3	40	0.9
19	0	ND	110.3	55.1	50	0.6
Tavurvur vent field. Area II						
0	32	0.31	113.0	40.4	36	0.2
15	0	ND	62.5	23.3	37	0.4
21	0	ND	47.0	28.6	61	0.2
Rabalanakaia vent field						
0	3.6	0.034	70.8	3.0	4	0.6
8	6.6	ND	141.2	5.6	4	0.7
14	0	ND	111.2	40.4	36	0.6
18	0	ND	85.8	30.0	33	1.2
23	0	ND	92.2	36.6	40	0.8

ND, no determinations; $P_{b.}$, bacterial production; $B_{b.}$, biomass of bacteria (after Tarasov *et al.*, 1993, 1999; Sorokin *et al.*, 1994, 1998).

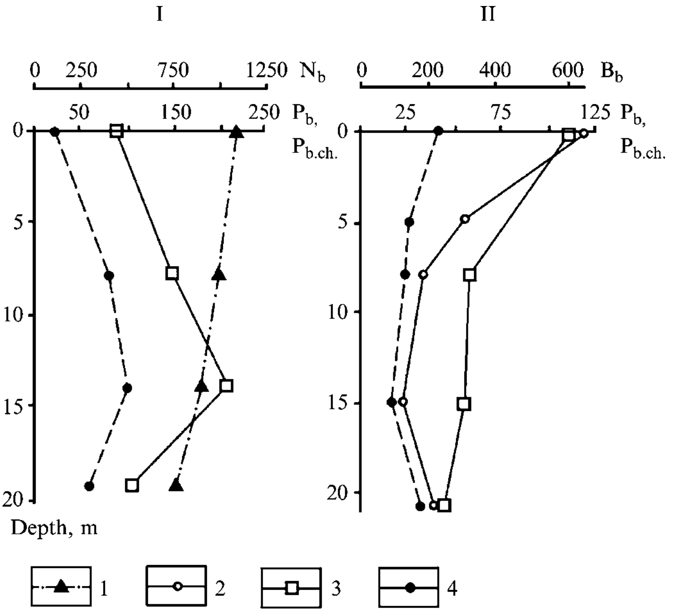

Figure 15 Number of bacteria (N_b, 10^3 cells ml^{-1}), biomass of bacteria (B_b, mg m^{-3} wet biomass), the bacterioplankton production and rate of bacterial chemosynthesis (P_b and $P_{b.ch.}$, both as mg m^{-3} d^{-1} wet biomass) in the water column of the eastern part of Matupi Harbour. I – Tavurvur area 1; II – Tavurvur area 2; 1 – number of bacterioplankton, 2 – biomass of bacterioplankton, 3 –bacterioplankton production, 4 – chemosynthesis (after Sorokin *et al.*, 1994).

In MacEwans Bight, Volcanic Crater (Whale Island) and Calypso area (Bay of Plenty), the maximum values of chemosynthesis, ~7 mg C m^{-3} d^{-1}, were recorded in the near-bottom layer (Tables 18 and 19) (Sorokin *et al.*, 1994, 1998). Apparently, such distribution of microorganisms in the water column reflects the distribution of volcanic compounds.

The maximum rate of methane oxidation was detected in the bottom layer. It was 1.13–2.10 μl CH_4 l^{-1} d^{-1} in Volcanic Crater, up to 0.60 μl CH_4 l^{-1} d^{-1} in the MacEwans Bay, whilst it was one order of magnitude lower in the Calypso area (Namsaraev *et al.*, 1994).

These data show that in spite of active hydrological conditions, the streams of venting fluids appreciably affect the primary productivity of water in open areas of the Bay of Plenty. Appreciable chemosynthesis was observed. In contrast to ambient seawater, bacterioplankton production in the bay increased with depth (Table 19).

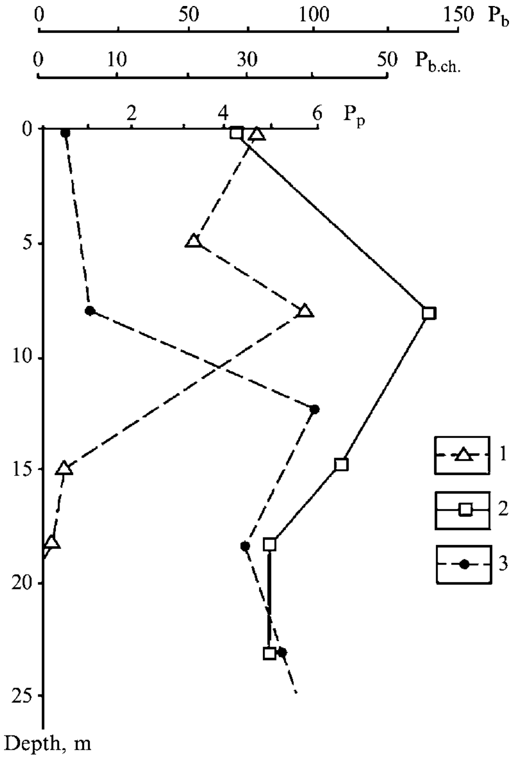

Figure 16 Photosynthetic production (P_p, mgC $m^{-3} \cdot d^{-1}$), bacterioplankton production and rate of bacterial chemosynthesis (P_b and $P_{b.ch.}$, both as mg m^{-3} d^{-1} wet biomass) in the water column of Rabalanakaia hydrothermal zone. (1) phytoplankton, (2) bacterial production, (3) chemosynthesis (after Sorokin *et al.*, 1994).

3.4. Planktonic protozoa

3.4.1. Kraternaya Bight

In Kraternaya Bight, there is a low population density and biomass of heterotrophic protozoans such as asymbiotic ciliates and zooflagellates (Table 17). The highest number and biomass of zooflagellates and small ciliates occurs in surface and near-bottom layers of the west basin. In the southeast venting zone, the population density and biomass of protozoans decreases noticeably, because of the effect of venting products on development of these groups of organisms. The total number of heterotrophic protozoans was two to three orders less than the population density of the symbiotic ciliate *M. rubrum*, and their biomass varied from 5 to 270 mg m^{-3}

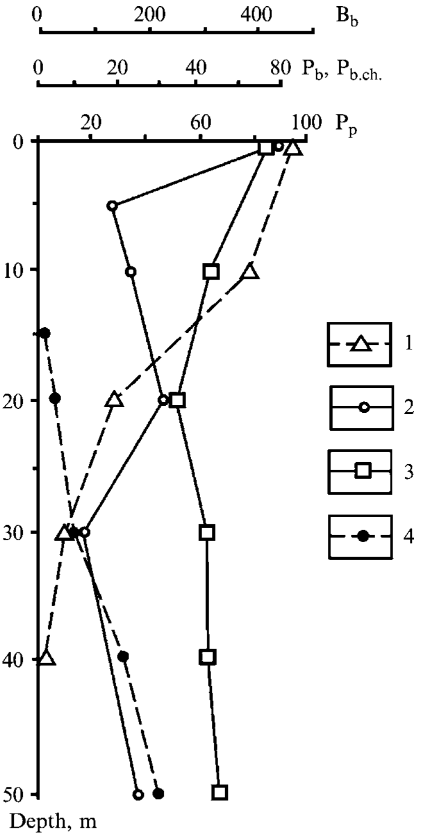

Figure 17 Photosynthetic production (P_p, mgC m^{-3} d^{-1}), biomass of bacteria (B_b, mg m^{-3} wet biomass), bacterioplankton production and rate of bacterial chemosynthesis (P_b and $P_{b.ch.}$, both as mg m^{-3} d^{-1} wet biomass) in the water column of central part of Matupi Harbour. (1) phytoplankton, (2) biomass of bacteria, (3) bacterial production, (4) chemosynthesis (after Sorokin *et al.*, 1994).

within the bight (Sorokin *et al.*, 1993, 1998). These values correspond to values of biomass typical of heterotrophic protozoans in mesotrophic and eutrophic sea basins (Sorokin, 1981), but their relative density was low for such a highly productive area as Kraternaya Bight.

3.4.2. Matupi Harbour

Zooflagellates, amoebae and asymbiotic ciliates are the commonest planktonic protozoans in the waters of Matupi Harbour (Sorokin *et al.*, 1993, 1998). Zooflagellates show the highest population density (up to $4.8 \cdot 10^5$ cells l^{-1}) in the surface layer of the central part of the bight and in Tavurvur Area II (Table 16). In the subsurface layer (3–5 m), the number of zooflagellates decreases four to six times and changes little with depth. An appreciable number of amoebae occur in the bottom layer of those areas.

The density of ciliates is at a maximum over venting areas in the bottom layers and reaches 2,300 cells l^{-1}. In the central part of the bay, abundant ciliates occur in the surface layer (770 cells l^{-1}). Below the surface layer, to a depth of 30 m, the density and biomass of ciliates vary little, but in the near-bottom layer, their number distinctly decreases (Table 16).

The total biomass of the planktonic protozoans in the bay was rather insignificant (5–24 mg m^{-3}), with the maximum being observed in the venting zone.

3.4.3. Bay of Plenty

In the open coastal areas with hydrothermal vents in the Bay of Plenty, the biomass of planktonic protozoans can reach 40–60 mg m^{-3}. Zooflagellates, amoebae and asymbiotic ciliates are distributed in the surface layer. In the near-bottom layer of MacEwans Bight, there are unusually high numbers of planktonic amoebae, which exceed the ciliates in their density and biomass. The density of amoebae reaches $3 \cdot 10^4$ cells l^{-1}, with a biomass of 15–25 mg m^{-3}. Such high biomass of planktonic amoebae in a marine ecosystem has not been recorded previously. The biomass of planktonic amoebae does not usually exceed 1–2 mg m^{-3} even in highly productive waters (Sorokin *et al.*, 1994, 1998).

3.5. Zooplankton

3.5.1. Kraternaya Bight

A few species dominate the zooplankton in Kraternaya Bight, and their distribution can be related to venting areas and the spreading of volcanic fluids (Kosihina and Malakhov, 1991) (Table 24).

The calanoid copepods *Paracalanus aculeatus, Clausocalanus furcatus* and *Clausocalanus abdominalis* flourish in the bight. Other species of calanoids are present outside, including *Metridia lucens, Calanus* sp., *Eucalanus* sp., *Scottocalanus* sp. and *Paraeuchaeta* sp. The vertical distribution of the abundance of these species varies. In the bight, large calanoids occur in very small numbers mainly in near-bottom waters, while outside the bight they are present in the surface layers at densities of 60–70 ind. m^{-3}. In the bight, small calanoids form aggregations in the intermediate layer (up to

Table 24 Density of some groups of plankton (ind m^{-3}) in the water column of Kraternaya Bight and outside Yankich Island

	Eastern basin			Eastern basin			Outside Yankich Island (background)			
	Layer in the water column									
Group of organisms	0–10 m	10–30 m	>30 m	0–10 m	10–30 m	>30 m	0–10 m	10–20 m	20–30 m	>30 m
calanoida: large size	3	—	7	—	—	6	60	20	10	7
small size	1250	8300	1050	1900	7000	1600	2200	1700	—	—
Cyclopoida: Oithona sp.	100	500	—	—	—	—	8250	5400	—	—
Oncea sp.	—	—	300	—	—	200	200	300	300	100
harpacticoida	—	—	300	—	—	400	100	100	100	—
chaetognatha, sagittoidea										
length: 1–2 cm	300	10	30	160	10	40	4	3	4	2
2–4 cm	3	10	4	2	10	10	—	—	—	—
appendicularia	—	—	—	—	—	—	10	4	3	2
Nauplii: *cirripedia*	100	—	—	1150	200	200	—	—	—	—
copepoda	11,000	3000	600	9500	1100	4200	2800	1200	—	—
Larvae: *ceriantharia*	—	20	10	—	10	—	—	—	—	—
gastropoda	300	600	—	—	100	—	100	100	100	—
bivalvia	900	5500	500	1500	5800	300	—	—	—	—
echinodermata	400	—	—	600	300	100	—	—	—	—

(—), not found in samples.

Source: Data from Kosihina and Malakhov, 1991.

8300 ind m^{-3}), where ambient seawater enters during high tide. In the outside waters at the same depth, the calanoid population density is only $\sim$1700 ind m^{-3}. The number of small calanoids in the bight is two to three times greater than outside Yancicha Island (Table 24).

Oithona sp. are the most abundant cyclopoid copepods, although densities in the bight are low (100–500 ind m^{-3}), with a maximum in the intermediate layers. Densities of $>8 \times 10^3$ ind m^{-3} of *Oithona* sp. are found in surface waters outside the bight, exceeding the densities inside by an order of magnitude. The population density of other cyclopoid species, including *Oncea* sp., is similar in the bight and outside.

Chaetognaths are always present in the bight. In September their population density reaches 300 ind m^{-3} in the surface layer of the east basin. This value is several times greater than the known density of chaetognaths in bays of the northwest Pacific (70–100 ind m^{-3}) (Nagasawa and Marumo, 1976; Sweat, 1980). The chaetognaths were the only carnivorous zooplankton found in Kraternaya Bight. Their abundance in the planktonic community could be explained by lack of competition. Analyses of food boluses in the intestine of the chaetognaths revealed that their basic food is copepods (Kosihina and Malakhov, 1991), as is well known for the group in open waters. The temperate-boreal species *Parasagitta liturata* inhabits the bight, while outside waters are inhabited by the cold-water and deep-water species *Eukrohnia bathypelagica*.

At the end of August/beginning of September, numerous larvae of barnacles, bivalves, echinoderms (mostly starfishes), and ceriantharians are present in the bight, but not recorded in the outside waters (Table 24). Copepod nauplii are also abundant, especially in the surface layer of the east basin, with values up to $1.1 \cdot 10^4$ ind m^{-3}.

Analysis of the vertical distribution of various groups of zooplankton shows a decrease of their number in the surface layer and an increase in the intermediate layer, except for chaetognaths and copepod nauplii.

The total biomass of zooplankton in the surface layers in the bight is >800 mg m^{-3}. This value exceeds the average biomass of zooplankton in the open waters of the Kuriles two to three times (Bogorov and Vinogradov, 1955; Shuntov, 2001). There are significant differences in biomass values at depths >10 m when waters of the bight are compared with ambient seawater outside. In the bight the biomass of zooplankton varies little with depth, varying from 500 to 900 mg m^{-3}, while in the outer waters it does not exceed 100 mg m^{-3} at depths between 20 and 30 m. An especially high biomass (up to 1000 mg m^{-3}) was observed southeast of the venting zone at a depth of 20 m. This area shows high primary production and abundance of bacterioplankton (Table 17). This food source appears to benefit the populations of the suspension-feeding zooplankters *Paracalanus* spp. and *Clausocalanus* spp. (Kosihina and Malakhov, 1991).

3.5.2. Matupi Harbour

The zooplankton of Matupi Harbour has high species diversity. There are >40 species of holoplankton and pelagic larvae of benthic animals including those of sea urchins, starfish, bivalve and gastropod molluscs, polychaetes and decapod nauplii (Chavtur, 1992). Thirteen species of cyclopoid copepod dominate the holoplankton, with small forms of *Oithona hamata* and species of the genus *Corycaeus* being the most common. Other plankton groups found in Matupi Harbour include a few species of Calanoida, Harpacticoida, Ostracoda, Chaetognatha and Euphausiacea.

In areas of volcanic activity, species of Cyclopoida comprise 50–60% of the total number of copepod species. Their proportion decreases with distance from the venting zone to the central part and to the outside of the bay, with cyclopoids being gradually replaced by calanoid species (Chavtur, 1992). Calanoid species dominate the control area in Blanche Bay. The overall population density of zooplankton varies little between the venting zones and the central and western parts of the bay. According to Chavtur (1992), the main mass of organisms in different areas of the bay is distributed in the surface layer with a population density 1.1–1.4 10^3 ind m^{-3}. The density of zooplankton decreases sharply (two to three times) below 10 m. The only exception was recorded in the Rabalanakaia venting areas, where surface waters had temperatures up to 50 °C. In these places the maximum zooplankton density ($\sim$1.4 10^3 ind m^{-3}) occurs at 10 m depth.

There are corresponding variations in the distribution of biomass. In the central part, the highest value, 640 mg m^{-3}, was recorded in the 0–10 m layer. In the deeper layers the value of biomass decreases four to five times, averaging 150 mg m^{-3} at 50 m depth. Over venting zones the values of biomass are appreciably higher in the 0–10 m layer and in the Rabalanakaia Area reach a maximum of up to 1,000 mg m^{-3}. The western part of the bay contains the lowest biomass value, 250 mg m^{-3}.

In the control area, Blanche Bay (Figure 7), zooplankton density reaches 400–740 ind m^{-3} with a biomass of 600–650 mg m^{-3} in the near-bottom layer above the coral reefs along the northern coast of the bay.

The main zooplankton species inhabiting venting areas of Matupi Harbour are organisms that are widespread in the open sea and oceans. The biomass of zooplankton off atolls of the Bismarck Sea averages 230 mg m^{-3} (maximum 340 mg m^{-3}) and in the open sea 40 mg m^{-3} (Geptner, 1979).

3.5.3. Bay of Plenty

There are fewer species of zooplankton in the venting zones of the Bay of Plenty than recorded for the Hauraki Gulf, to the north of the Bay of Plenty.

The zooplankton in the Bay of Plenty is mostly composed of small organisms up to 2 mm (Jillett, 1971; Chavtur, 1992). Calanoida dominate by species number (~30% of all the fauna) in Hauraki Bay, whereas in the vicinity of Whale Island they were not so numerous, representing ~15% of the total number of species.

In the coastal waters of Whale Island, Chavtur (1992) has identified abundant holoplanktonic and meroplanktonic species including *Oikopleura* sp. (Appendicularia), an unidentified species of harpacticoid, *Corycaeus aucklandicus* (Cyclopoida), *Temora turbinata* (Copepoda) and echinoderm larvae, whose population densities were 1,400, 700, 300, 100 and 300 ind m^{-3}, respectively. These values are an order of magnitude less than the densities of zooplankton recorded in Hauraki Gulf (Jillett, 1971).

In MacEwans Bay and in Volcanic Crater, the number of zooplankton species decreases with increase in depth. The most typical feature is an increase in population density and biomass of Harpacticoida in the bottom layer in the immediate vicinity of vent outlets, where other zooplankton are not found.

3.6. Summary

In shallow-water venting zones of island arcs at different latitudes (temperate and tropical) in the western Pacific, the phytoplankton community is composed of a small number of diatom species (four to five species) of the genera *Thalassiosira, Chaetoceros* and *Melosira*, with high density and biomass (Tarasov, 1999).

In Kraternaya Bight, the ciliate *Mesodinium rubrum* with symbiotic microalgae is also important as a photoautotrophic component of the ecosystem. As a whole, the pattern of daily vertical migrations of *M. rubrum* is similar to the blooms and migrations of these ciliates in upwelling zones and eutrophic bays (Ratkova *et al.*, 1980; Lindholm, 1985).

The bloom of *Mesodinium* in Kraternaya Bight, as in other sea areas, stems from the ability of the organism to reproduce rapidly and to employ both phototrophic and heterotrophic metabolism (Lindholm, 1985). Night migrations to 6–10 m depth in Kraternaya Bay appear to be driven by the need to obtain nutrients for the symbiotic microalgae. The concentrations of mineral matter (i.e., algal nutrients) at that depth are several times greater than in the upper layer (Table 4, Figure 18). The ciliates do not apparently feed on bacteria during these night migrations. In the daytime, *M. rubrum* gathers in the surface layer, which provides optimum conditions for photosynthesis of the endosymbionts.

At tropical latitudes in Matupi Harbour, cyanobacteria and chemosynthesising microorganisms dominate the autotrophic component of the plankton

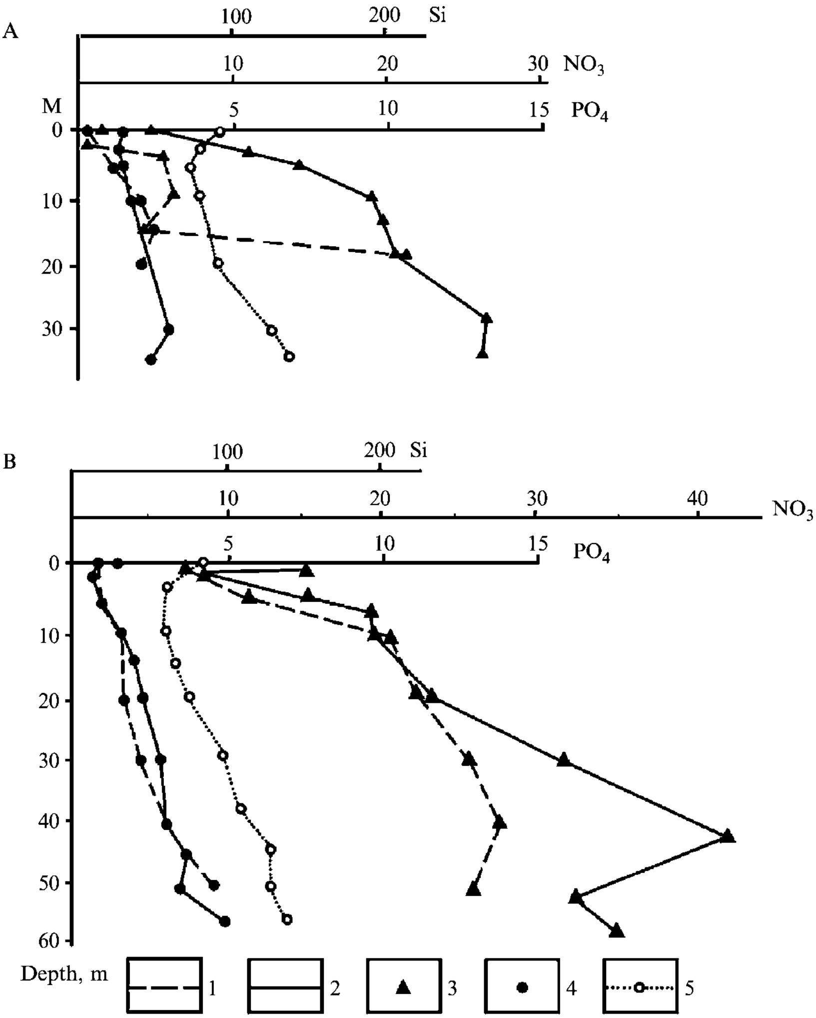

Figure 18 Concentration of algal nutrients in the water column of Kraternaya Bight. (1) in 1985, (2) in 1986, (3) nitrate (μM), (4) orthophosphate (μM), (5) silicon (μM). (A) eastern basin; (B) western basin (after Propp *et al.*, 1989).

community in zones of venting of hydrogen sulfide at high temperatures (>50 °C). Environmental conditions in Matupi Harbour are governed by the vent fluids that issue from littoral and sublittoral gas-hydrothermal vents of the Tavurvur Volcano.

An abundance of algal nutrients (SiO_3^{2-}, PO_4^{3-}, NO_3^-, etc.), gases (CO_2, H_2) and reduced compounds (CH_4, C_nH_n, S_o, H_2S, $S_2O_3^{2-}$, NH_4^+) under shallow-water hydrothermal vent conditions allows autotrophic organisms to employ two sources of energy: sunlight (photosynthesis) and oxidation-reduction reactions (bacterial chemosynthesis). Chemosynthesis in zones of shallow-water volcanism occurs near the seabed in areas of immediate venting fluid, whilst intense photosynthetic processes are observed in the surface layer of the water column. In the surface layers of the water column, the region of most intense photosynthesis occurs below the layer of chemosynthesis, which is related to the distribution of hydrothermal fluids on the water surface. The contribution of each of these processes to primary production depends on the physical and chemical conditions created by the vents and on the range of potential adaptation of the photosynthesising organisms.

Intensive production processes occur over a very narrow range of depth. For example, in Kraternaya Bight intensive production is confined to the surface layer of water (0–3 m), in which a large biomass of organic matter is being produced at a level greater than found in other marine ecosystems (Figures 3 and 5, Tables 17, 21 and 22). The pycnocline is continuously maintained by volcanic activity in the subsurface layer. Tidal phenomena have little effect on the temperature gradient. Because of different values of water density at depths of 1–2 m, a sort of "liquid ceiling" has arisen and is maintained. At this level there are large numbers of the basic groups of photosynthesising microorganisms. Suspended at 1–3 m depth these concentrations of diatoms and infusorians are seen by SCUBA divers as numerous and long strips of brown colour. Because of the abundance of these organisms, light intensity is much reduced at depths >10–15 m.

Hydrochemical and geochemical analyses show that in the surface layer the mineral nutrients required by photoautotrophs are not limiting (Tarasov, 1999, 2002). Upward diffusion of hydrothermal fluids saturated with trace elements brings them to the surface. Synthesis of vitamins and other biologically active substances by bacteria and microheterotrophs should also be favourable factors for the photosynthesising organisms. The high concentrations of dissolved metals do not seen to have an appreciable effect on the population density and biomass of the photosynthesising organisms. It appears that development of phototrophs and the rate of photosynthetic production in Kraternaya Bight are determined by nontrophic regulatory correlations connected to excretion of metabolites that are toxic for development of other groups of microalgae, or to autoinhibition of further growth of diatoms and protozoans, as shown elsewhere (Vinogradov, 1977). Thus, in all areas of shallow-water hydrothermal venting reviewed here, an abundance of primary organic matter is created by a combination of photosynthesis and chemosynthesis.

A rather high concentration and steady flow of reduced compounds is needed for development of chemosynthesising organisms (Sorokin *et al.*, 1993, 1994, 1998, 2003). Measurements and estimations of chemosynthetic activity can be used as an indicator of vent activity and give a guide to the composition of the venting fluids. High activity of chemosynthesising bacteria indicates that the products of volcanism are usually quickly oxidised by bacterial activity, and this should be taken into account, for example, in estimations of the absolute concentration of hydrocarbon gases in seawater when assessing reserves of oil and gas in shelf sediments.

All the organisms that form the main biomass of the phytoplankton community in areas of shallow venting are widely distributed species that inhabit several regions of the World Ocean. Their dominance in zones of shallow-water venting is related to their ability to grow in conditions that are unfavourable for most other species. Apparently, before colonising venting areas or before the start of volcanic activity in coastal waters, these species already possessed biochemical mechanisms that could respond to a wide range of temperature, to high concentrations of gases, and to various toxic compounds, including dissolved heavy metals.

The characteristics of the marine environment in venting areas determine changes in structure and distribution of the heterotrophic component of plankton communities. All shallow-water volcanic areas are characterised by extremely high bacterial population density and bacterioplankton production (Sorokin *et al.*, 1993, 1994, 1998, 2003). Maximum values of bacterial production are seen in the surface layers of semiclosed basins, but in the near-bottom layer in open areas where currents and water turbulence are slight. In Kraternaya Bight and Matupi Harbour the bacterioplankton is characterised by the large size of the microbial cells. Their average size is two or three times that of bacterial cells developing in typical coastal temperate and tropical waters (Tarasov, 1999).

The abundance of heterotrophic microplankton (zooflagellates, asymbiotic ciliates, planktonic amoebae) and zooplankton in areas of shallow venting depends on the distribution of organic matter and bacterioplankton.

Compared to normal coastal waters, zooplankton in venting areas has low diversity but high biomass. As is the case with the phytoplankton communities, it is not possible to identify species or groups of organisms among the zooplankton that could be regarded as specific inhabitants of shallow-water vents.

4. BENTHIC COMMUNITIES

4.1. Thermophilic bacteria

The occurrence of bacteria in volcanic structures was known at the beginning of the last century (Emoto, 1929, 1933, cited by Zavarzin *et al.*, 1967, p. 606), but their important role in biogeochemical processes was determined more recently (Kuznetsov, 1955; Zavarzin and Zhilina, 1964). Zavarzin *et al.* (1967) and Ivanov *et al.* (1968) showed that sulfuric acid in terrestrial volcanic springs results from the activity of sulfur bacteria.

Later, a large number of new bacterial taxa, including thermophilic bacteria and specific microbial communities were identified from various regions on land and at vents in deep-water, able to utilise practically all reduced compounds or gases and other products of volcanic origin as energy sources (Brock, 1969, 1978; Brock *et al.*, 1972; Gorlenko *et al.*, 1977; Loginova, 1982; Gerasimenko *et al.*, 1983; Stetter *et al.*, 1983; Zilling *et al.*, 1983; Jannasch, 1985; Belkin *et al.*, 1986; Fiala *et al.*, 1986; Jannasch *et al.*, 1986; Stetter, 1986; Wirsen *et al.*, 1986; Zavarzin *et al.*, 1989; Bonch-Osmolovskaya, 1991).

Thermophilic bacteria can be divided into three groups related to their temperature requirements: (1) mesothermophilic bacteria that develop in the range from 40 to 70 °C (optimum 55–60 °C); (2) extreme thermophilic bacteria that grow at 50–80 °C (optimum 70–75 °C); and (3) hyperthermophilic bacteria that grow at 70–110 °C (optimum 85–105 °C) (Bonch-Osmolovskaya, 2002). Most mesothermophilic and extreme thermophilic bacteria belong to the Bacteria domain, while hyperthermophiles are classed in the Archaea domain (Stetter, 1996).

Isolation of cultures and description of thermophilic bacteria from shallow-water vents began in the early 1980s on the coast of Italy, then off Iceland, Azores, Africa and the Kurile Islands (Dando *et al.*, 1999; Bonch-Osmolovskaya, 2002).

4.1.1. Kraternaya Bight

A new species of extreme thermophilic Archaebacteria, *Thermococcus stetteri*, growing in anaerobic environments in the temperature range 55–94 °C, has been isolated and described from the hydrogen sulfide vents of Kraternaya Bight (Miroshnichenko *et al.*, 1989b). These bacteria ferment complex organic substrates (peptides and polysaccharides) and reduce elemental sulfur to hydrogen sulfide, which accumulates in the environment in significant amounts (up to 20 mM) (Miroshnichenko *et al.*, 1989a,b). Complete fermentation of organic matter does not occur, and isomers of volatile fatty acids, butyric and valeric, are produced concurrently with hydrogen sulfide and carbonic acid. In the southern part of the bight, the population density of those bacteria reaches 10^8 cells ml^{-1} in hot (55–60 °C) silty sediment in the zone of strong gas-hydrothermal vents at depths of 23 m (Bonch-Osmolovskaya *et al.*, 1991). The rate of bacterial reduction of elemental sulfur can reach 0.94 $\mathrm{g\ l^{-1}\ d^{-1}}$ during the fermentation of organic matter. Abiotic chemical reduction of elemental sulfur in controls without bacteria was only 1–10% of bacterial sulfur reduction (Bonch-Osmolovskaya, 1994).

This type of microorganism lives in terrestrial, littoral and sublittoral vents, sediments and bacterial mats in the south and southeast parts of Kraternaya Bight (Miroshnichenko *et al.*, 1989a; Bonch-Osmolovskaya

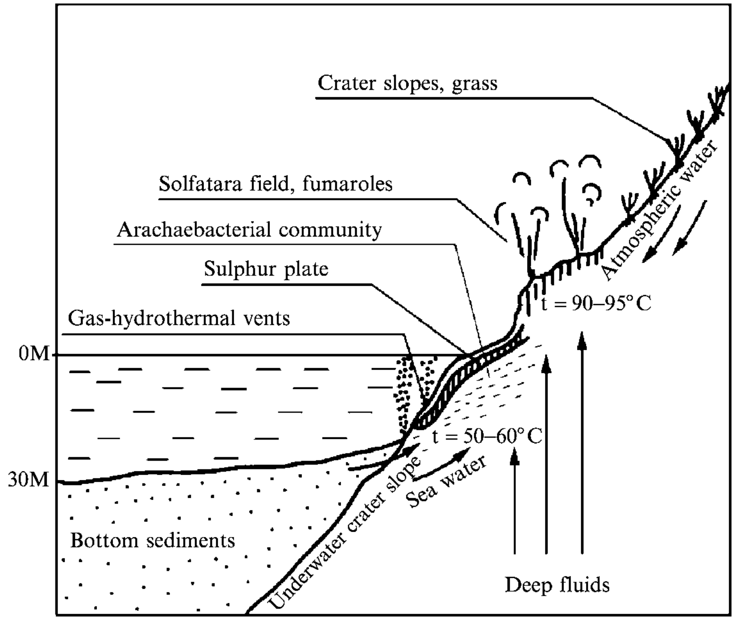

Figure 19 Vertical section of Ushihir Volcano in the area of the terrestrial hydrosolfatar field, Kraternaya Bight (from Bonch-Osmolovskaya *et al.*, 1991).

et al., 1991). Sampling of the pebble-gravel beach at the base of solfatara field and examination of underwater slopes shows the sediment contains a layer of clay and a stratum of elemental sulfur at depths of 1.5–2.0 m and under silty-sand sediments on the slopes. Hot fluid (>60 °C), saturated with hydrogen sulfide and containing Archaebacteria, circulates under these strata (Figure 19). It appears that a community of extreme thermophilic bacteria exists deep in the hydrothermal system of the Ushishir Volcano. Uptake of organic matter (i.e., a substrate for development of Archaebacteria) occurs through seepage of seawater deep in the volcanic structure and from circulation induced by gas-steam jets.

4.1.2. Matupi Harbour

Another hyperthermophilic archaebacterium, *Thermococcus litoralis*, has been isolated from samples taken from vents at Matupi Harbour (Kostyukova *et al.*, 1999; Bonch-Osmolovskaya, 2002). These bacteria, with population densities up to 10^6 cells ml^{-1}, came from soft bottoms with a temperature of 70–90 °C at Tavurvur venting Area II. *Thermococcus litoralis*

Table 25 Rate of bacterial sulfur-reducing (mgS_0 m^{-2} day^{-1}) in hot bottom sediments of Matupi Harbour

Locality, object	T, °C	S_0 content in sediment mg l^{-1}	Rate of bacterial S_0-reduction
Tavurvur vent field: Area II:			
Sand sediments under the bacterial mat	60–85	1434.2	2306.0
Silty sand, depth 5 m	55	775.2	8.6
Rabalanakaia vent field:			
Silty sand, depth 27 m	85	0	2.1
Eastern part of Matupi Harbour:			
Silty sand outside the vents field, depth 10–15 m	27	0	26.0

Data from Bonch-Osmolovskaya, 1991; Namsaraev *et al.*, 1994.

is another anaerobic fermenter and grows mostly on peptides in the presence of elemental sulfur. Surplus hydrogen (H^+), generated in the course of bacterial fermentation, reduces the sulfur to hydrogen sulfide.

A new genus and species of mesothermophilic sulfur-reducing bacteria, *Hippea maritima*, has been isolated and described from the same zone of sediments in Matupi Harbour, at temperatures <60 °C. The optimum temperature for growth of this species is 52–54 °C. It uses hydrogen, acetate, pyruvate and saturated fatty acids as substrates and produces CO_2 and H_2S (Miroshnichenko *et al.*, 1999).

The populations of hyperthermophilic archaea and mesothermophilic bacteria have a maximum density (10^5–10^6 cells ml^{-1}) in littoral and sublittoral hot bottom sediments of Tavurvur venting Area II. In other volcanic areas of Matupi Harbour, their density is lower, varying from 10 to 10^3 cells ml^{-1}. Biological processes of sulfur reduction occur in the upper layer (0–2 cm) of black silty sand or at bottom sites covered by bacterial mats. Very high rates of sulfur reduction reaching 72 mM S m^2 d^{-1} have been observed at temperatures of ≥60 °C. The sulfur reduction rate is two to three orders of magnitude lower at water depths of 5–10 m and decreases with depth in the sediment (Table 25).

4.1.3. Bay of Plenty

Two other new species of hyperthermophilic sulfur-reducing Archaebacteria of the genus *Thermococcus* have been described from open sea areas of gas-hydrothermal activity in the Bay of Plenty. These are *T. gorgonarius*, from littoral vents around Whale Island, and *T. pacificus*, from hot silty sediment of the Volcanic Crater (Bonch-Osmolovskaya *et al.*, 1993;

Table 26 Rate of bacterial sulfur reduction (mgS^0 m^{-2} day^{-1}) in hot bottom sediments in areas of gas-hydrothermal vents in Whale Island

Locality, object	T, °C	S^0 content in the sediment, mg l^{-1}	Rate of bacterial S^0-reduction
Volcanic crater:			
Clay-silt bottom	81	67.2	0.52
Clay-silt bottom	65	19.0	3.15
MacEwans Bight:			
Sand sediments under the bacterial mat *Thiothrix* sp.	55	115.0	1.10

Data from Bonch-Osmolovskaya, 1991; Namsaraev *et al.*, 1994.

Miroshnichenko *et al.*, 1998; Kostykova *et al.*, 1999). These bacteria grow within a temperature range of 55–100 °C, with an optimum of 85–88 °C. Like other species of this genus, they are fermenters of peptides and other complex organic substrates and reduce elemental sulfur to hydrogen sulfide (Bonch-Osmolovskaya, 2002).

In Volcanic Crater, at a temperature of 81 °C, the rate of sulfur reduction is low (0.52 mg S^{2-} m^{-2} d^{-1}), although the population density of hyperthermophilic Archaebacteria is high, 10^7 cells ml^{-1}. The rate increases with decreasing temperature (Table 26). The mesothermophilic sulfur-reducing bacteria *Hippea maritima* occurs in silty sediments of Volcanic Crater at temperatures <55 °C, like in Matupi Harbour (Miroshnichenko *et al.*, 1999).

In MacEwans Bight there are populations of thermophilic sulfur-reducing eubacteria at densities of 10^4–10^5 cells ml^{-1} in silty-sand bottoms at temperatures of 50–60 °C. In contrast to the Archaebacteria, they use low-molecular-weight compounds, including acetate and other organic acids, as an energy source, reducing sulfur to hydrogen sulfide (Bonch-Osmolovskaya *et al.*, 1993). Bacilliform fermenting eubacteria dominate among these bacteria. Their morphology is similar to that of *Desulfurella acetivorans*, a mesothermophilic freshwater eubacterium that reduces elemental sulfur while fermenting acetate (Bonch-Osmolovskaya *et al.*, 1990; Bonch-Osmolovskaya, 1994). The rate of sulfur reduction in these eubacteria was 1.1 mg S^{2-} m^{-2} d^{-1}, comparable to the rate of extreme thermophilic Archaebacteria in Volcanic Crater (Table 26).

4.2. Bacterial mats and microphytobenthos

Bacterial mats are benthic communities consisting of various microflora, the products of their metabolism, and particles of sediment. They are found in many marine habitats but are extremely common in zones of shallow-water gas-hydrothermal venting and seepage of volcanic fluids. In these conditions, they can be found from the littoral zone down to 30 m depth.

The mats in zones of shallow-water venting can be divided into diatom, bacterial and algobacterial according to the dominant group of microorganisms (Tarasov *et al.*, 1985, 1986, 1990, 1991; Starynin *et al.*, 1989; Namsaraev *et al.*, 1991; Nesterov *et al.*, 1991; Tarasov, 1999, 2002). The mats form the basis for complex communities and sustain a high population density of meiobenthos and macrozoobenthos.

4.2.1. Kraternaya Bight

In Kraternaya Bight the diatom mats show the greatest development in the venting zone of the northern part of the bight, which does not contain hydrogen sulfide, at depths from 5 to 15 m (Figure 20). In this area the mats are located on and between boulders, at sites of gas emission. The mats consist of filiform colonies of the diatom *Melosira sulcata*, together with particles of sediment and metal oxides attached to the surface of diatom cells. The deposit under the mat is often of ochreous, being rich in iron, up to 43% of dry weight of the sediment (Shulkin, 1989, 1991, 1992a). The mats have a pillow-like form up to 2 m^2 area and 20–30 cm thick and provide a substratum for numerous burrowing molluscs, tubicolous polychaetes and cerianthids (Plate 3A). In the surface layer of the mats, the content of chlorophyll *a* ranges from 0.8 to 1.5 g m^{-2}, and the phaeophytin content from 2.5 to 3.0 g m^{-2}.

The diatom *Thalassiosira anguste-lineata*, population density 2.2×10^{10} cells m^{-2}, dominates the microphytobenthos in the southeast part, in the region of the stream mouth, on the warm (up to 20 °C) pebble bottom, and in the southwest part (area of the outlet from the bay) on underwater slopes at depths from 1 to 10 m (Figure 20). The population density of the diatoms was so high in some areas that they covered the surface of rocks, pebbles and sandy bottom with a thin film, colouring the seabed red-brown.

Bacterial mats (Plates 1B, 3B, 9A) develop in zones of hydrogen sulfide venting (Figure 20). The temperature in the littoral areas where they develop ranges from 20 to 30 °C, whereas ambient temperature even in summer is only 8–12 °C. The hydrogen sulfide content in these vents is 6–7 mg l^{-1}. Photosynthesising bacteria dominate in such mats: purple sulfur bacteria *Thiocystis violacea* (10^8 cells ml^{-1}), *Thiocapsa roseopersicina* (10^3 cells ml^{-1}), non-sulfur purple bacteria *Rhodobacter* sp. (3×10^8 cell ml^{-1}), and anaerobic green bacteria *Prosthecochloris aestuarii* (5×10^3 cells ml^{-1}). In addition, there are abundant sulfur-oxidising and methane-oxidising bacteria. Aerobic lithoautotrophs, including *Thiobacillus* sp. (10^6 cells ml^{-1}), *Thiomicrospira*

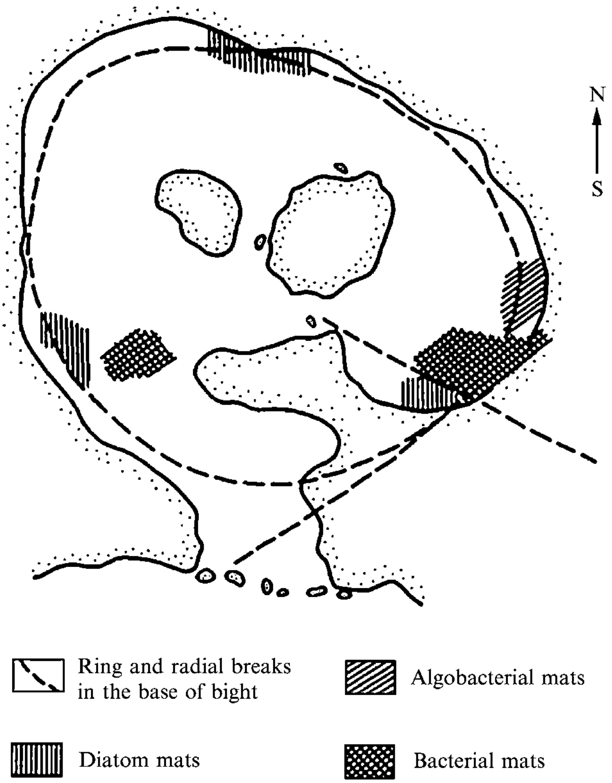

Figure 20 Distribution of the different types of mats on the bottom sediments in Kraternaya Bight.

pelophila (10^4 cells ml^{-1}) occur there together with the facultative autotroph *Thiosphaera* sp. (10^6 cells ml^{-1}) (Starynin *et al.*, 1989; Namsaraev *et al.*, 1991; Nesterov *et al.*, 1991).

Mats of colourless sulfur-oxidising bacteria of the genus *Thiothrix* also occur in the littoral zone in areas of hydrogen sulfide venting that have comparatively low sulfide content (0.2–2.2 mg l^{-1}). These microorganisms are often seen as a white fouling on the brown seaweed *Fucus evanenscens*, and as a secondary epiphyte on filiform green microalgae growing on the *Fucus* (Starynin *et al.*, 1989; Namsaraev *et al.*, 1991; Nesterov *et al.*, 1991).

The number of photosynthesising bacteria decreases with increasing depth (<1–2 m), but the population density of *Thiobacillus* and *Thiothrix* is higher than in the littoral mats. The activity of these bacteria leads to a large amount of elemental sulfur (up to 55.1 mg l^{-1}) in the sediment under the mats (Nesterov *et al.*, 1991).

Bacterial mats occur in two areas of the bight at greater depths (Figure 20). These deeper mats are most common in the southeast area, at 5–30 m. Gas-hydrothermal vents are rich in hydrogen sulfide (240–340 μmol), ammonia (up to 40 μM), orthophosphate (up to 10 μM), silicate (up to 3,000 μM) and in dissolved heavy metals. The mats form on underwater slopes of pebbles, gravel, sand and silt around the vents as loose white formations 1–2 cm thick, and up to several square metres in area (Plate 3B). In such places the temperature of the bottom varies from 12 to 40–50 °C. (Tarasov, 1999). Sulfur bacteria *Thiobacillus* sp. or colourless sulfur bacteria *Thiothrix* sp., *Beggiatoa mirabilis*, or bacteria formerly attributed to the group of colourless filiform thiobacteria known as *Thiodendron* (Perfilyev and Gabe, 1969; Schmidt, 1981), dominate the mats. In 1993 this latter genus was described as a syntrophic association of bacteria made up of free-living spirochaetes (three new spirochaete species of the genus *Spirochaeta* have been described from mats of Kraternaya Bight) and sulfate-reducing *Desulfobacter* (Dubinina *et al.*, 1993a,b; Leshcheva, 1997). The old name "Thiodendron" has been continued here (Plate 4A). Beyond these groups of bacteria, non-sulfur purple bacteria *Rhodobacter* sp. of density 10^3–10^6 cells ml^{-1} and a small number of diatoms *T. anguste-lineata* occur in mats at depths of 15–25 m (Nesterov *et al.*, 1991; Tarasov *et al.*, 1991). The distribution and development of *Rhodobacter* sp. in mats under conditions of low light have been explained by their ability to combine photoautotrophic and chemoheterotrophic growth (Nesterov *et al.*, 1991). The varying temperatures at different vents (12–50 °C) do not seem to alter the species composition and structure of the mats.

Where the underwater slopes of Kraternaya Bight flatten into a rather silty bottom (deeper than 25 m), bacterial mats can be seen on the seabed as white perforated films <1 mm thick, occupying areas of up to 100 m^2. The base of the mats is composed of sulfur-oxidising microbes and the colourless sulfur bacterium *Beggiatoa mirabilis*. The interstitial water under these mats has a high content of H_2S (>200 μM), high NH_4 (up to 40 μM) and high orthophosphate (8–12 μM).

A second area of distribution of bacterial mats is in the southwest part of the bight (Figure 20). Mats develop at the bottom of a sandy slope at depths of 10–15 m. The mats cover areas of 1–2 m^2 and consist mostly of bacteria of the "Thiodendron" association (Plate 4A).

Algobacterial mats form along the east and southeast coasts of the bight at depths from 2 to 10 m in zones of gas-hydrothermal venting and seepage of volcanic fluids (Figure 20; Plates 4B, 5A). They are layered and jelly-like formations 1–3 cm thick, located on sandy-gravel and pebble bottoms with a high content of elemental sulfur. The temperature of the sediments under the mats ranges from 20 to 40 °C. The mats reach maximum thickness at temperatures of 30–40 °C; their wet weight is $\sim$25–30 kg m^{-2}, with a dry weight of 5–6 kg m^{-2}. Most of the dry mass of mat (95–98%) consists of inorganic material, mostly silica and particles of sulfur. These mats are inhabited by a great number of psammophilic ciliates *Trachelorapsis incaudatus, Trachelorapsis* sp., *Prorodon* sp., with population densities of 47 ± 20 10^4 cells m^{-2} and biomass 90 mg m^{-2} (Medvedev, 1991). Nematodes (up to 2×10^6 ind. m^{-2}) (Plates 5B, 6A) and small polychaetes are abundant. The water under these mats contains trace amounts of oxygen and high concentrations of hydrogen sulfide (up to 90 μM), ammonia (up to 23 μM) and orthophosphate (12 μM). The fluids also contain heavy metals (Shulkin, 1989). The outer surface of the mats is covered with a thin but dense film of white or brown colour. This film is made up of particles of elemental sulfur, together with sulfur-bacteria and colourless sulfur bacteria (Starynin *et al.*, 1989). Under the outer film, there is a loose layer of diatoms, dominated by *Melosira moniliformis, Comphonemopsis exiqua* and *T. anguste-lineata*. The population density of microalgae is $4.6 \pm 0.9 \times 10^{10}$ cells m^{-2}, and the biomass is 80.8 ± 10.8 g m^{-2}. Photosynthesising bacteria *Thiocystis violacea* and *Rhodobacter* sp. (up to 10^6 cells ml^{-1}) can be chemotrophic in darkness and occur in the same layer. Anaerobic green sulfur bacteria, anaerobic saprophytes and sulfate-reducing bacteria occupy the bottom layer of the mat (Starynin *et al.*, 1989; Tarasov *et al.*, 1990; Nesterov *et al.*, 1991).

The algobacterial mats have a high content of chlorophyll *a*, and values were similar in different years, being 1.31 ± 0.5 in 1987 and 1.30 ± 0.3 g m^{-2} in 1988; pheophytin values reached 4.3 ± 1.2 and 5.9 ± 0.9 g m^{-2} in respective years.

After removal of 25 × 25 cm patches of mats from zones of seepage of volcanic fluids, the mat cover was restored in 25 days (Tarasov *et al.*, 1991; Tarasov, 1999).

In the remaining areas of Kraternaya Bight, two diatom species, *T. angustelineata* and *Pleurosigma* sp., with population densities up to 1.6×10^{10} cells m^{-2}, dominate the microphytobenthos in sand and silt-sand at depths from 3 to 20–30 m.

At depths exceeding 25 m, below which the steep slopes of the underwater part of the crater level off to a flat silty seabed, autotrophic and facultative autotrophic sulfur-reducing bacteria of the genera *Thiobacillus, Thiomicrospira, Thiosphaera* (up to 10^3–10^6 cells ml^{-1}) occur, together with the colourless sulfur bacterium *Beggiatoa mirabilis* (Nesterov *et al.*, 1991).

4.2.2. Matupi Harbour

In Matupi Harbour, bacterial mats occur only in Tavurvur venting Area II (Figure 8; Plate 6B). Their species composition and thickness (from 0.5 up to 2 cm) vary according to depth and bottom character (Tarasov *et al.*, 1999).

In the littoral zone and to a depth of 1 m, where the temperature of surface of the silty-sand bottom is 50–65 °C, the microbial mats have a loose or perforated film structure up to 0.5 cm thick. This consists of the filamentous "Thiodendron" bacterial association together with the colourless sulfur bacteria *Beggiatoa*. Cyanobacteria and benthic diatoms occur in small numbers.

The thickness of the mat increases to 1.0–1.5 cm at depths of 4–6 m, where numerous vents break through the sand ground, with a seabed temperature of 50 °C. The upper layer containing abundant filiform cyanobacteria can be identified by a high content of chlorophyll *a* (86 mg m^{-2}). There are only a few diatoms. Under the layer of cyanobacteria, there is a loose white structure, consisting of abundant "Thiodendron" association, the sulfur bacteria *Beggiatoa* sp. and *Thiovolum* sp., as well as particles of elemental sulfur, silt and slime.

In the same volcanic zone, there is strong venting at depths of 3–5 m, issuing between hardened lava streams and boulder blocks. Bacterial mats up to 2 cm thick form in cracks and on the lateral walls of lava blocks and boulders. Flows of hot fluids, traceable by their whitish colour, wash the mat surface and carry particles and scraps of bacterial mat to the water surface. The temperature of these vents varies from 45 to 75 °C at different sites. The vent flow contains much hydrogen sulfide, up to 760 μM. These mats also include the "Thiodendron" association, with numerous sulfur bacteria and cyanobacteria in the upper layer.

4.2.3. Bay of Plenty

In the Bay of Plenty, algobacterial and bacterial mats are formed only in MacEwans Bight (Whale Island), with a thickness of 0.3–1.0 cm. The algobacterial mats are found mostly at 3–7 m depth. Individual patches of diatom mats occur on the seabed at temperatures of 30–35 °C.

Mats 0.3–0.5 cm thick occur in the bay between jets of gas at a depth of 4 m, with seabed temperatures of up to 55 °C. The hydrogen sulfide content of the water under the mats is only 1.2 μM. The mats contain a loose layer of diatoms, with the surface covered by a film composed of the "Thiodendron" bacterial association, filamentous colourless sulfur bacteria *Beggiatoa* sp., large unicellular forms of thiobacteria *Thiovolum* sp. and particles of elemental sulfur and silt.

The algobacterial mats increase in thickness up to 1 cm on silt-sand bottoms at the depths of 7 m where there is a trace of hydrogen sulfide and a seabed temperature of 30 °C. The upper layer of these mats consists mostly of a film of the "Thiodendron" bacterial association, under which diatoms are settled. The chlorophyll *a* concentration in the Bay of Plenty mats is lower than in the mats at Kraternaya Bight, only 170 mg m^{-2}.

With an increase in depth, the number of diatoms in the mats decreases. At depths exceeding 7 m, the 0.3–0.5 cm thick mats consist of the "Thiodendron" bacterial association, with *Beggiatoa* sp. and thiobacteria. The concentration of hydrogen sulfide under the mats was 1.3 μM.

In some bottom areas, mats of colourless *Thiothrix* and thionic bacteria can also occur at various depths from 3 to 12 m. They form a thin film, 0.1 cm thick, differing from the "Thiodendron" mats in containing small white lumps.

4.3. Meiobenthos

4.3.1. Kraternaya Bight

In Kraternaya Bight, there are 19 taxonomic groups of meiobenthos. A full description of species structure has been made only for the Foraminifera (Lukina and Tarasova, 1991), and some nematodes of the genus *Theristus* (family Xyalidae) and the genus *Gobbia*, of which a new species, *Gobbia kamenevi*, has been described (Fadeeva and Malyusheva, 1991).

The different taxonomic groups of meiobenthos differ in their distribution (Tables 27–30). In the east part of the bight, the number of species within each taxon is low, relative to the western part of the bight. For example, in the east basin, species diversity of Foraminifera decreases 2.0–2.5 times, and in the zone of hydrogen sulfide gas-hydrothermal vents, the Foraminifera, of which *Eggerella advena* was a major species, are much reduced in species

Table 27 Density (10^3 ind m^{-2}) of major groups of meiobenthos in the surface layer (0–1 cm) of soft bottom of the littoral of Kraternaya Bight

Taxon	Southern part of the eastern basin	Area of mouth volcanic brook	Eastern zone of gas-hydrothermal vents	Strait, eastern shore	Outside Yankich Island (background)
Nematoda	723	990	10.4	27	77
Harpacticolda	5	0	0	2	232
Amphipoda	1.4	0	0.1	0	0
Ostracoda	1.6	0	0	0	0
Polychaeta	1	0	0	0	0
Turbellaria	0	320	0	51.2	0
Cillata	0	5	0	70	722
Gastropoda	0.2	0	0	0	0
Total:	732.2	1315	10.5	150.2	1031

Source: Unpublished data of Professor A. Adrianov, Institute of Marine Biology and Professor V. Malakhov, Moscow State University.

Table 28 Density (10^3 ind m^{-2}) of major groups of meiobenthos and their vertical distribution in the brush of sedentary polychaete *Polydora vulcanica* in Kraternaya Bight

	Layer of the brush, cm				
Taxon	0–1	1–2	2–3	3–4	16–17
Nematoda	9672	3750	1716	1670	859
Harpacticoida	853	10	0	0	0
Turbellaria	285	150	140	0	500
Cladocera	142	0	0	0	0
Ciliata	140	0	0	0	0
Polychaeta	130	0	0	0	0
Bivalvia	9	9	8	0	0
Foraminifera	0	0	0	0	0.6
Total:	11,059	3919	1864	1670	1359.6

Source: Unpublished data of Professor A. Adrianov, Institute of Marine Biology.

Table 29 Density (10^3 ind m^{-2}) of major groups of meiobenthos in the mats and in the surface (0–1 cm) of bottom sediments in sublittoral of the eastern basin of Kraternaya Bight

	Bacterial mat	Algobacterial mat	Sand	Silty-sand	Silt in zone vents	Silt
	Depth, m					
Taxon	2–5	3–5	7–10	15	20–25	30–40
Nematoda	23.3	1004	37	84	589	197
Harpacticoida	0	44	1.7	33	16	18
Halacaridae	0	0	0	0	9	0
Ostracoda	0.6	28	0	0	0	0
Cladocera	0	9	0	0	0	0
Polychaeta	0	0	0.5	0	50	1.7
Turbellaria	0	35	0	1	9	0
Nemertini	0	0	0.5	0.6	0	0
Hydrozoa	0	0	0	0.1	0	0
Bivalvia	0	0	9.5	0.5	0	0
Ciliata	1	160	0	61	0	0
Foraminifera	0	0	0.5	0.4	0	0.1
Total:	24.9	1280	49.7	181	673	216.8

Source: Unpublished data of Professor A. Adrianov, Institute of Marine Biology, and Professor V. Malakhov, Moscow State University.

Table 30 Density (10^3 ind m^{-2}) of major groups of meiobenthos in the diatom mat and in the surface (0–1 cm) of bottom sediments in sublittoral of the western basin of Kraternaya Bight

Taxon	Diatom mats in the northern vents	Sand bottom in the southwestern part of the bight	Sand bottom between two islets of the bight	Silt bottom		Sand bottom outside Yankich Island (near Kolpak Rock)
	Depth, m					
	8–12	5–7	20–25	40	55	30
Nematoda	128	296	3.3	350	364	66
Harpacticoida	196	156	23	9	0	240
Halacaridae	0	0	2.7	0	0.5	0
Ostracoda	200	9.6	0.5	9.5	0	2
Gastrotricha	0	3	0	0	0	1
Amphipoda	0	2.6	0	0	0	0.5
Isopoda	0	0	0.5	0	0	0.5
Tanaidacea	0	0	1.1	0	0	0
Polychaeta	3.7	4.8	44	0	0.6	0.8
Oligochaeta	0	0	0	0	18	0
Turbellaria	0	3.2	0	8.5	0	0
Nemertini	0	5	10.3	0	0	0
Hydrozoa	0	5	0	0	0	0
Anthozoa	0	0	0.5	0	0	0
Bivalvia	0	14.8	0.5	0	0	0
Gastropoda	0	1.6	0	0	0	0
Priapulida	0	0	0.4	0	0	0
Ciliata	30	2	0	0	0	1.5
Foraminifera	16	3.2	0.5	0.1	0.1	0.5
Total:	573.7	506.8	87.7	377.6	383.8	312.8

number and population density. Species with calcareous shells are absent in all venting areas (Lukina and Tarasova, 1991), probably as a result of low pH values in the bottom sediments, through which the hydrothermal fluids diffuse. The species composition of the calcareous Foraminifera in the bight did not differ much from that of the waters outside Yankicha Island, but the shells in Kraternaya Bight were much smaller than shells of the same species inhabiting ambient seawater outside the bight.

In the littoral zone of the east basin the greatest number of taxa occurs in its southern part, over a large area of the seabed where the surface is covered with silted coarse sand, particles of iron oxide and with rocks protruding from the bottom (Table 27). During low tide numerous small gas-hydrothermal vents can be seen, containing abundant iron, manganese and other metals (Plate 7A). On the seabed there are sites of dead thalli of *Fucus evanescens* and polychaete tubes covered with iron oxides. Here, nematodes dominate the meiobenthos, accounting for 99% of the total number of organisms.

The composition of the seabed changes closer to the mouth of the volcanic brook. Stones and pebbles often have a yellow colouring resulting from deposits of elemental sulfur. The surface of the bed between stones was covered with a thin layer of clay particles coming from vents and the brook. Species diversity of meiobenthos is poor there, but population density is appreciably greater, compared with the area outside the venting zone (Table 27). Small nematodes (75% of the total quantity of meiobenthos) and Turbellaria (24%) dominate the fauna. The population density of these groups of animals was extraordinarily high for such types of bottom sediments (e.g., nematodes, $\sim 10^6$ ind m^{-2}). This appears to be related to the high number of diatoms and sulfur bacteria (see Section 4.2) that form the basic food of the meiobenthos.

Groups of the sedentary polychaete *Polydora vulcanica*, with a population density of $\sim 10^6$ ind m^{-2}, occur in the lower littoral zone in the western basin near the channel, where the basement fault of the bight runs under the bottom sediments. Their tubes formed dense "brushes" of up to 1–2 m^2 area and 15–20 cm high. These brushes are covered by a film inhabited by diatoms and the filamentous colourless sulfur bacterium *Beggiatoa mirabilis*. The highest density of meiobenthos occurs in such polychaete settlements. On the surface layer of the brush (0–1 cm), the numbers of meiobenthos can exceed 1.1×10^7 ind m^{-2} (Table 28). Tubes of polychaetes and fine-grained sand between the tubes serve as substratum for meiobenthos. The interior and exterior surfaces of a single polychaete tube can contain 10–20 individual nematodes and 2–3 turbellarians. Large ciliates of the genera *Trachelorhaphis* and *Condylostoma* (2–3 ind.) and Harpacticoida (2 ind.) are also found.

Quantitative data on the surface layer of the brush and vertical distribution of population density of basic taxa are given in Table 28. The density of nematodes and harpacticoids is maximal there, higher even than in enclosed highly eutrophic bays with silty bottoms or in regions of aquaculture, in which densities may reach several million individuals per square metre (Galtsova, 1991). A sharp decrease of population density of harpacticoids and ciliates in the lower layers of the brush is explained by lack of food, diatoms and bacteria, which mostly live in the surface layer of the brush. Small mobile turbellarians and large *Leptoplana* (Polyclada) were distributed uniformly in deeper layers together with nematodes. The brush constitutes a porous entity that provides aeration of all layers, both from above and from below. During high tides, water rises from the underlying layer of sand. The maximum population density of meiobenthos in the littoral zone was observed in these local settlements of polychaetes, which in their turn form aggregations in sites of gas-hydrothermal venting.

In the same region of the bight, in the sand bottom of the littoral zone of the channel (outside the brushes of *Polydora*), the abundance of meiobenthos is two orders of magnitude lower. Meiobenthos are here represented mainly by three taxa (Table 27), in which ciliates form 47%. The population density of all groups of animals was low (1.5×10^5 ind m^{-2}). There are strong tidal currents in this area, which agitate the sand bottom and change bottom relief. This mobility of the substratum under the effect of the tidal flow appears to be a major factor determining the poor species diversity and low density of meiobenthic populations.

In the sublittoral zone of the bight, the qualitative and quantitative characteristics of meiobenthos and the vertical distribution of the animal groups differed appreciably between the mats and different types of bottom sediments (Tables 29 and 30).

The meiofauna in bacterial mats in the southeast part of the bight at depths from 1 to 20 m is characterised by low species diversity and population density (only $\sim 2.5 \times 10^4$ ind m^{-2}) Nematodes prevailed (94% of total number of organisms). The main mass occurred in the most superficial layer of the mat (Figure 21). In mats of *Beggiatoa mirabilis* at depths exceeding 20 m, the meiobenthos is chiefly nematodes and oligochaetes of the family Tubificidae. Population density of these settlements was high, $1.0–1.5 \times 10^5$ ind m^{-2}.

In the algobacterial mats, there is an abundance of meiofauna (Table 29; Plate 6A). Nematodes constitute the greatest component of the population (78%, exceeding 90% at some sites). Their density reaches 1.8×10^6 ind m^{-2}. Nematodes and large ciliates occupy the surface layer of the mat, between the layer of thionic bacteria and a loose mass of diatoms. Other meiofauna groups are present in the lower layers of the mat.

In other areas of the east basin, the composition of the meiofauna depends mostly on the character of the bottom sediments. At shallow depths (5–15 m) on steep slopes of sand and silty sand, only a few taxa at rather

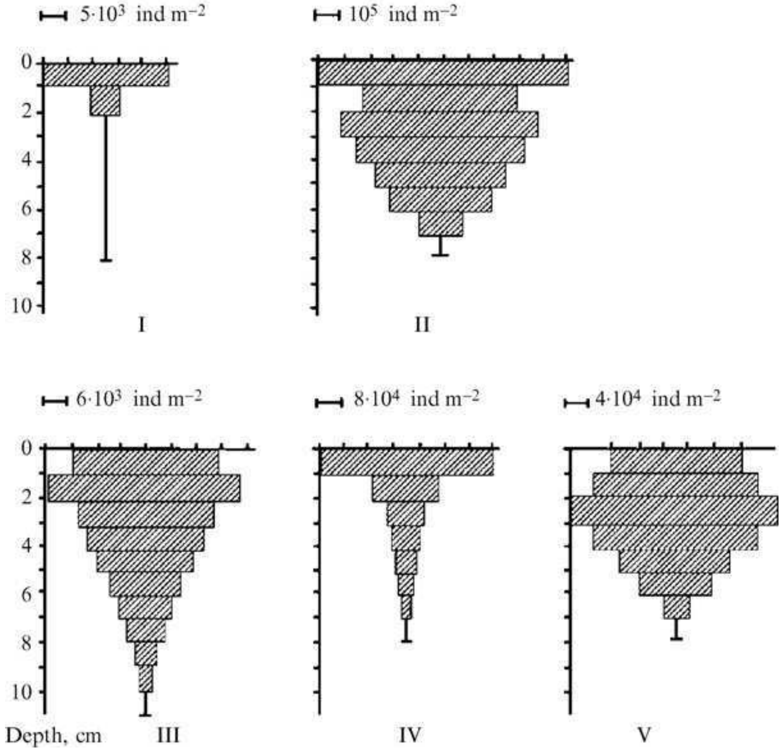

Figure 21 Vertical distribution of nematodes in the mats and bottom sediments of the eastern basin of Kraternaya Bight. (I) bacterial mats; (II) algobacterial mats; (III) silty-sand sediments; (IV) silt bottom in zone of strong vents at 20–25 m depth, (5) silt bottom in the central part of eastern basin at 40 m depth (unpublished data, courtesy Professor A. Adrianov, Institute of Marine Biology).

low population density have been recorded (Table 29). There is a decrease of population density with depth into the sediment (Figure 21).

A rich fauna of nematodes (88% of the total number of meiobenthos) and small polychaetes (7%) develops at a depth of 20–25 m in silty bottoms where there are strong outflows from gas-hydrothermal vents (Table 29). The tube walls of *Cerianthus lloydii* and the mucous sheaths of the large polychaete *Myxicola infundibulum* provide peculiar additional substrata for meiobenthos and form settlements of high population density in that region of the bight. The tubes of these animals penetrate deep in the silty bottom, and movement of the polyps and worms inside the tubes provides aeration. As in the littoral brushes of *Polydora*, this habitat is extensively inhabited by meiobenthos, including small polychaetes such as *Pholoe minuta* and *Eteone* *longa*. Nemertines (Hoplonemertini) are also numerous, as are the larger nematodes of the genus Leptosomatidae.

In silty sediments in the centre of the east basin at depths of 30–40 m, the population density of the meiobenthos is reduced (Table 29). Nematodes dominate there (91%), the number of individuals increasing with depth in the sediment. Population density is at a maximum at 2–3 cm depth (Figure 21).

Compared to the east basin, there is greater taxonomic diversity of meiobenthos in the sublittoral zone of the west basin, but in diatom mats, the density of the dominant nematodes is significantly less (Tables 29 and 30).

In the northern part of the venting area, three taxa prevail in the diatom mats: ostracods (35%), harpacticoids (34%) and nematodes (22%). A significant increase in crustaceans in the diatom mats is probably related to the absence of hydrogen sulfide in the hydrothermal fluids of this part of the bight. In the mats the maximum numbers of crustacea occur in the surface layer, but nematodes are commoner at 4–5 cm depth (Figure 22).

The richest meiofauna is found in the southwest part of the west basin (Table 30), with nematodes (58%) and harpacticoids (31%) dominating. Other groups of crustaceans also inhabit the surface layer of sand and occur under the surface of diatom mats that cover the seabed. For all crustaceans (Table 30), the taxonomic diversity and abundance increase away from the southeast part, where the maximum venting is observed. It is worth noting that the bivalve *Mysella kurilensis* and juveniles of *Macoma* in that area are overgrown by solitary hydroid polyps, which are absent in other parts of the bight. Small sedentary maldanid worms are the dominant polychaetes.

A few taxa occur in part of the bight on a silty bottom at 40 m depth (Table 30). The commonest are nematodes with high population density, up to $4 \cdot 10^5$ ind m^{-2} and 93% occurrence. The vertical distribution of nematodes in sediments shows two peaks, one in the surface layer and another at 3 cm depth (Figure 22).

Nematodes (95%) and oligochaetes (5%) occur in the meiobenthos in silt sediments of the centre of the west basin at depth 55 m (Table 30). The maximum population density of nematodes is found in silty bottoms at a depth of 2–3 cm, but large numbers occur in deeper layers of sediment (Figure 22). Tubificid oligochaetes occur mostly in the 2–3 cm layer.

Outside Yankicha Island, in the vicinity of Kolpak Rock, there is a rich fauna of meiobenthic organisms with a high population density (3×10^5 ind m^2) at depths of 30 m in coarse sand with slight silting. The fauna consists mostly of harpacticoids (76% of total population density of meiobenthos) and nematodes (21%). The rest consists of ostracods, infusorians and gastrotrichs (Table 30).

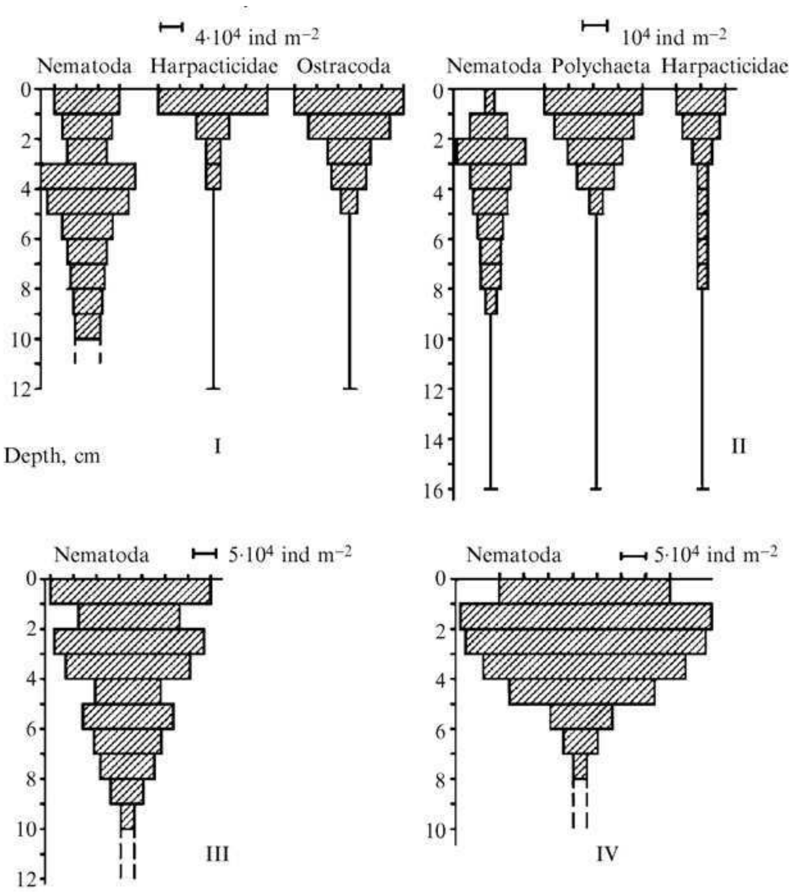

Figure 22 Vertical distributions of some group meiobenthos in the soft bottom of the western basin of Kraternaya Bight. (I) diatom mats in the northern venting zone; (II) sand bottom; (III) silt bottom at 40 m depth; (IV) silt bottom at 55 m depth (unpublished data, courtesy Professor A. Adrianov).

The meiobenthic fauna of Kraternaya Bight is thus characterised by rather high taxonomic diversity, compared with other marine bays and fjords. The greatest numbers of taxa occur in the outlet area in the southwest part of the bight, the least in the zone of littoral hydrogen sulfide gas-hydrothermal vents and in bacterial mats in the southeast part of the bight. Nematodes and ciliates are found at very high population densities in algobacterial mats and in aggregations of macrozoobenthos (cerianthids, polychaetes and bivalves) around vent outlets.

4.3.2. Matupi Harbour

In Matupi Harbour, the taxonomic structure and distribution of bottom invertebrates is mainly determined by volcanic activity, bottom relief and the distribution of soft and hard substrata within the bay (Tarasov *et al.*, 1999).

In Tavurvur venting Area I (Figure 8), at sites of hot fluid seepage (85–90 °C) through black volcanic sand, there is no flora or fauna in the littoral zone or down to 6–8 m deep. Meiobenthic nematodes (70% of the total number of animals) and harpacticoids (30%) in the upper layer of sediment increase with depth, with decrease of temperature at the seabed to 50–60 °C and with silting of the surface of bottom slopes (Table 31). The taxonomic diversity of the meiobenthos is greater at depths exceeding 10 m, with a further increase of silting and a temperature decrease to 30–40 °C, nematodes and harpacticoids being dominant by population density. The remainder of the meiofauna is not significant (Table 31).

In Tavurvur venting Area II, small *Polydora* sp. prevail in the meiobenthos of bacterial mats at depths of 0.5–6.0 m, covering hot (>60 °C) underwater sandy slopes through which gas and thermal fluids seep (Plate 6B). These worms build tunnels penetrating the mat and upper layers of bottom sediment under mats to a depth of 2–3 cm. The tunnel walls in the sediment are covered with a layer of filamentous colourless sulfur bacteria. The population density of spionid polychaetes reaches 2×10^3 ind m^{-2}, comprising >90% of total meiobenthos (Table 31).

At depths exceeding 8–10 m, the silty-sand bottom of the slopes showed small conic structures or hillocks perforated by numerous apertures of 0.5–1.0 cm in diameter. These hillocks and apertures represented recent gas activity, which is variable at that site. Scraps and particles of bacterial mats, which roll down the slope from above, accumulate between the hillocks, silting the seabed, and increased numbers of meiofauna taxa occur there. Nematoda (up to 70%) and Polychaeta (25–30%) are commonest. At sites where the bottom temperature is 50–60 °C, the density of nematodes decreases significantly while harpacticoids increase (Table 31).

The Rabalankaia volcanic zone (Area III) is distinguished by extensive areas of hot seabed and strong output of hydrothermal fluids, which occur from the littoral zone to depths of 27 m. From the edge of the water to depths of 5 m, the seabed consists of a hot (50–60 °C) rocky platform covered with clay particles. Only one species of large oncholaimid nematode, with a population density of 1.3×10^5 ind m^{-2}, was found in meiobenthos in this area (Table 31).

The rocky platform ends 5 m deeper, and the seabed changes to a sandy slope with exposed boulders. The temperature in the surface layer of sand is

Table 31 Density of meiobenthos (10^3 ind m^{-2}) in bacterial mat and bottom sediments (0–1 cm layer) in Matupi Harbour

	Tavurvur (Area I)			Tavurvur (Area II)					Rabalanakaia				Western part		Central	Blanche Bay	
	Silty-sand			Bacterial mat	Silty-sand				Silty-sand				Silt		Silt	Silt	Sand
	Depth, m																
Taxon	8	14	20	6[a]	11	16[a]	16	20	5[a]	9	18	27[a]	2	8	50	10	22
Nematoda	29	33.1	44.6	0.2	3.8	1.5	4.6	8.7	131	7.7	25	3.1	83.9	65.5	+	+	+
Harpacticoida	12.7	5.4	15.8	0	0.4	1.5	0.2	1	0	1.5	1.9	1.2	11.5	2	+	+	+
Ostracoda	0	0	0	0	0	0	0	0.2	0	0	0	0	+	+	+	+	+
Polychaeta	0	3	3	2	1.2	0	2.1	2.7	0	1.5	1.9	1.2	2.7	3.9	+	+	+
Konorhyncha	1.1	0.7	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sipunculida	0	0	+	0	0	0	+	+	0	0	0	0	0	2	0	0	0
Turbellaria	0	0	0	0	0.4	0	0	0	0	0	0	0	0	0	0	+	0
Total:	42.8	42.2	68.4	2.2	5.8	3.0	6.9	12.6	131	10.7	28.8	5.5	98.1	73.4	+	+	+

[a] Sediment T° 50–60 °C; "+", only single individuals present.

Source: After Tarasov *et al.*, 1999.

30–45 °C. The number of taxa of meiofauna increases, but the population density of animals is still low. Nematodes dominate by their relative number, 83–93%.

At depths of 25–27 m, between ring- and conical hydrothermal structures and hot diffuse vents (Tarasov *et al.*, 1999), the bottom consists of silty sand containing abundant sponge spicules. No meiobenthic animals are found in the sediments between ring-structures and around them. Nematodes, harpacticoids and polychaetes occur in the bottom sediment only near the outer slopes of ring hydrothermal structures.

In the western part of Matupi Harbour, where vents do not occur, the bottom slopes gently (20–30 degrees) and is covered by silty sediments from the littoral zone to depths of 30 m. A high diversity and population density of meiobenthos is found here. Nematodes dominate (79–89%), while harpacticoids (3–11%) and polychaetes (3–5%) also occur. The total number of meiobenthic animals reaches 9×10^4 ind m^{-2} (Table 31).

In the central part of Matupi Harbour, and in the Rabalanakaia area, at depths of 45–55 m where the sediments are silty and contain numerous sponge spicules, there is little meiofauna or macrofauna. Single nematodes and small polychaetes occur, together with harpacticoids, ostracods and sipunculids, to a total density of <100 ind m^{-2}.

4.3.3. Bay of Plenty

In the Bay of Plenty, in MacEwans Bight, there are the highest population densities and biomass of benthic animals recorded in all the studied areas of shallow gas-hydrothermal activity. There is a rich meiobenthic fauna in the algobacterial and bacterial mats in this bight (Table 32), with nematodes (up to 2.11×10^5 ind m^{-2}) and harpacticoids (up to 3.9×10^4 ind m^{-2}) dominant. Three nematode species of the family Desmodoridae have been recorded in bacterial mats. Exosymbiotic bacteria occur on the surface of the cuticle of these (Tarasov, 1999), and judging from intracellular inclusions of sulfur, the microbes belong to the group of colourless sulfur bacteria. Their cells merge at one end of the body of the nematode to form a continuous layer, leaving free the anterior end as far as the secretory pore and the caudal part up to the anus (Figure 23).

Outside the zones of volcanic activity only a few nematodes occur in the sand bottom (Table 32). In Volcanic Crater only single nematodes occur in the meiobenthos, and other groups of meiofauna are not found. In the Calypso area, nematodes, harpacticoids, small polychaetes and copepods are present in the meiofauna on silt bottoms at depths of 150–200 m.

Table 32 Density (10^3 ind m^{-2}) of major groups of meiobenthos in the mats and in the surface (0–1 cm) of bottom sediments in the gas-hydrothermal zones of MacEwans Bight

Taxon	Algobacterial mat	Bacterial mat	Silty-sand sediments covered with iron oxides		Silty-sand sediments outside the vents area (control)
Nematoda	211.0	75.6	7.0	5.5	1.2
Harpacticoida	11.0	39.2	5.6	1.4	0
Ostracoda	14.0	47.6	0	0	0
Amphipoda	1.5	2.8	5.6	0.6	0
Isopoda	0	4.2	0	0	0
Tanaidacea	1.5	0	0	0	0
Cumacea	0	1.4	0	0	0
Polychaeta	1.5	0	0	0	0
Kinorhynchia	0	0	0	0.3	0
Gastrotricha	0	0	0	0.3	0
Total:	240.5	170.8	18.2	8.1	1.2

Source: Unpublished data of Professor V. Malakhov, Moscow State University.

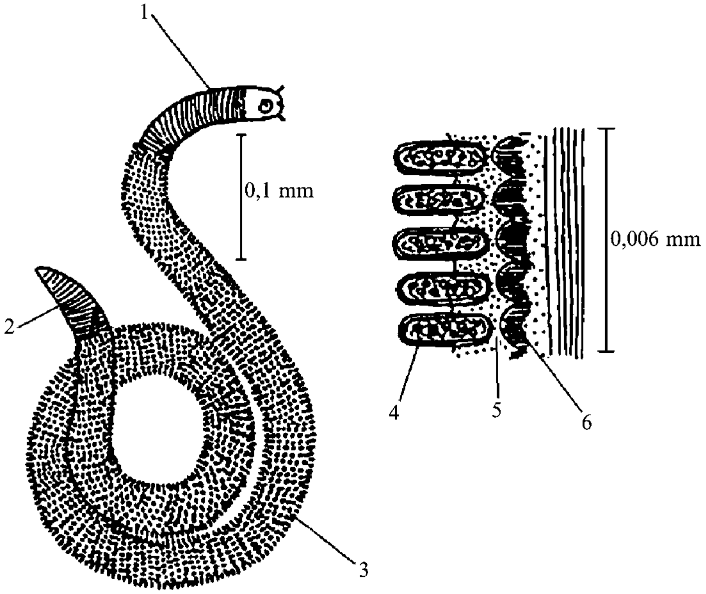

Figure 23 Colourless sulfur bacteria located on the body surface of an individual of the nematode family Desmodoridae. (1) head of nematode free of bacteria; (2) caudal part of nematode; (3) bacterial cover; (4) bacteria with elemental sulfur in the cell; (5) mucus attaching bacteria to the cuticle, (6) cuticle (unpublished data, courtesy Professor V. Malakhov, Moscow State University).

4.4. Macrobenthos

4.4.1. Kraternaya Bight

The macrobenthos has been the most comprehensively studied of all the basic biological components of the ecosystem of the bight. The composition and structure of the bottom communities, both in the bight and outside, have been recorded by Tarasov *et al.* (1985, 1986, 1990), Kamenev (1991a,b, c), Kostina (1991), Levenets (1991), Kussakin and Kostina (1996) and Tarasov (1999, 2002). Patterns of distribution of individual species, as well as of groups of zoobenthos, their taxonomic composition and characteristics of new species have been described (Kamenev, 1989, 1990; Buzhinskaya, 1990; Bagaveyeva, 1991; Budnikova, 1991; Moshchenko and Gladkov, 1991; Radashevsky, 1994; Kamenev *et al.*, 2004). Oxygen metabolism, bacterial endosymbiosis, some biochemical and genetic characteristics of the common species of macrobenthos and mats, and microelemental composition of brown algae have been analysed (Khristoforova and Malinovskaya, 1991; Khotimchenko, 1991; Kuznetsov and Gebruk, 1991; Nikiforov and Zaslavskaya, 1991; Muzyka and Tarasov, 1991; Tarasov, 1991c; Zhukova *et al.*, 1991, 1992; Nikiforov, 1993; Kharlamenko *et al.*, 1995; Nikiforov, 1997; Tarasov *et al.*, 2003). Full lists of species, population density and biomass of macrobenthos of the bight are given by Kamenev (1991b,c), Kostina (1991), Levenec (1991) and Kussakin and Kostina (1996).

4.4.1.1. Littoral zone

The littoral (=intertidal) zone of Kraternaya Bight, with a tidal range of 0.8–1.2 m, is mostly composed of gravel, stones and boulders. Insignificant indentation of the coastline of the bight and an almost homogenous granulometric sediment structure determine the zonal distribution of intertidal communities of macrobenthos (Kostina, 1991; Kussakin and Kostina, 1996). Only along the south coast of the east basin is the littoral zone extensive and flat, with sediments and numerous small vents containing an abundance of iron. In the south part of the west basin, the littoral zone of the inlet or channel is sand.

Some 22 macrophytes and 60 animal species have been described from the intertidal of Kraternaya Bight (Kostina, 1991; Levenec, 1991). *Fucus evanescens* dominates the biomass of seaweeds, and the commonest animals are the gastropod *Littorina sitkana* and the barnacle *Balanus crenatus*. Species diversity increases appreciably from the upper to the lower margins of the intertidal (the supralittoral and infralittoral fringes according to Stephenson and Stephenson [1972]). Species number becomes less near hydrogen sulfide vents and only 7 species of macrophytes and 25 species of zoobenthos are then present (Kussakin and Kostina, 1996).

The richest intertidal biota occur immediately at the entrance to the bight, on stones and boulders. A new genus and species of laminarian alga, *Undariella kurilensis*, has been described from this area (Petrov and Kussakin, 1997).

In areas of gas-hydrothermal venting, there are appreciable changes in the qualitative and quantitative composition of the littoral communities, compared with other parts of the bight. Macrobenthic animals are not found in the mouth of the volcanic brook at temperatures of 30–40 °C. However, below the mouth of the brook, the upper intertidal subzone is inhabited by *Littorina sitkana*, the mid-littoral by irregular patches of *Fucus evanescens*; and in the low-littoral, some stones are covered by *Balanus crenatus*.

To the west of the mouth of the brook, *F. evanescens* and aggregations of *B. crenatus* and *Littorina sitkana* occur in the mid- and low-littoral on a silty flat with small vents and on exposed boulders. Brushes of the sedentary polychaete *Polydora vulcanica* with population densities exceeding 10^5 ind m^{-2} and biomass >8.5 kg m^{-2} are found in the low-littoral (Kostina, 1991; Kussakin and Kostina, 1996) and in the southwest part of the bight. These communities of *P. vulcanica* carry a high density of meiobenthic settlements and microflora, as already noted (p. 346). *Polydora vulcanica* from Kraternaya Bay is a new species of spionid (Radashevsky, 1994). Most of the colonies of this spionid are located in the vicinity of gas-hydrothermal vents or volcanic seeps and the area occupied by each varies from one up to 4 m^2. These aggregations of *Polydora* provide a substratum for small numbers of the sea anemone *Charisea saxicola* and the amphipod *Amphithoe volki*.

In southeast and eastern parts of Kraternaya Bight, in areas of release of hydrogen sulfide from vents, *L. sitkana* tends to dominate the upper littoral subzone, and its biomass ($\sim$3.0 kg m^{-2}) is higher than at sites outside the venting zone. In the mid-littoral, brushes of *P. vulcanica* and irregular patches of *Fucus* are covered by bacterial mats of *Thiothrix* sp. Numerous amphipods, nemertines and oligochaetes also live under stones and pebbles here. The brown algae *Pleuropterum paradiseum* and *Alaria marginata*, of low biomass (1440 g m^{-2}), grow in the low littoral. The thalli of the seaweeds are often covered with a white film of *Thiothrix*. The polychaete *Nereis pelagica*, the bivalve *Turtonia minuta* and the barnacle *Balanus crenatus* dominate the zoobenthos at this level, with a total biomass of $\sim$250 g m^{-2} (Kostina, 1991).

In the northern part of the bight, in an area of cooler vents without hydrogen sulfide, the composition of the flora and fauna in the upper and mid-littoral subzones does not show any appreciable differences from areas of the bight located outside of zones of volcanic impact. However, there are populations of *Alaria angusta* with a biomass exceeding 26 kg m^{-2} on the stones and boulders in the low littoral; other seaweeds also occur there, including *Ulvaria splendens, Acrosiphonia duriuscula* and *Melanosiphon* *intestinalis*. In addition to abundant populations of the barnacle *B. crenatus* (1.8 kg m^{-2}) and the predatory gastropod *Nucella freycinettii* (270 g m^{-2}), there are high numbers of amphipods and polychaetes (from 500 to 20,000 ind. m^{-2}) (Kussakin and Kostina, 1996).

A remarkable point about the communities in Kraternaya Bight is the abundance of the barnacle *B. crenatus* in the main part of the intertidal zone (Kussakin and Kostina, 1996). Elsewhere this circumboreal cold-water species is restricted to the sublittoral fringe, the sublittoral zone and shelf-sea bottoms. It appears the larvae are retained within the bight, allowing a high density population to build up.

4.4.1.2. Sublittoral zone

Up to the present, 154 species and subspecies of macrophytes and animals have been identified in the sublittoral of Kraternaya Bight, with polychaetes (45 species) and amphipods (40 species) dominant. Most of the species are widely distributed boreal (42%) and boreoarctic (35%) forms (Kamenev, 1991a).

Two new species and one subspecies of polychaete, *Syllis (Haplosyllis) cratericola, Spio butleri kurilensis* (Buzhinskaya, 1990), *Polydora vulcanica* (Radashevsky, 1994) and one bivalve *Macoma lukini* (Kamenev, 1989, 1990) have been described from Kraternaya Bight. Under this name (*M. lukini*), this species appeared in many subsequent hydrobiological, genetic and biochemical studies (Kamenev, 1991a,b,c; Zhirmunsky and Tarasov, 1991; Muzyka and Tarasov, 1991; Nikiforov and Zaslavskaya, 1991; Zhukova *et al.*, 1992; Kharlamenko *et al.*, 1995; Tarasov, 1999, 2002). However, additional studies have shown that *M. lukini* should be considered a synonym of *M. golikovi*, previously described as *Macoma orbiculata* by Scarlato (1981) (Scarlato and Kafanov, 1988; Kafanov, 1999; Kamenev *et al.*, 2004).

About 80% of biomass of benthic macrophytes and animals in Kraternaya Bight consists of only 12 species. These are the algae *F. evanescens, Alaria fistulosa, Alaria angusta* and the invertebrates *Cerianthus lloydii, Balanus crenatus*, polychaetes *P. vulcanica* and *Pectinaria hyperborea*, the bivalves *Macoma golikovi* and *Macoma calcarea*, the sea urchin *Strongylocentrotus droebachiensis*, and the holothurians *Psolus fabricii* and *Eupentacta pseudoquinquesemita*.

The structure of the flora and fauna in the bight shows little similarity with the biota of outside waters of Yankicha Island. There are only 17 common species, most of them being crustaceans, found in the coastal zone of Simushir Island (middle Kuriles), and other semienclosed caldera bays of the Kuriles-Broughton Bay (Simushir Island) and Lion's Mouth Bay (Iturup Bay) (Kamenev, 1991b). Kamenev (1991b,c) has carried out cluster and discriminant function analysis of biomass and population density of the flora and fauna and has distinguished 10 bottom communities and 2 ecotone

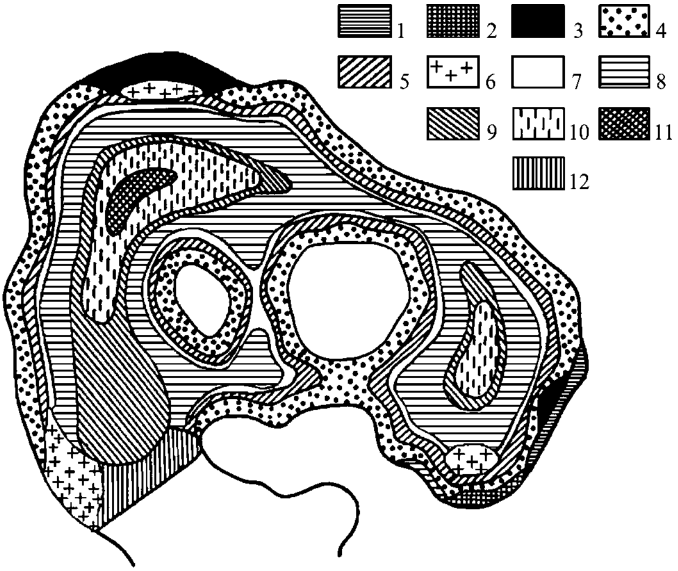

Figure 24 Distribution of the bottom communities and ecotone groups of macrobenthos in Kraternaya Bight. (1) *Fucus evanescens* + *Balanus crenatus* community; (2) *Balanus crenatus* + *Polydora vulcanica*; (3) *Alaria* spp. + *Balanus crenatus*; (4) *Strongylocentrotus droebachlensis*; (5) *Psolus fabricii* + *Macomal golikovi*; (6) *Cerianthus lloydii* + *Macoma golikovi*; (7) *ecotone Macoma golikovi*, *M. calcarea, Hiatella arctica* and *Mya usenensis*; (8) *Macoma calcarea* + *Hiatella arctica* community; (9) ecotone *M. calcarea*, *H. arctica* and *Pectinaria hyperborea*; (10) *Pectinaria hyperborea* community; (11) *Capitella capitata*; (12) *Capitella capitata* + amphipod species (after Kamenev, 1991b).

groups (Figure 24). This author has grouped the species found in zones of vent release and seepage of volcanic fluids into distinct associations:

1. *F. evanescens* + *B. crenatus* occupies a small site on boulder-gravel ground in the east part of the bight at 1 m depth (Figure 24). The community comprises 47 species with total biomass exceeding 4000 g m^{-2}, in which the biomass of *Fucus* and barnacles is, respectively, 2700 g m^{-2} and >700 g m^{-2}. The proportion of dominant species was 82% of the total biomass.
2. *B. crenatus* + *P. vulcanica* is located on coarse gravel and on some boulders in the south part of the east basin at depth 1 m, in the region of the mouth of the volcanic brook with small sulfide vents. This association includes 28 macrobenthic species with total biomass exceeding 5100 g m^{-2}. Macrophytes were represented by irregular patches of *F. evanescens* (150 g m^{-2}). Compared with other areas of the bight, there is a rather high biomass of barnacles, >3000 g m^{-2}, or 59% of the total biomass of flora and

fauna. As in the littoral zone, brushes of *P. vulcanica* up to 2 m^2 in area develop at these depths. In the immediate vicinity of vents, bacterial mats develop on the surfaces of the polychaete brushes. The population density of *P. vulcanica* was 8×10^4 ind. m^{-2}. Other polychaete species, *Harmothoe imbricata* and *Nereis pelagica*, are also widespread in the community, their total biomass being 400 g m^{-2} at a population density $\sim 4 \times 10^3$ ind. m^{-2}. In the barnacle settlements, there is a large number of amphipods, leptostracans and small bivalves, from 1300 up to 6000 ind. m^{-2}. The proportion of dominant species in the community is 81% of the total biomass.

3. *Alaria* spp. + *B. crenatus* occupies small sites only in the eastern region of hydrogen sulfide gas-hydrothermal and northern hydrothermal vents, occurring on boulders and stones at depths from 1 to 6 m (Figure 24). This association includes 32 species of macrobenthos. The macrophytes comprise 90% of the total biomass. *Alaria angusta*, with a biomass of 8.5 kg m^{-2}, develops in the zone of sulfide vents, while *Alaria fistulosa* and *Arthrothamnus bifidus*, with a joint biomass of ~31 kg m^{-2} occur in the northern part of the bight. The thalli of the *Alaria* in the bight, in contrast to the same species inhabiting outside waters of the island, show partial reduction of rhizoids, thinning of the stipe, and a short and thin thallus. In this association, there are 27 species of animals with a biomass 2316 g m^{-2}, comprising mainly (88%) *B. crenatus* (2050 g m^{-2}). There were numerous amphipods and caprellids among the macrophytes, with a population density from 10^2 to 10^3 ind. m^{-2}. Errant and sedentary polychaetes are also abundant.

4. *Strongylocentrotus droebachiensis* occurs on hard-rock bottoms around almost all the perimeter of the bight and around the islets inside at depths from 1 to 7 m (Plate 7B). Macrophytes are very few in this association, but there are 40 species of animals with a biomass exceeding 3000 g m^{-2}. The biomass of the dominant species, *S. droebachiensis*, is ~2400 g m^{-2} (74%) at a population density of 226 ind. m^{-2}. The maximum values of numbers and biomass are usually observed at depths of 2–3 m. The sea urchins completely cover the surface of boulders in the southwest part of the bight away from venting zones. Their average biomass is then 6455 ± 629 g m^{-2} at a population density 403 ± 10 ind. m^{-2}. The number of sea urchins and their biomass decreases with distance from the entrance into the bight along the west and east coasts to the venting areas in the south part of the bight (Figure 25). In the vicinity of the volcanic brook, the sea urchin biomass was 769 g m^{-2} at population density 77 ind. m^{-2}. In hydrothermal vent zones at depths of 2–7 m, where the rocky sea bed is mixed with gravel and covered with a blanketing layer of silt, the number of polychaetes increased appreciably, including *Eteone longa* (>350 ind. m^{-2}), *Harmathoe imbricata* (up to 160 ind. m^{-2}), the newly described *Syllis (Haplosyllis) cratericola* and subspecies *Spio butleri kurilensis* (Buzhinskaya, 1990). Under the blanketing layer of silt, the gravel was inhabited by burrowing bivalves *Macoma*

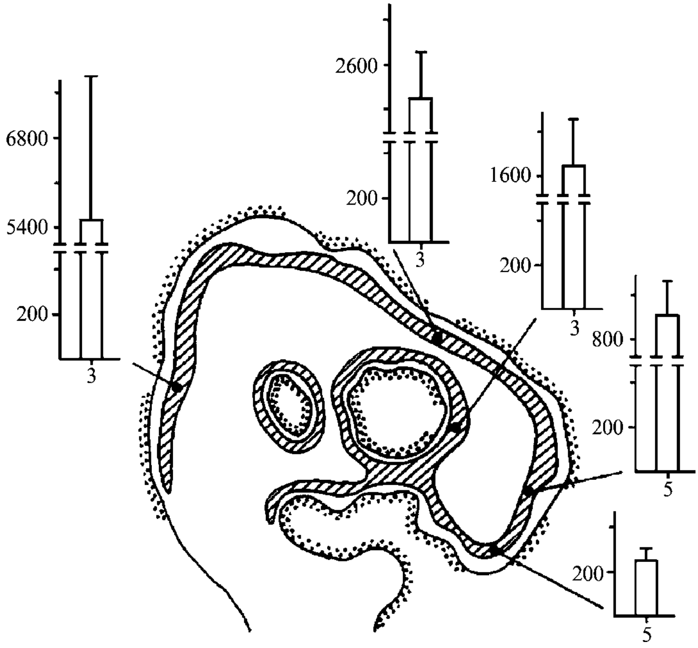

Figure 25 Average values of the biomass of the sea-urchin *Strongylocentrotus droebachiensis* in Kraternaya Bight. Abscissa. depth, m; ordinate, wet biomass, g m^{-2} (after Kamenev, 1991b).

golikovi and *Mya usenensis*. Some boulders carried *P. vulcanica* (density 3000 ind. m^{-2}, biomass 333 g m^{-2}) and *B. crenatus* (up to 220 ind. m^{-2}).

5. *Psolus fabricii* + *Macoma golikovi* community is distributed around the perimeter of the bight and around islets, on boulders and stones that alternate with areas of the silt-sand and silty bottom at depths from 5 to 20 m (Figure 24).

The greatest number of animal species found is 64, with a total biomass of >2600 g m^{-2}. Macrophytes, including the coralline algae *Callophyllis rhynchocarpa* and *Clathromorphum compactum*, also the noncalcareous alga *Turnerella mertensiana*, form small patches. The corallines occur mainly in the region of the outlet from the bight, the channel. The algal biomass is comparatively low, up to 123 g m^{-2}. The total biomass of animals in this community reaches 2500 g m^{-2}, in which the dominant species is a holothurian, *Psolus fabricii*, which forms 40% of the fauna. The holothurians live on boulders and stones, often forming aggregations (Plate 8A). Their population density on boulders at depths of 10–15 m is 16 ± 2 ind. m^{-2}, with a biomass of 1600 ± 162 g m^{-2}. The greatest population densities occur in the

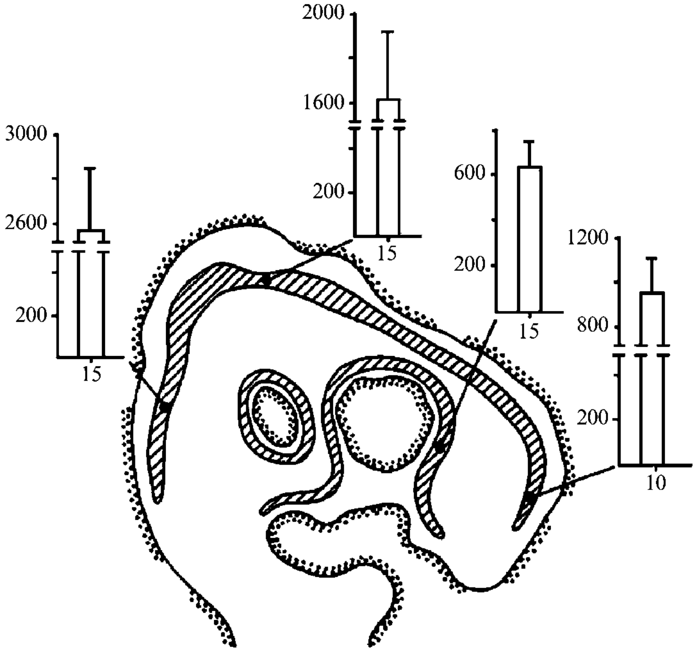

Figure 26 Average values of the biomass of the holothurian, *Psolus fabricii* in Kraternaya Bight. Abscissa, depth, m; ordinate, wet biomass, g m^{-2} (after Kamenev, 1991b).

area of outlet from the bight, where the holothurians cover all surfaces of the boulders, reaching 104 ind. m^{-2}, with a biomass up to 10 kg m^{-2}.

In the east basin and near sulfide vents, *Psolus fabricii* was less abundant than in the west basin or in the area of the northern vents (Figure 26).

A second holothurian species, *Eupentacta pseudoquinquesemita*, is also present at an average population density of 5.3 ind. m^{-2} and a biomass of 45.2 g m^{-2}. Like *Psolus*, this species can form large aggregations on boulders, where there can be a density of up to 417 ind. m^{-2} and biomass of 2869 g m^{-2} (Plate 8B). In addition to the holothurians, there can be a significant number of *S. droebachiensis* with a population density 78 ind. m^{-2} and biomass 417 g m^{-2}. Occasionally, the ascidian *Ciona intestinalis* and the small starfish *Leptasterias hirsuta* and *L. alaskensis asiatica* can be observed.

An abundant fauna of burrowing bivalves, including *Macoma golikovi, M. calcarea, M. usenensis* and *Hiatella arctica*, is present in the soft bottom between rocks and on slopes at the bottom of the crater. The mean total bivalve biomass reaches 846 g m^{-2}, of which the dominant species, *Macoma* *golikovi*, forms 593 g m^{-2}, or 23% of the total, at an average density of 605 ind. m^{-2}. *M. golikovi* reaches a biomass of 910 ± 180 g m^{-2} at a population density 460 ± 120 ind. m^{-2} under layers of silted pebbles and gravel at depths of 3–5 m in the vicinity of the mouth of the volcanic brook (Kamenev *et al.*, 2004). *M. golikovi* also occurs at a population density of 450 + 172 ind. m^{-2} and biomass 381 ± 158 g m^{-2} in diatom mats and aggregations of *C. lloydii* in the north venting area. Only *M. golikovi* and scattered individuals of *Mya usenensis* and *H. arctica* occur in sediments up to the depth of 10 m. The population density of *M. golikovi* decreases with increasing silt content of the bottom, which increases with depth (Kamenev *et al.*, 2004). *Macoma calcarea* (density 153 ind. m^{-2}, and biomass 185 g m^{-2}), *M. usenensis* and *Axinopsida orbiculata orbiculata* (20–30 ind. m^{-2}) begin to occur in bottom sediments at depths of 15 m and deeper. The infauna here includes polychaetes (total biomass 68 g m^{-2}), among which *Amphitrite cirrata* dominates (density 36 ind. m^{-2}, biomass 31 g m^{-2}).

6. *Cerianthus lloydii* + *M. golikovi* community is found on various types of a bottom sediments at depths of 2–25 m in zones of gas-hydrothermal venting (Figure 24). There are 55 species identified in this community, with a total biomass of 2700 g m^{-2}, in which 68% is *C. lloydii* and *Macoma golikovi* (Kamenev, 1991b).

In the southeast part of the bight, this community occurs on silt around outlets of strong sulfide vents at depths of 20–25 m, among mats of *Beggiatoa mirabilis* and the bacterial association “Thiodendron” (Plate 9A).

In the northern venting area, the settlements of ceriantharians were located only in diatom mats. Diatom mats with ceriantharians present a pillow-like form on the surface of boulders and rocks, between boulders or among *Alaria* rhizoids at depths of 6–12 m. In the southwest part of the bight, in the region of the strait, the community also occurs on sandy bottoms among diatom mats at depths from 2 to 17 m (Plate 9B).

The cerianthid is always present in clumps or aggregations. The maximum density, 1360 ind. m^{-2} at a biomass of ~1700 g m^{-2}, occurs in the southeast part of the bight in a zone of hydrogen sulfide vents where there are numerous small individuals. The highest biomass (2670 g m^{-2}) is found in the southwest part of the bight where the population density of larger cerianthids reaches 345 ind. m^{-2} (Figure 27; Plate 9B). The second dominant species, *M. golikovi*, forms settlements with a density of 517 ind. m^{-2} and biomass of 428 g m^{-2}.

A great number of molluscs are sympatric with *M. golikovi*. In the southeast part of the bight, they are mostly *M. calcarea* and *H. arctica*, with an average biomass of 1326 ± 371 g m^{-2} and a joint density of 500 ± 141 ind. m^{-2}. In the north part of the bight *H. arctica* has a biomass up to 600 g m^{-2}.

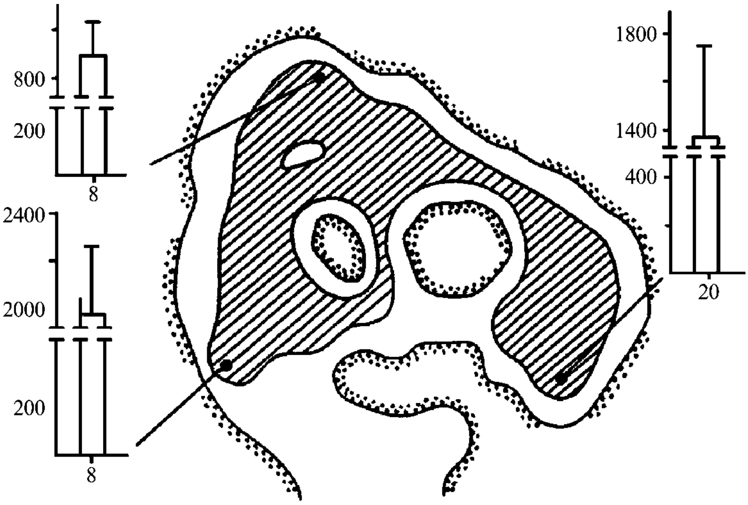

Figure 27 Average biomass of *Cerianthus lloydii* in Kraternaya Bight. Abscissa, depth, m; ordinate, wet biomass, g m^{-2} (after Kamenev, 1991b).

In the southwest part of the bight, at 10 m depth, there are numerous small *M. usenensis*, (population density 1384 ± 494 ind. m^{-2}, biomass 405 ± 121 g m^{-2}), and *Mysella kurilensis* (2539 ± 721 ind. m^{-2}).

This community is also characterised by an abundance of various species of sedentary and errant polychaetes. In the northern area, concurrently with aggregations of cerianthids, the diatom mats carry large polychaetes, *M. infundibulum* and *Thelepus plagistoma*, with population densities from 10 up to 60 ind. m^{-2} and biomass from 100 up to 2000 g m^{-2} (Plate 10A). (Moshchenko and Gladkov, 1991). In the southwest part, in sand under diatom mats, there are numbers of small *Mediomastus californiensis* (up to 4×10^4 ind. m^{-2}) and *Capitella capitata* ($>6 \times 10^3$ ind. m^{-2}).

Outside the zones of venting and seepage of volcanic fluids in Kraternaya bight, it is possible to distinguish four other communities and two ecotone groups on the sea bed (Figure 24).

4.4.2. Matupi Harbour

In Matupi Harbour, the macrobenthic associations are governed by the nature of the bottom (old lavas, hard and soft bottoms) and the temperature of the gas-hydrothermal vents. The species composition of the animals has been listed by Tarasov *et al.* (1999). In all zones of volcanic activity, there are no plants and animals in the intertidal zone.

In the Tavurvur volcanic Area I at 6–8 m depth, in the zone of seeps with temperatures of 50–60 °C, individual small crabs *Hippa* sp. and *Macrophalmus* sp. occur and reach a total biomass 1.2 g m^{-2}. At 10–20 m depth, where the sediment temperature is 30–40 °C, the total biomass of epifauna and infauna increases considerably. Sponges (*Petrosia, Scleritoderma* and *Stromatoderma*) reach a biomass of 137 g m^{-2} on rocks. Sabellid polychaetes (*Sabella* sp., from 3000 to 10,000 ind. m^{-2}) and small crabs (*Hippa* sp. and *Macrophalmus* sp.—in total 175 ind. m^{-2}) are abundant on silty-sand. Other benthic forms include the gastropod *Conus eburneus* on sand and *Peristernia* sp. and *Chicoreus ramosus* on rocks (Tarasov *et al.*, 1999). The macroinfauna at 20 m includes polychaetes (the families Sabellidae and Spionidae) and bivalves (Veneridae and Corbulidae). Also present is a species of *Thyasira* (6–9 ind. m^{-2}), 5–8 mm in diameter, which shows the enlarged gills typical for forms with endosymbiotic bacteria. Macrofaunal numbers decrease below 30 m depth.

In the Tavurvur volcanic Area II on steep sandy slopes with hot sediments (60 °C) devoid of bacterial mats, the macrofauna is represented by polychaetes of the family Spionidae (*Polydora* sp.) (Plate 6B) and small crabs (*Macrophalmus* sp.) (total biomass ~1 g m^{-2}). At a depth of 3–6 m, on bacterial mats, the macrofauna is markedly richer and includes crabs (*Actea* sp., *Macrophthalmus* sp. and *Pilumnus* sp.), polychaetes (Sabellidae and Spionidae) and small cerianthids (total biomass 20 g m^{-2}).

Below the zone of hot vents, numerous small gastropods (*Nassarius* sp.) occur on the sand, reaching a density of 13 ind. m^{-2} and a biomass of 5.6 g m^{-2}. A few hermit crabs (*Dardanus* sp., *Pagurus* sp.), crabs (*Hippa* and *Macrophthalmus*), small amphipods and polychaetes (Nereidae and Syllidae) are also present and total macrofauna biomass is 12 g m^{-2}. The fauna is richer at 20–25 m depth, where the rocks are colonised by ascidians (*Didemnum* sp., up to 337 ind. m^{-2} and 34.5 g m^{-2}), while polychaetes (*Sabella* sp.) are abundant on sand (7000–12,000 ind. m^{-2}). Also recorded are gastropods (*Lataxiena fimbriata*), bivalves (Veneridae, Corbulidae and Thyasiridae) (Plate 10B), crabs and infaunal polychaetes (Spionidae, Capitellidae and Nereidae), and the total biomass of macrofauna biomass is 332 g m^{-2}. The abundance of the macrofauna is less at greater depths (Tarasov *et al.*, 1999).

A diverse scleractinian community occurs near the southern lava cape in Tavurvur volcanic Area II at 3–10 m depth, in the zone of gas-hydrothermal vents on a steep slope covered with rock blocks 2–3 m across. The coral community contains 17 species and is dominated by the lamelliform species *Pectinia lactuca* and *P. alcicornis*, whose growth appears to be inhibited by ferruginous silt that covers the surface of the colonies (Tarasov *et al.*, 1999). Gas bubbles through the coral structures. Small colonies of *Porites* sp. (3–5 cm) and *Dendrophyllia* sp. are also abundant. Less common species include *Plerogyra sinuosa* reaching 30 cm, small irregular colonies of *Galaxea fascicularis* (7–8 cm) and large colonies of *Turbinaria bifrons*. In addition, *Favites abdital, Mycedium elephantotus, Goniopora stokesi* and black corals *Antipathes* sp. occur. At 4–10 m depth the spatial coverage of corals reaches 90–100%. Sponges (*Petrosia, Scleritoderma* and *Stromatospongia*), boring bivalves (*Lithophaga kuehnelti* and *L. simplex*), large gorgonarians (up to 1 m) densely colonised by the bivalves *Pteria coturnix, Septifer bilocularis* and small ophiuroids are also abundant.

There is hot sediment (50–60 °C) in shallower depths (1–5 m) of the Rabalanakaia volcanic zone and no epifauna. Below 5 m, the epifauna includes crabs (*Dardanus, Macrophthalmus, Hippa*), hermit crabs (*Pagurus*), polychaetes (*Polydora*) and bivalves (*Corbula*). At 27 m depth, in the zone of ring-structures and hot diffuse vents (Tarasov *et al.*, 1999), there is a dense population of sponges (?*Oceanapia* sp.), reaching a biomass of 1,010 g m^{-2}. The sponges are colonised by numerous small ascidians (*Diplosoma*). The sediment contains large numbers of sponge spicules.

There is a more diverse coral fauna in the eastern part of the Rabalanakaia volcanic zone, where lava flow has formed a small cape, extending stepwise underwater. Corals, mainly *Pachyseris rugosa*, begin to occur at ~0.5–1.0 m depth in the hot water layer (60 °C.) On the upper part of the slope, the colonies are small and undeveloped, with some parts dead. There is intensive venting through the coral masses. Deeper down the slope, *Pachyseris* colonies are larger, exceeding 0.5 m in height. Other common corals include branched and massive forms such as *Porites, P. alcicornis* and *Oxypora glabra. Leptoseris explanata, Plerogyra sinuosa, Hydnophora rigida, Acropora* sp., *Pocillopora damicornis* and *Favites abdita* are less common. Black corals and small gorgonians are also present. In general, the coral fauna in this area is the richest in Matupi Harbour, and below 3–4 m depth, it covers 90–100% of the surface of the substratum. Among other epifaunal forms, the bivalves *Barbatia* sp. and *Septifera bilocularis*, feather stars, sponges and grey anemones with symbiotic fish are present (Tarasov *et al.*, 1999).

In the lower, less steep part of the slope (15–20 m), only two forms of corals are present: *Pectinia lactuca* and *Oxypora glabra*, with the greater part of the colonies killed by heavy sedimentation.

In the western part of the bight, where volcanic activity has not been recorded, the macrofauna is very poor: single amphipods, hermit crabs (*Pagurus*), polychaetes (Nereidae and Syliidae) occur in silty sand. The total biomass of macrobenthos does not exceed 1 g m^{-2} between 1 and 30 m depth.

In the central part of Matupi Harbour at a depth of 45–55 m, the sediment is silty and contains very high numbers of sponge spicules. The macrofauna and meiofauna are extremely poor; single nematodes and polychaetes were recorded together with harpacticoids and ostracods, with a total density of <100 ind. m^{-2} (Tarasov *et al.*, 1999).

At a depth of 0.5–5.0 m in the coastal zone of Blanche Bay, the area used as a control (Figure 7), the seabed consists of coarse volcanic sand mixed with dead corals and silt. The fauna contains only a few taxa. Occasional rocks are covered by patches of the coral *Pocillopora damicornis*, also sea grasses with height of stalk no more than 5 cm. There is no infauna.

Beginning at 5 m deep, the bottom slopes steeply to 30 m and more and consists mainly of crystalline volcanogenic material, lapilli, 0.5–1.0 cm in diameter, and there are traces of landslips at some sites. There is dense cover of filiform Rhodophyta at depths of 5–10 m. These algae are inhabited by nematodes, polychaetes, harpacticoids and numerous amphipods. The structure of the bottom sediments does not change with depth. Only small settlements of transparent anastomotic sponges, 5–6 cm high, with a population density of 2–3 ind. m^{-2} present on the bottom. The slope remains steep to a depth of 30 m and more. It is inhabited by the small fungoid coral *Diaseris distorta*, in clusters of some tens of individuals per square metre. Large anemones are also present.

No significant changes in bottom relief, character of ground and structure of biota can be seen in other parts of Blanche Bay near the exit from the bay. Judging from SCUBA-diving observations, development of the benthic flora and fauna there is limited by mobility of the substratum and occurrence of landslips.

Near the exit from Blanche Bay, there is a bottom composed of boulders and gravel, which carries a typical coral reef community. From the point of view of geomorphology, this community is at a stage of formation of reef-flat (i.e. its uppermost part is not exposed to the air during low tide) (Sorokin, 1990b). This young reef is formed by development of massive colonies of *Porites solida*, anastomic *Porites nigrescens, Galaxea fascicularis Acropora digitifera* (Tarasov *et al.*, 1999). The cover of corals on this reef flat reaches 75%. There is a small bed of coralline red algae. At 3–15 m and deeper, the outer slope of reef is composed mostly of entangled branches of large colonies of *Acropora caroliniana* and *Pocillopora* spp.; the cover here approaches 100%. The bivalves *Tridacna squamosa* and *Barbatia* sp., coniid gastropods, large Amphinomidae, regular sea urchins of the family Diadematidae, brittle stars, sea lilies, sponges, sea anemones and numerous small coral fishes live in the coral structures and among and under boulders.

4.4.3. Bay of Plenty

In areas of gas-hydrothermal venting in the Bay of Plenty, at 3–12 m depth, where there are various types of mats, and bottom temperatures of 20–50 °C, there are populations of the burrowing bivalve *Tawera spissa* and of the gastropod *Cominella adspersa* at high density and biomass (Kamenev *et al.*, 1993). The biomass of bivalves reaches an average of 5121 ± 445 g m^{-2} at a population density of 1581 ± 135 ind. m^{-2}. The commensal crab *Pinnotheres novaezelandiae* occurs in the mantle cavity of >30% of the bivalves. The biomass of *Cominella adspersa* averages 84 ± 15 g m^{-2} at a population density 511 ± 97 ind. $m^{-2.}$ It occurs on the seabed or in the mats that form a layer (0–5 cm) over bottom sediments. Groups of three to four individuals of *C. adspersa* aggregate on living shells of *Tawera spissa*, on which they prey.

The burrowing starfish *Astropecten polyacanthus* occurs in aggregations of molluscs. In addition, the gastropod *Penion dilatatus*, the isopod *Exosphaeroma obtusum*, polychaetes of the families Spionidae, Capitellidae and Lumbrineridae, small hermit crabs and juvenile cerianthids are present in mats and in the silty-sand seabed.

Outside the zone of venting and mats, the bottom fauna includes *Astropecten polyacanthus, Cominella adspersa*, hermit crabs, small polychaetes and amphipods. The average biomass of all animals is here only 1.4 ± 0.9 g m^{-2}.

Despite the high temperature of the bottom sediments, the fauna of the gas-hydrothermal venting area in Volcanic Crater has a notably high population density, but low biomass (Table 33). Macrophytes have not been recorded. The macrobenthos includes the small crab *M. hirtipes*, the gastropod *Cominella maculosa* and the amphipod *Proharpinia* sp.

The animals are not distributed uniformly at the bottom of Volcanic Crater. This appears to be linked to an increase of temperature at the seabed as we progress from the margins of the crater (17 °C) to the centre, where the temperature reaches 81–86 °C (Figure 28). At temperatures of 40 °C, only eunicid polychaetes, the crab *Macropthalmus hirtipes* and the amphipod *Proharpinia* sp. have been recorded in the macrobenthic fauna (Table 33). The population density and biomass of these animals is three to four times less than the macrofaunal biomass at the crater margins. At high temperatures (60–65 ° C), a species of the pogonophore genus *Siboglinum* has been reported to have a population density of 8 ind. m^{-2}. *Macropthalmus hirtipes* also occurs at a density 24 ind. m^{-2} (Table 33). In the centre of the Volcanic Crater, at a temperature 81 °C, *Macropthalmus hirtipes* (16 ind. m^{-2}) is the only fauna. The animals present in Volcanic Crater are exposed not only to high temperatures but also to high concentrations of methane (30–100 $\mu l\ l^{-1}$) (Table 12).

On a sandy bottom at depths of 20 m around Volcanic Crater, only individual small polychaetes and brittle stars have been reported.

In the Calypso Area, a diverse benthic fauna is present on silty bottoms at depths of 150–200 m. Sedentary and errant polychaetes, sipunculids, echiurids and holothurians are abundant. Sea urchins with numerous goose barnacles attached to their spines, bivalves, starfishes, sea lilies, brittle stars, sea anemones, crabs and shrimps are also present. Hydroids, small gorgonians and scleractinian corals occur on small stones and on mollusc shells taken in samples of silty-sand sediments. *Siboglinum* sp., which appear similar to

Table 33 Density (N, ind. m^{-2}) and biomass (B, g m^{-2}) of macrobenthic animals in bottom sediments at different temperature in Volcanic crater near Whale Island

Taxon, species		17 °C	18 °C	18 °C	19 °C	20 °C	30°C	40 °0	50 °C	65 °C	81 °C
Polychaeta:											
Glycera sp.	N	0	0	0	4	0	0	0	0	0	0
	B	0	0	0	1.7	0	0	0	0	0	0
Eunicidae gen. sp.	N	8	0	0	4	20	0	4	0	0	0
	B	3.0	0	0	0.3	3.0	0	0.1	0	0	0
Lumbrinereis sp.	N	0	0	4	0	12	0	0	0	0	0
	B	0	0	0.1	0	0.1	0	0	0	0	0
Nephtys sp.	N	8	0	4	0	4	0	0	0	0	0
	B	0.7	0	0.03	0	0.09	0	0	0	0	0
Spionidae gen. sp.	N	0	16	0	4	0	8	0	0	0	0
	B	0	0.3	0	0.08	0	0.1	0	0	0	0
Amphipoda:											
Proharpinia sp.	N	112	196	220	220	300	176	52	52	0	4
	B	0.4	0.8	0.7	0.8	1.1	0.6	0.1	0.2	0	0.01
Decapoda:											
Macropthalmus hirtipes	N	24	28	16	16	20	12	8	4	24	16
	B	12.4	8.4	10.0	4.8	5.0	2.8	1.6	1.4	4.4	4.6
Gastropoda:											
Cominella maculosa	N	8	28	4	0	4	4	0	0	0	0
	B	38.8	31.6	5.8	0	2.9	1.4	0	0	0	0
Pelicaria vermis	N	4	0	0	4	0	0	0	0	0	0
	B	3.2	0	0	2.5	0	0	0	0	0	0
Echinodermata											
Ophiuroidea	N	12	0	28	8	12	0	0	0	0	0
	B	0.8	0	0.4	0.09	0.2	0	0	0	0	0
Pogonophora:											
Siboglinum sp.	N	0	0	0	0	0	0	0	0	8	0
	B	0	0	0	0	0	0	0	0	0.06	0

Source: From Kamenev *et al.*, 1993.

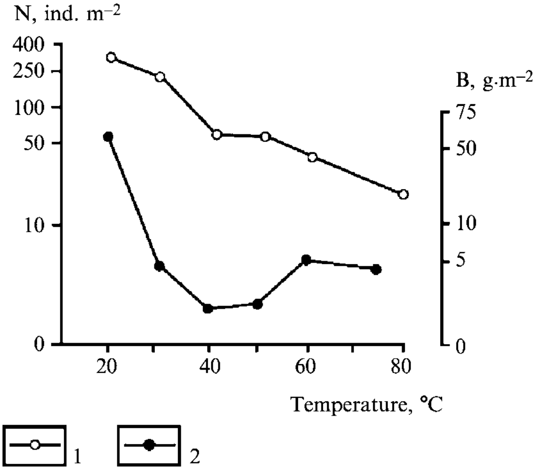

Figure 28 Density (N, ind. m^{-2}) and biomass (B, g m^{-2}) of macrobenthic animals in the bottom sediment of Volcanic Crater in relation to temperature. (1) density of animals; (2) wet biomass (after Kamenev *et al.*, 1993).

those recorded from the hot deposits of Volcanic Crater, occur in the silt samples from Calypso, together with thyasirid bivalves.

4.5. Photosynthesis, chemosynthesis and breakdown of organic matter

4.5.1. Kraternaya Bight

In the venting area of Kraternaya Bight, oxygenic and anoxygenic (=bacterial) photosynthesis, chemosynthesis and heterotrophic production have all been measured in the various types of mats and on the bottom (Starynin *et al.*, 1989; Nesterov *et al.*, 1991; Tarasov *et al.*, 1991; Tarasov, 1999) (Tables 34 and 35).

Oxygenic photosynthesis, which reaches 1 g C m^{-2} d^{-1}, was measured in the diatom mats in the northern part of the bight (Tarasov *et al.*, 1991; Tarasov, 1999). At the mouth of the volcanic brook in the southeast part of the bight, the rate of oxygenic photosynthesis reaches 91.8 ± 7.5 ml O_2 m^{-2} h^{-1}, or 0.65 g C m^{-2} d^{-1}, on pebble and rocky ground covered with a thin film of diatoms at depth 2–5 m. High rates of photosynthesis, 0.9 g C m^{-2} d^{-1}, have also been recorded in the diatom films that develop on slopes of the sandy bottom near the outlet from the bight (Tarasov *et al.*, 1991; Tarasov, 1999).

Table 34 Rate of CO_2-assimilation (gC m^{-2} day^{-1}) of photosynthetic and chemosynthetic bacteria in bacterial mats and silt sediments of Kraternaya Bight

		Photosynthesis			Share of the group bacteria in dark CO_2-fixation, %		
Depth, m	CO_2-assimilation (total)	Microalgae (oxigenous)	Bacteria (anoxygenous)	CO_2-fixation (dark)	Heterotrophic	Thiobacteria (lithotrophic)	Nitrifiers
Bacterial mats:							
0.1	2.20	0.80	1.20	0.20	0	100	0
0.5–1.0	1.60	0	1.00	0.60	0	100	0
1–2	0.80	0.20	0	0.60	60	40	0
3	0.14	0	0	0.14	65	35	HO
5	0.08	ND	ND	0.08	ND	ND	ND
15	0.06	0	0	0.06	22	56	22
20	0.10	ND	ND	0.10	ND	ND	ND
Silt sediments:							
25	0.09	0	0	0.09	56	22	22
45	0.06	0	0	0.06	ND	ND	ND

ND, no determinations.

Source: Data from Nesterov *et al.*, 1991; Namsaraev, 1992.

Table 35 Rate of bacterial sulfur reduction (mgS^0 kg^{-1} day^{-1}) in bacterial mats of Kraternaya Bight

Depth, m	S^0 content in the mat (mg kg^{-1})	Rate of bacterial S^0-reduction
0.5–1.0	55,137	160.7
1–2	412	3.8
15	517	5.4
20	949	32.7

Source: Data from Bonch-Osmolovskaya, 1991; Namsaraev *et al.*, 1991.

Within the bight, in the zone of volcanic activity up to a depth of 10 m, the rate of oxygenic photosynthesis of the diatom mats and of microphytobenthos of the sandy bottom varies from 0.7 up to 1.0 g C m^{-2} d^{-1}. These values are an order of magnitude higher than observed values of primary production of microphytobenthos communities of sand and silt bottoms of the sublittoral zone in temperate latitudes without hydrothermal venting (Smith, 1973; Nixon *et al.*, 1976; Cherbadzhi and Tarasov, 1980; Propp *et al.*, 1980; Herndl *et al.*, 1989).

High rates of primary production also occur in bacterial mats growing in areas of hydrogen sulfide venting and seeping of volcanic fluids through the bottom. In the intertidal zone (depth <1 m), the total assimilation of carbon dioxide by the bacterial mats is 1.6–2.2 g C m^{-2} d^{-1} (Table 34). Bacterial photosynthesis is higher than other primary production, constituting 54–64% of the total. This high rate appears to be caused by the high population density of photosynthesising bacteria, whose development is connected to high exposure to light and the high concentration of hydrogen sulfide coming from the littoral vents. There is also a high rate of dark assimilation of CO_2 in these mats (0.2–0.6 g C m^{-2} d^{-1}), involving chemosynthesis by sulfur bacteria (Starynin *et al.*, 1989; Nesterov *et al.*, 1991) (Table 34).

The rate of primary production in the microbial mats becomes less (0.8 g C m^{-2} d^{-1}) at depths exceeding 1–2 m. At this level, oxygenic photosynthesis by diatoms comprises 25% of the total production, whereas bacterial photosynthesis has not been recorded (Table 34). Chemosynthesis by sulfur bacteria contributes 30% of total carbon assimilation, with heterotrophs providing the remaining 45% (Nesterov *et al.*, 1991; Namsaraev, 1992).

In algobacterial mats, the total rate of photosynthesis of diatoms and photoautotrophic bacteria varies from 0.6 to 3.7 g C m^{-2} d^{-1} (Starynin *et al.*, 1989). This type of mat also has a high rate of oxygenic photosynthesis, 106.7 ± 15.1 ml O_2 m^{-2} h^{-1} (Tarasov *et al.*, 1991).

Experimental data from flow-through systems measuring oxygen and carbon dioxide metabolism show that the algal-bacterial mats in Kraternaya

Bight produce more oxygen than is consumed by heterotrophic microflora, chemosynthesising bacteria and microbenthos and meiobenthos (Tarasov *et al.*, 1990, 1991; Tarasov, 1999). The level of oxygenic photosynthesis in the algobacterial mats in the bight has probably been underestimated, because of oversaturation of oxygen in the water above the mats, and its release from the mats in the form of bubbles. During SCUBA-diving in the daytime, it is possible to see numerous small gas bubbles on the surface film of the mats, detaching and rising to the sea surface. Elsewhere, it has been shown that oxygen microbubbles form in cyanobacterial mats when rates of photosynthesis exceed 5–10 g C m^{-2} d^{-1} (Cohen *et al.*, 1975; Jorgensen and Revsbech, 1983).

Photosynthesis has not been recorded in bacterial mats at depths from 3 down to 30 m. Synthesis of primary organic matter in these depths is carried out by sulfur bacteria. Dark assimilation of CO_2 has been measured at 80–140 mg C m^{-2} d^{-1} in depths of 3–5 m and at 60–100 mg C m^{-2} d^{-1} in depths of 15–20 m. Of these values, 35% and 56%, respectively, can be attributed to chemosynthesis by bacteria (Nesterov *et al.*, 1991; Namsaraev, 1992) (Table 34).

A large number of bacterial groups are involved in decomposition of organic matter in the bottom sediments of Kraternaya Bight including (1) aerobic saprophytes; (2) heterotrophic bacteria that hydrolyze biopolymers; (3) unspecialised heterotrophic microorganisms able to reduce nitrates, elemental sulfur and oxidised forms of iron and manganese; (4) bacteria using partially reduced products of fermentation, including sulfate-reducing, sulfur-reducing, and methane-producing bacteria; and (5) anaerobic bacteria that use hydrogen (i.e., methane-producing and acetogenic bacteria). Qualitative and quantitative characteristics of these groups of bacteria have been considered in detail elsewhere (Borzenkov, 1989; Karnachuk *et al.*, 1989; Namsaraev *et al.*, 1989, 1991, 1994; Odintsov and Propp, 1991; Bonch-Osmolovskaya 1991, 1994; Namsaraev, 1992). This review considers only those processes of breakdown of organic matter that are related to volcanic activity.

In the venting zone, mostly in the east part of the bay, sulfur-reducing bacteria, including thermophilic Archaebacteria, take an appreciable part in transformation of $C_{org.}$ and sulfur (see Section 4.1). Most of these bacteria are fermenters and use elemental sulfur as an electron acceptor. Groups of these bacteria occur in microbial mats at depths from 0.5 up to 20 m in areas of high elemental sulfur content. The highest concentration of sulfur and the highest rate of sulfur reduction have been found in the bacterial mats of the littoral zone (Table 35).

Colourless sulfur bacteria *Thiothrix* sp. and the bacterial association "Thiodendron" also participate in breakdown of organic matter in bottom communities. The colourless sulfur bacteria include various taxonomic and physiological groups of microorganisms. Their only common trait is the ability to store elemental sulfur in the cell. The role of sulfur compounds in metabolism of those microorganisms still remains unclear, because of the difficulty of isolating colourless sulfur bacteria in pure culture. Different species of colourless sulfur bacteria can differ significantly in their metabolism and in their paths of oxidation of inorganic sulfur compounds, and such differences may be found within species (Strohl and Larkin, 1978; Dubinina, 1989).

Inorganic sulfur compounds are used by sulfur bacteria in four ways: (1) as electron donors during CO_2 fixation (chemoautotrophy); (2) for assimilation of organic substrates in growth (chemolithoheterotrophy); (3) for detoxication of products of incomplete reduction of oxygen; and (4) as electron acceptors during anaerobic respiration (Pringsheim, 1967; Zavarzin, 1972; Mezzino *et al.*, 1984; Dubinina, 1989; Bonch-Osmolovskaya, 1991).

Studies on the bacterial mats of *Thiothrix* sp. and "Thiodendron" in Kraternaya Bight have shown that these microorganisms possess a chemoorganotrophic metabolism and participate in breakdown of organic matter (Namsaraev *et al.*, 1991; Dubinina *et al.*, 1993a; Dultseva, 1996; Leshcheva, 1997). They are able to grow only in the presence of reduced compounds of sulfur, mainly hydrogen sulfide and thiosulfate. The rates of oxidation of these compounds in the mats are quite high, 21–202 mg H_2S m^{-2} d^{-1} and 6–346 mg $S_2O_3^{2-}$ m^{-2} d^{-1}, respectively. Elemental sulfur accumulates in the bacterial cells. These processes occur concurrently with normal decomposition of organic matter as is typical for marine basins. Breakdown of organic matter is also effected by groups of thermophilic bacteria, including thermophilic and hyperthermophilic Archaebacteria living in hydrothermal systems, in addition to other groups of sulfur-reducing microbes and mats of colourless sulfur bacteria and the "Thiodendron" association.

In bottom sediments of the bight outside the zone of venting, the decomposition of organic matter occurs mostly under anaerobic conditions with participation of various groups of bacteria, mainly those of the sulfur cycle (Karnachuk *et al.*, 1989; Namsaraev *et al.*, 1989, 1991; Namsaraev, 1992).

4.5.2. Matupi Harbour

In Matupi Harbour, there is also high production in bacterial mats (Table 36). Photosynthesis in mats was not detected in the intertidal zone or to a depth of 1 m. However, intense oxygenic photosynthesis with rates up to 1.5 g C m^{-2} d^{-1} has been measured in mats that contain abundant cyanobacteria at 4–6 m depth. The rate of dark assimilation of CO_2 was also high there.

Table 36 Rate of CO_2-assimilation (mgC m^{-2} d^{-1}) in bacterial mats of Matupi Harbour

Depth, m	CO_2-assimilation (total)	Photosynthesis Microalgae (oxigenic)	Photosynthesis Bacteria (anoxygenic)	CO_2-fixation (dark)
1	380	0	0	380
3–5	940	240	110	590
4–6	2020	1490	0	530

Source: From Tarasov *et al.*, 1999.

Mats located on rigid lava flows among outputs of strong vents at depths of 3–5 m (Tavurvur venting Area II) were characterised by low values of oxygenic and anoxygenic photosynthesis and by a high rate of dark CO_2 fixation (Table 36). It was not possible to make accurate estimates of the proportion of chemosynthesis and heterotrophic assimilation involved in carbon dioxide fixation (Tarasov *et al.*, 1999; Tarasov, 1999). On the whole, the rate of production in Matupi Harbour mats was comparable to that of Kraternaya Bight mats.

Sorokin (1991) has shown that in the microbial mats and bottom sediments of Tavurvur venting Area II, bacterial chemosynthesis involves oxidation of reduced forms of sulfur (S^{2-}, $S_2O_3{}^{2-}$ and S^0). Chemolithotrophic sulfur bacteria have been recorded at densities up to 10^9 cells ml^{-1}. In addition, sulfur compounds are oxidised also by lithoheterotrophic and heterotrophic sulfur bacteria (10^3–10^5 cells ml^{-1}). Sorokin (1992) has isolated and described a new genus and species of bacterium, *Catenococcus thiocyclus*, from these groups of bacteria. Heterotrophic sulfur bacteria, with a maximum density of 10^6 cells ml^{-1}, dominate bottom sediments of all other venting areas of the bight, together with chemolithoautotrophic microorganisms observed at lesser numbers (10^2–10^5 cells ml^{-1}) (Sorokin, 1991).

In areas where the vents contain high concentrations of hydrogen sulfide (up to 30 mg l^{-1}), this undergoes intense oxidation in bacterial mats at rates up to 2.73 g S^{2-} m^{-2} d^{-1} (Table 37). The proportion of the total H_2S undergoing bacterial oxidation is ~60%, the remainder being oxidised abiotically. Molecular sulfur is the main end product of bacterial oxidation of H_2S under these conditions (Sorokin, 1991).

Thiosulfate and elemental sulfur are most actively oxidised in areas with bacterial mats. Such processes occur at lower rates or are below limits of detection in other venting areas.

In addition to breakdown of organic matter by anaerobic fermentation by hyperthermophilic archaea and mesothermophilic bacteria (Section 4.1),

Table 37 Bacterial oxidation of sulfide, thiosulfate and elemental sulfur in the bacterial mat and the uppermost sediment layer in Matupi Harbour

Locality, object	H_2S content, mg l^{-1}	Oxidation rate		S^0-content, mg l^{-1}	Rate of $S_2O_3^{2-}$ + SO_4^{2-} formation from S^0
		H_2S	$S_2O_3^{2-}$		
		mg m^{-2} d^{-1}			mg m^{-2} d^{-1}
Tavurvur zone, Area I:					
Sand, depth 1–5 m	0	0	0.42	0.1	0.17
Tavurvur zone, Area II:					
Bacterial mat,					
depth 0.5–1.0 m	26.0	2728	3.58	ND	ND
depth 5 m	28.2	2124	2.18	173.0	77.30
Rabalanakaia zone, volcanic ring-structure:					
Depth 27 m	0	0	0.68	0	0
Blanche Bay (control):					
Sand, depth 1 m	0	0	0.46	0	0

ND, no determination.

Source: After Sorokin, 1991; Tarasov *et al.*, 1999.

organic matter in mats and bottom sediments in the venting zone is a substrate for sulfate reducing and cellulolytic bacteria. The rates of these processes vary from 2.0 to 18.0 mg C m^{-2} d^{-1} (sulfate reduction) and from 0.1 up to 34.0 mg C m^{-2} d^{-1} (cellulose breakdown) (Table 38). This great variation probably reflects the heterogeneous distribution of substrates and bacteria within the limits of the same mat (Namsaraev, 1992; Namsaraev *et al.*, 1994).

The role of methanogenesis in diagenetic transformations of $C_{org.}$ appears to be small. Of the total methane generated from biological process in soft sediments of Matupi Harbour, 82% was formed from H_2 and CO_2 (Namsaraev, 1992).

Thus, as in Kraternaya Bight, the hot bottom sediments of Matupi Harbour that contain elemental sulfur are characterised by the existence of populations of hyperthermophilic, extreme thermophilic and mesothermophilic sulfur-reducing bacteria that participate in the decomposition of organic matter. Bacterial mats are formed only in the zone of release of hydrogen sulfide from vents. In contrast to the microbial mats of Kraternaya Bight, where benthic diatoms are the dominant photosynthesising organisms, and where cyanobacteria are not present, the mats of Matupi Harbour carry cyanobacteria as the primary photosynthetic producers.

Table 38 Rate of decomposition of organic matter (mgC m^{-2} d^{-1}) in some of anaerobic processes in the bottom sediments and mats of Matupi Harbour

Locality, object	Breakdown of cellulose	Sulfate reduction	Methanogenesis
Central part, depth 55 m:			
Silt, sediment layer (cm):			
0–10	ND	0.300	0.140 (18%)
20–40	ND	0.320	0.287 (5%)
40–60	ND	728.700	0.087 (40%)
80–100	ND	70.400	0.010 (10%)
Tavurvur zone, Area II:			
Littoral mats	8.0–7.1	2.0–11.0	0.1–2.0 (NC)
Sublittoral mats	0.1–34.0	4.3–18.0	0.8–2.8 (NC)
Depth 15 m, silty sand, sediment layer (cm):			
0–0.5	ND	5.750	0.028 (3%)
0–1	ND	2.290	ND
1–3	ND	2.480	ND
Rabalankaia zone, depth 27 m:			
Silty sand, sediment layer (cm):			
0–1	ND	1.850	0.298 (6%)
1–2	ND	2.750	0.054 (10%)
2–4	ND	0.800	0.001 (HC)
Blanche Bay (control), depth 15 m:			
Silty sand	ND	1.560	0.030 (70%)

ND, no determinations; minimal and maximal values are given where available; in parentheses, proportion of methane formed from CO_2; NC below limits of measurement.
Source: Data from Namsaraev, 1992; Namsaraev *et al.*, 1994.

4.5.3. Bay of Plenty

Production processes are low in the mats in MacEwans Bight, Bay of Plenty. Oxygenic photosynthesis was measured in algobacterial mats at 3–8 m depth, with a maximum at 4 m of 0.62 g C m^{-2} d^{-1} (Table 39). A high rate of dark fixation of CO_2 was also recorded. However, again it was not possible to assess the proportions of chemosynthetic and heterotrophic assimilation of carbon dioxide in different mat structures. Bacterial photosynthesis was registered only in the shallowest zone (Table 39).

Microbiological investigation of anaerobic processes in the mats of MacEwans Bight shows that the basic role in mineralisation of C_{org} is played by two groups of bacteria: sulfate-reducing and cellulose-decomposing (Namsaraev, 1992) (Table 40). The rate of cellulose decomposition in algobacterial mats was considerably higher than that of sulfate reduction, which

Table 39 Rate of CO_2-assimilation (mgC m^{-2} d^{-1}) in mats of MacEwans Bight

		Photosynthesis		
Depth, m	CO_2-assimilation (total)	Microalgae (oxigenous)	Bacteria (anoxygenous)	CO_2-fixation (dark)
Algobacterial mat:				
4	860	620	30	210
7	350	280	0	70
Bacterial mat:				
8	30	0	0	30
12	40	0	0	40

Source: From Tarasov *et al.*, 1999.

corresponds to the data on quantitative bacterial composition and is related to the abundance of diatoms (Namsaraev *et al.*, 1994).

The total rates of aerobic and anaerobic processes of breakdown of organic matter in the algobacterial mats are lower than primary production by photosynthesis and chemosynthesis.

The mats in MacEwans Bight show high rates of oxidation of sulfide, elemental sulfur and, to a lesser extent, thiosulfate (Table 41). Oxidation of reduced compounds of sulfur (S^{2-}, $S_2O_3{}^{2-}$ and S^0) in mats is carried out by several groups of physiologically different sulfur bacteria, among which chemolithoautotrophic organisms prevailed. Sulfate was the end product of oxidation, and 20–30% was produced by abiotic oxidation (Sorokin, 1991).

No photosynthetic processes have been recorded in the bottom sediments of Volcanic Crater. Chemolithoautotrophic (up to 10^6 cells ml^{-1}) and heterotrophic thiosulfate oxidising microorganisms (up to 10^7 cells ml^{-2}) occur in the surface layer of the sediment and in near-bottom water, where the temperature is much lower than deep in the sediment (Sorokin, 1991). The growth of these microorganisms is based on utilisation of hydrogen sulfide generated from processes of bacterial sulfur reduction and sulfate reduction deeper in the sediment, but hydrogen sulfide was not detected in gas emissions and in the near-bottom layer. In the surface layers of the sediment, methane oxidation also occurred. The maximum rate of this process was found in the 0–0.5 cm layer, where it reached 373.3 μl CH_4 m^{-2} d^{-1} (Namsaraev, 1992).

In Volcanic Crater, in addition to sulfur-reducing archaea and eubacteria and thiosulfate-oxidising microorganisms, there are sulfate-reducing bacteria among the groups of bacteria participating in the breakdown of organic matter. *Desulfobacter postgatii* is the most abundant species (10^5 cells ml^{-1} in acetate) in cultures; *Desulfobacter autotrophicus* reaches a density of

Table 40 Rate of decomposition of organic matter (mgC m^{-2} d^{-1}) in some of anaerobic processes in the bottom sediments and mats of the Bay of Plenty

Locality, object	Breakdown of cellulose	Sulfate reduction	Methanogenesis
Volcanic crater near Whale Island:			
Silt, sediment layer (cm):			
0–0.5	ND	0.428	0.129 (96%)
0.5–1.0	ND	4.576	0.151 (40%)
1–3	ND	1.864	0.034 (6%)
3–6	ND	5.454	0.003 (100%)
6–9	ND	9.602	0.051 (50%)
10–15	ND	0.082	0.010 (40%)
18–22	ND	0.021	0
25–27	ND	0.011	0.188 (35%)
MacEwans Bight:			
Algobacterial mat	9–48	8–27	0.01–0.58
Bacterial mat	0.1–27	4–25	0.01–1.00
Calypso zone:	0	9.0–74.5	0.42–1.32 (20%)

ND, no determinations; minimal and maximal values are given where available; in parentheses, part of methane formation from CO_2.

Source: Data from Namsaraev, 1992; Namsaraev *et al.*, 1994.

Table 41 Bacterial oxidation of sulfide, thiosulfate and elemental sulfur in bacterial mat and the uppermost sediment layer of bottom sediment in the Bay of Plenty

		Oxidation rate			Rate of $S_2O_3^{2-}$ + SO_4^{2-} formation from S^0
		H_2S	$S_2O_3^{2-}$		
Locality, object	H_2S content, mg l^{-1}	mg m^{-2} d^{-1}		S^0-content, mg l^{-1}	mg m^{-2} d^{-1}
Volcanic crater near Whale Island:					
Silt	0	17.5	1.4	0	0
MacEwans Bight:					
Algobacterial mat	0.13	36.7	3.3	ND	ND
Bacterial mat *Beggiatoa* sp.	0.07	34.9	3.2	115	552
Bacterial mat *Thiothrix* sp.	0.07	0	6.2	ND	ND
Calypso zone:	0.01	6.3	0	0	0

ND, no determination.

Source: After Sorokin, 1991; Tarasov *et al.*, 1999.

10^6 cells ml^{-1} in the presence of hydrogen. There were also methane-producing bacteria in other sediments, where acetate-using bacteria had a population density 10^2 cells ml^{-1} and hydrogen oxidisers 10^3 cells ml^{-1} (Namsaraev, 1992; Namsaraev *et al.*, 1994).

The sulfate reduction rate was low, the maximum occurring 6–9 cm deep in the sediment and at a temperature of 50 °C (Table 40). Methanogenesis occurred at a greater rate in the surface layer of the sediment, where methane was mostly generated from acetate and in lesser amounts from formate. In deeper layers of the sediment (25–27 cm), CH_4 was mostly formed from CO_2 and H_2 (Namsaraev *et al.*, 1994) (Table 40).

The bottom sediments of the Calypso venting area showed oxidation of methane and hydrogen sulfide with rates of 1.61 μl CH_4 m^{-2} d^{-1} and 6.30 mg S^{2-} m^{-2} d^{-1}, respectively. In the surface layer of sediment (0–2 mm), chemolithoautotrophic sulfur bacteria, up to 10^6 cells ml^{-1}, and heterotrophic sulfur bacteria, up to 10^6 cells ml^{-1}, were recorded (Sorokin, 1991).

A high rate of sulfate reduction was associated with breakdown of organic matter (Table 40). The maximum rate was observed in the uppermost surface layer (0–0.5 cm), related to the high content of organic carbon in the sediments. The C_{org} content in soft bottoms reached a maximum of 10% around the gypsum dome (Sarano *et al.*, 1989).

Bacterial methanogenesis, with rates up to 1.324 mg Cm^{-2} d^{-1}, was recorded in bottom sediments of the Calypso area (Namsaraev, 1992; Namsaraev *et al.*, 1994).

Thus, in bottom sediments of shallow-water venting zones of the Bay of Plenty, thermophilic archaea and eubacteria develop concurrently with a great number of groups of microorganisms, participating in transformations of sulfur compounds. In areas of low water exchange (MacEwans Bight), microorganisms formed various types of mats at sites of venting.

4.6. Summary

The major and characteristic biological components of marine ecosystems in zones of shallow water venting are an abundance of thermophilic bacteria and microbial mats undergoing a variety of biogeochemical processes.

In zones of hydrogen sulfide venting, the leading role belongs to bacteria of the sulfur cycle, which oxidise and reduce various forms of sulfur, as part of a process of primary production (bacterial photosynthesis and chemosynthesis), and in the mineralisation of organic matter. Sulfur-reducing hyperthermophilic and extreme thermophilic bacteria (including new species of Archaebacteria), and mesothermophilic eubacteria are specific links in the sulfur cycle and breakdown of organic substrates (Miroshnichenko *et al.*, 1989a,b, 1999; Bonch-Osmolovskaya, 1991; Bonch-Osmolovskaya *et al.*, 1991, 1993; Kostyukova *et al.*, 1999). Such bacteria are found deeper in the hydrothermal systems, in bottom sediments and in vents, in both temperate (Kuriles and New Zealand) and tropical (Papua New Guinea) latitudes of the west Pacific. These groups of bacteria participate in anaerobic breakdown of organic matter and can reduce elemental sulfur to hydrogen sulfide at high temperatures (>50–60 °C). Peptides and polysaccharides are among the substrates for growth of the extremely thermophilic bacteria, but complete breakdown of organic matter does not occur in such processes. Intermediate metabolic products of extreme thermophilic bacteria (acetate, formate, propionate) are oxidised by mesothermophilic sulfobacteria at lower temperatures, usually <50 °C. In all these processes, there is a high rate of reduction of elemental sulfur to hydrogen sulfide, up to 2.3–3.2 g S^{2-} m^{-2} d^{-1} (Bonch-Osmolovskaya, 1991; Bonch-Osmolovskaya *et al.*, 1991, 1993; Namsaraev *et al.*, 1994). Data on fatty acids in deeper fluids of the hydrothermal system and waters of Kraternaya Bight show that the substrate for these processes is mostly organic matter in seawater coming through bottom sediments from the deep part of the volcanic structure (Figures 1 and 19). These processes of mineralisation of organic matter by thermophilic sulfur bacteria and reduction of elemental sulfur were formerly unknown for coastal ecosystems.

On the seabed in the zone of shallow-water venting, microorganisms form mats that consist of bacteria of various physiological groups, plus microalgae, and products of their metabolism, either as deposits or in suspension. Diatom mats develop around vents that do not contain hydrogen sulfide. Mats and films cover significant areas of the seabed and their thickness, depending on environmental conditions, ranges from 0.3 mm to 20–30 cm.

Various groups of bacteria that oxidise and reduce sulfur compounds develop concurrently with diatoms in the algobacterial mats. The sulfur cycle is thus bound both to synthesis and to breakdown of organic matter. A high diversity of purple, green and colourless sulfur bacteria is found in these mats.

Bacterial mats contain *Thiobacillus, Thiomicrospira, Thiosphaera* (up to 10^6 cells ml^{-1}) or the filamentous sulfur bacteria *Thiothrix* and *Beggiatoa*, and most oxidation of hydrogen sulfide and thiosulfate occurs there (Dubinina, 1989; Nesterov *et al.*, 1991; Sorokin, 1991; Namsaraev *et al.*, 1994). Colourless bacteria are able to switch to chemoorganotrophic metabolism (i.e., to participate in mineralisation of organic matter) in sites of simultaneously high content of organic substrates and hydrogen sulfide. The algobacterial and bacterial mats show both synthesis and breakdown of organic matter and function as a biogeochemical barrier to hydrogen sulfide, oxidising it to elemental sulfur. In most mats, the microorganisms are in a syntrophic relation with each other, producing and decomposing organic matter and using various energy sources and substrates. Noteworthy, at a temperature up to 40 °C and at a hydrogen sulfide content up to 90 μM there is an abundance of the diatom *T. anguste-lineata* in the algobacterial mats of Kraternaya Bight. This species also dominates the phytoplankton of the bight. In MacEwans Bight, Bay of Plenty, diatoms live in algobacterial mats at even higher temperatures, up to 55–60 °C.

Development of the mats is affected by benthic organisms. Benthic communities of high population density and biomass occur in the diatom mats, near or under algobacterial, bacterial or diatom mats and in bottom sediments. Nematodes and harpacticoids are common forms of meiobenthos in diatom mats. In algobacterial and bacterial mats, concurrently with prevailing nematodes and ciliates, there are sedentary polychaetes at high population density and biomass. These animals feed on the bacteria and microalgae of the mats. Additionally, particles and scraps from the mats are carried out by vertical flow into the water column and distributed to the benefit of the fauna over a wider area (Tarasov *et al.*, 1985, 1986, 1991, 1999; Kamenev, 1991a,b; Kamenev *et al.*, 1993; Tarasov, 1999).

All estimations of the rate of primary production of organic matter in mats (up to 3.7 gC m^{-2} d^{-1}) confirm that the mats are important in the trophic system in zones of shallow-water venting. Oxygenic photosynthesis of benthic diatoms, bacterial photosynthesis (anoxygenic photosynthesis) and autotrophic chemosynthesis in algal-bacterial and bacterial mats generate primary organic matter, which is an essential addition to the primary organic matter synthesised in the water column. For example, in Kraternaya Bight the rate of primary production in diatom and algobacterial mats and in microphytobenthic communities is 0.6–3.7 gC m^{-2} d^{-1} compared to a background rate of $\sim$10 gC m^{-2} d^{-1} rate for primary production in the water column. In algobacterial mats of MacEwans Bight, production is comparable to that of the entire water column, 0.9 and 1.2–2.4 gC m^{-2} d^{-1}, respectively. In Matupi Harbour, in the gas-hydrothermal venting zone, the average production of cyanobacterial mats exceeds the rate of photosynthesis and chemosynthesis (cyanobacteria, diatoms and bacteria) in the water column 0.9–2.0 and 0.5–0.6 gC m^{-2} d^{-1}, respectively.

In these ecosystems, there is, in addition to intense primary production, active breakdown of organic matter. A complex of thermophilic sulfur-reducing bacteria break down organic matter to carbon dioxide in the mats and in bottom sediments at high temperatures, 50–90 °C. This process is slower at lower temperatures. In addition to these specific groups of bacteria, other bacterial groups that are common in coastal sediments also take part in the breakdown of organic matter in areas of shallow-water venting (Borzenkov *et al.*, 1989; Namsaraev *et al.*, 1991, 1994; Namsaraev, 1992).

We must note that in all zones of shallow-water venting, an important biogeochemical role belongs to the heterotrophic bacteria that are able to reduce and oxidise iron and manganese. For example, the number of manganese-oxidising and iron- and manganese-reducing bacteria reaches, respectively, 10^8 and 10^6 cells ml^{-1} in soft bottoms of venting areas (Namsaraev *et al.*, 1991).

The high rates of production, abundance of various organic substrates in the water column and intense development of the microflora on the bottom drives the formation of an abundant benthic fauna (Tarasov *et al.*, 1985, 1986, 1991, 1993, 1999; Kamenev, 1991c; Kamenev *et al.*, 1993; Tarasov, 1999).

The taxonomic structure and abundance of meiobenthos of shallow-water vents depend on the temperature of the seabed and the content of hydrogen sulfide in the fluids. Nematodes dominate the meiobenthos, their population density varying from 2×10^3 ind. m^{-2} in bacterial mats of Matupi Harbour up to 1.8×10^6 ind. m^{-2} in algobacterial mats of Kraternaya Bight. Very high numbers of nematodes, $\sim 10^7$ ind m^{-2}, are found in aggregations (brushes) of the sedentary polychaete *P. vulcanica*, on which bacterial mats form. Such intensive populations of nematodes, especially in mats, appear to result from the wide range of morphological and biochemical adaptations of the group to environmental conditions, which enables them to master new biotopes and sources of food. Nematodes of the family Oncholaimidae, which inhabit venting zones in Matupi Harbour at population densities exceeding 1.3 10^5 ind m^{-2}, were also found in shallow-water venting areas off Milos Island in the Aegean Sea (Thiermann *et al.*, 1994, 1997; Dando *et al.*, 1995). Bacterial mats are also inhabited by animals with special adaptations, such as the nematodes of the family Desmoridae, which carry exosymbiotic sulfur bacteria (Tarasov, 1999, 2002). In cerianthid tubes at shallow vents, there are commensal nematodes of the family Leptosomatidae, and colourless sulfur bacteria (*Beggiatoa*) form a web-like thin film. The mats also provide a habitat for animals that carry endosymbiotic bacteria (Zhukova *et al.*, 1991, 1992; Malakhov *et al.*, 1992).

In all shallow venting areas, the macrozoobenthos has low species diversity. The taxonomic structure in these areas appears to be determined by the geographical region of the ocean (temperate or tropical latitudes), the character of the seabed (hard or soft bottoms, rigid lava flows or hydrothermal constructions on the bottom), the temperature of the bottom sediments and volcanic fluids and the chemical composition of the vent fluids (sulfide or nonsulfide).

Cerianthids, burrowing bivalves and polychaetes dominate the biomass in some parts of zones of shallow-water venting at temperate latitudes of the Pacific (Kuriles and New Zealand). In Kraternaya Bight and MacEwans Bight, representatives of these taxa form communities of very high population density and biomass, up to several kilograms per square metre.

In Matupi Harbour, in the tropics, the commonest animals living close to vents are the sponge *Oceanapia* sp., with ascidians, molluscs, spionid polychaetes, various species of crabs and scleractinian corals, whose colonial growth is depressed, compared with typical coral reefs of the Bismarck Sea (Tarasov *et al.*, 1999). Development of sponge settlements on hydrothermal structures is probably helped by the high content of silicate (up to 2.0 mM) in the volcanic fluids (Propp *et al.*, 1997). Gas-hydrothermal activity in Matupi Harbour is more intense than in Kraternaya Bight or in MacEwans Bight. Matupi Harbour is characterised by the high temperature of a great number of the vents and their flow rate and by the hot bottom sediments. It is probable that the high temperature is a key factor controlling the rather low biomass and population density of animals found there.

5. ECOSYSTEMS OF SHALLOW-WATER VENTING

The occurrence of gas-hydrothermal systems along island arcs depends on the periods of activity and the life span of the volcanoes or the volcanic massif. The average duration of activity of a single volcano within the complete cycle of development to termination of any activity has been estimated as 40–50 thousand years (Masurenkov, 1979). There has been no common pattern in the number of eruptions and their periodicity, and postvolcanic stages may last for thousands of years. Eruptions of volcanoes are related to the behaviour of the magmatic centre (intrusion) and to thermal condition of the magma.

In the studied areas of the Pacific reviewed here, the time since the last volcanic eruptions (i.e., the age of the hydrothermal system) has been estimated as some thousands of years for Ushishir Volcano (Kraternaya Bight) (Bondarenko, 1991) and 9000 years for Whale Volcano (Whale Island, the Bay of Plenty) (Duncan and Pantin, 1969; Lloyd, 1974). In Matupi Harbour the modern hydrothermal stage began after the last eruptions of volcanoes Tavurvur and Volcano ~50 years ago (Greene *et al.*, 1986; Archbold *et al.*, 1988). However, we must note that strong eruptions of Tavurvur Volcano occurred in September 1994. At present we have no data on the impact of these eruptions on underwater venting and the biota of Matupi Harbour.

Despite the differences in duration of the hydrothermal stages, the data on qualitative and quantitative structure of the vents, physical and chemical parameters of the water environment and bottom sediments show that the effect of modern volcanism on the marine environment in shallow-water areas has similar characteristics and does not depend on the geographical position of such areas in the ocean.

According to the classification of Kononov (1983), known terrestrial, littoral and sublittoral gas-hydrothermal vents belong to (1) the hydrogen sulfide-carbonic-sulfate-chloride type; (2) the magnesium-sodium type; or (3) the carbonic-sulfate-chloride type. This classification is rather inconvenient for analysing biological processes in zones of venting, as it defines only the liability of hydrothermal solutions to leaching and to formation of ore components. To consider volcanic solutions from the perspective of bacterial oxidising-reducing processes and the effects of the vents on vital functions of marine organisms, all shallow-water vents can be divided in two groups: (1) those with hydrogen sulfide and (2) those without reduced sulfur.

Shallow-water vents emit gases and volcanic fluids at temperatures from 10 to 98 °C, all containing an abundance of dissolved metals and compounds, including algal nutrients. In island arcs or single volcanoes, the vents are located mostly in rift sites, on the bottom of bays and gulfs. Terrestrial and underwater vents are formed from one volcanic centre, as a result of high-temperature interaction of seawater with adjoining volcanic rock or sediment masses on the bottom. Juvenile water is present but does not exceed 3–4%. Terrestrial thermal vents often contain appreciable amounts of meteoric (atmospheric) water, and they are thus fresher than littoral and sublittoral vents. The share of meteoric water increases with a decrease of temperature of the volcanic fluids.

In shallow-water venting zones, enrichment of seawater by products of volcanic activity is determined by the gas and chemical composition of the vent water, particularly the ratios of the various gases, elements and their compounds. Much depends on the rate of flow of the vents, their number and occupied area, on the degree of openness or isolation from the open sea and on depth and dynamics of the water masses.

The greatest impact of volcanic activity on the environment is found in semi-enclosed bays (Kraternaya Bight and Matupi Harbour) with low water exchange with the open sea but also occurs in shallow water (3–15 m depth) in open bays (MacEwans Bight), in the immediate zone of venting. There is an enrichment of the seawater by products of volcanism, gases, heavy metals, sulfur compounds, silicon, phosphorus and other nutrient elements, two or three orders of magnitude greater than in normal shallow seas.

The water column in the semi-enclosed bays is stratified, because of tidal water exchange and a distinction in physical and chemical characteristics of surface and underlying layers of the water, caused by spreading of hydrothermal fluids lighter than seawater. Water exchange with the surrounding ocean occurs in the lower layers of the water column, and the distribution of the seawater depends on the strength of the tidal phenomena and the physical structure of the bays. Beneath the surface layer the characteristics of the near-bottom layer also change. The physical conditions and the chemical composition of the lower layers are controlled by the effect of the vents and sedimentation metal particles and organic matter, and by biogeochemical transformations of organic matter in bottom sediments and remobilisation of nutrients and metals in the near-bottom layer.

In the open water areas (Volcanic Crater and Calypso area, Bay of Plenty) with high-speed tidal currents, the gas-hydrothermal venting affects mostly the near-bottom layers and bottom sediments, although volcanic gases can be traced to the surface, mainly as a result of their abundance and intense emission. At these vents, carbon dioxide is the predominant gas, enriching the seawater to such an extent that some escapes to the atmosphere. Where hydrogen sulfide, hydrogen, methane and other hydrocarbons are in high concentration in the vent fluids, their concentration in the marine environment (the degree of enrichment) increases. The same is observed in metals and in compounds of volcanic origin. In semi-enclosed water areas, especially in Kraternaya Bight, a significant portion of incoming hydrogen sulfide is oxidised abiogenically by chemical reactions in the surface layer of the water column, which carries high concentrations of oxygen (150–200% saturation). In spite of this high oxygen saturation, the flow of hydrothermal fluids is so high that hydrogen sulfide is continuously present in the water column concurrently with oxygen.

Enrichment of seawater by nutrients is also related to the flow of hydrothermal fluids and their distribution at the water surface. Beyond the direct intake from vents, there are three other sources of mineral substances required for development of microflora. These sources are indirectly connected to volcanic activity and to the structure of the bays and include (1) bottom regeneration of nutrients and their upwelling into the surface layer of the water column by vertical convective diffusion, created by heat of the volcanic centre; (2) nutrients coming with outside seawater during flood tide; and (3) terrigenous drainage from terrestrial slopes of volcanoes during periods of rain.

The data on composition and content of various forms of metals (dissolved and suspended forms) in vents, water column, suspension, phytoplankton and zooplankton, bottom sediments, on sedimentation rate of suspension, and on destruction of suspended organic matter during sedimentation, suggest a relevant role for metals in the biogeochemical processes occurring in the bays. In the surveyed areas, transition of metals into the suspended form depends on production, development and distribution of phytoplankton and bacterial communities (Shulkin, 1995). With an increase of population density of microflora in the water column, there is increased adsorption of metals onto suspended biogenic material. Rates of removal of metals from the water column by sedimentation to the seabed of semi-enclosed bays vary significantly, depending on latitude (temperate or tropical latitudes). In the tropical venting areas, there are high rates of removal of metals, related to the rather low content of biogenic suspension (microflora) or its absence. In the temperate venting zones, with high levels of biogenic suspension, the rate of removal of metals from the water column is lower. Shulkin (1995) has suggested that this difference in rates of removal of metals between venting areas of tropical and temperate latitudes could be related to different values of density of the seawater. The observed rate of sedimentation is four to five times lower in Kraternaya Bight than in Matupi Harbour. As a result, the residence time of suspended material in the water column in Kraternaya Bight is 20–38 days, while in Matupi Harbour it is only 3–10 days. Iron and manganese occur at high concentrations in the near-bottom layer but are low in bottom sediments. This could imply redistribution (or remobilisation) of various forms of metals in biogeochemical processes in bottom sediments and reverse intake into suspension of a part of the reactive forms of iron and manganese from bottom sediments. Thus, there is apparently a circulation of metals with variable valency at the boundary between the near-bottom layer and seabed sediments. This in turn is connected to the productivity of the water column, to the abundance of biogenic suspension, to the rate of its sedimentation in the water column and in near-bottom layer, to density of water and to intensity of biological and chemical processes in the bottom sediments. In Matupi Harbour such a phenomenon was not observed as the water column as a whole is characterised by low values of primary production, abundance of microflora and suspended material of biogenic origin. In addition, the water column has a low organic content and there is a low rate of biogeochemical processes in the sediments away from the zone of direct impact of venting.

Variation in the chemical composition and properties of bottom sediments is connected to volcanic activity. In the bays, most of the bottom sediments are of hydrothermal or volcanic origin. In open areas, the physical and chemical characteristics of soft bottoms adjacent to the venting zone change considerably as a result of uptake of gases and thermal solutions through them. High temperatures at the seabed, bubbling of gases through the sediments and biogeochemical redistribution of various forms of metals with variable valency are the key factors that determine the observed changes.

The dissolved forms of metals emitted by vents into the marine environment are transformed into oxides deposited on the seabed. The amount of oxide and hydroxide forms of metals, both in suspension and in surface layers of bottom sediments, is high in zones of shallow-water gas-hydrothermal vents (Shulkin, 1991, 1992a,b, 1995). In some sediments, the concentration of iron reaches ore level (>10% of dry weight), rising to 45% close to the vents (Sazonov, 1991; Shulkin, 1991, 1992b).

The redox index in the sediments is related to the flow of metals from the vents, to the availability of oxidised forms of iron and manganese, which have higher concentrations than the other metals in liquid and solid phases in bottom sediments, and to biogeochemical transformations of forms of metals. In environments with sufficient organic matter, the iron, being a highly reactive element, changes from oxide to protoxide form, giving one portion of the oxygen to oxidation of organic substances and another to the generation of water (Kapchenko, 1974; Ilichev, 1989):

$$\mathrm{Fe(OH)_3 = Fe(OH)_2 + OH; 2OH = H_2O + 1/2O_2} \tag{1}$$

A considerable amount of iron can go into solution when there is a high carbon dioxide content in the sediments:

$$\mathrm{Fe(OH)_2 + 2CO_2 = Fe(HCO_3)_2} \tag{2}$$

The iron further reacts with hydrogen sulfide and turns into pyrite under reducing condition:

$$\mathrm{Fe(OH)_2 + H_2S = FeS\ nH2O; FeS + H_2S = FeS_2 + H_2} \tag{3}$$

Unfortunately, the role of metals with variable valency in the balance of organic matter in marine sediments in zones of shallow-water volcanism still remains unexplored. It is unknown which part of C_{org} is used for reduction of iron and manganese, how these processes are mated with bacterial sulfate reduction and sulfur reduction and with hydrogen sulfide of hydrothermal origin and whether oxide forms of iron and manganese are able to oxidise other reduced compounds in bottom sediments.

The data on the amount of various forms of metals and hydrogen sulfide, on the sulfate reduction rate in various layers of soft bottom in areas of shallow-water vents, nevertheless, show that iron and manganese, and to a lesser degree other metals, can bind hydrogen sulfide, thus providing the geochemical barrier that impedes its penetration into the surface layer of bottom sediments. An important role in these processes also belongs to bacterial activity, which is able to oxidise or reduce compounds of iron, manganese and sulfur.

Summarising the data on structure, abundance, distribution and dynamics of gases, metals and various compounds in vents, the water column and in bottom sediments, it is possible to conclude that special conditions of the environment, determined by venting flows and by hydrological conditions, exist in zones of shallow-water volcanism. Comparison of areas of shallow and deep-water venting reveals a number of differences, related mostly to depth, dynamics of the water masses and processes of mineralisation and ore formation, but all are connected to global volcanic processes.

From the point of view of volcanology and geology, the Calypso area should be distinguished from the other venting areas considered here. It is characterised not only by a great number of vents located over a large bottom area at a depth of 160–180 m, but also by an extremely high content of arsenic, antimony, mercury, uranium and molybdenum in the sediments (Sarano *et al.*, 1989). The cause of the high concentration of these elements is still unresolved.

The abundance of mineral nutrients (SiO_3^{2-}, PO_4^{3-}, NO_3^-), gases and other inorganic compounds (CO_2, H_2, CH_4, C_nH_n, S^0, H_2S, $S_2O_3^{2-}$, NH_4^+) enables autotrophic organisms to use two energy sources: sunlight (photosynthesis) and oxidation of reduced compounds (chemosynthesis). It is important to note that in contrast to all known marine basins, in areas with shallow-water volcanism, chemosynthesis occurs not only near the seabed, in the immediate vicinity of the venting, but also in the surface layer of the water column, where intense photosynthetic processes are also observed (Plate 11). The photosynthetic layer in the surface waters often occurs below the layer of chemosynthesis, as it is related to the distribution of hydrothermal fluids in surface waters. The contribution of each process to the production of primary organic matter depends on the physical and chemical conditions created by the vents and on the range of adaptation potential of the photosynthesising organisms.

Most of the organisms forming the main biomass of the phytoplankton community at shallow vents are common species, widely distributed in various regions of the World Ocean. Recent research shows that the basic primary producers of the phytoplankton community in zones of shallow-water volcanism include the following: a small number of diatom species; the ciliate *Mesodinium rubrum* with its symbiotic microalgae; and cyanobacteria. Where the environment is extremely specialised (high temperature and strong flow from vents) (e.g., the zones of littoral and sublittoral vents of Tavurvur Volcano, Matupi Harbour), cyanobacteria and chemosynthesising bacteria prevail in the autotrophic component of the plankton community. In such zones, the proportion of bacterial chemosynthesis in the total primary production of the water column reaches 30–50%.

A large amount of primary organic matter is generated during photosynthesis and chemosynthesis in areas of shallow-water volcanism. A high production of biomass and high rates of assimilation of CO_2 are especially characteristic of Kraternaya Bight.

The characteristics of the water environment determine changes in the composition and distribution of the heterotrophic component of the pelagic community. Volcanic areas are characterised by extremely high population densities and production of bacterioplankton (Sorokin *et al.*, 1998, 2003). In bays the maximum values of bacterial production are reached in the surface layer, whilst in the open areas it is the bottom layer, where currents and turbulence are less significant, that is most productive.

The distribution of planktonic protozoa (zooflagellates, planktonic amoebae, asymbiotic ciliates) is related to the distribution of organic matter and bacterioplankton. Zooplankton in venting regions is of low species diversity, but great biomass, when compared to normal seawater communities. As with the phytoplankton communities, the zooplankton does not contain any species or group of organisms that can be identified as obligate inhabitants of shallow-water venting areas.

Various microbial communities, including hyperthermophilic bacteria that are specific to the zone of volcanic activity, form in bottom communities of shallow-water venting areas. These communities develop deep in the hydrothermal systems, in vents, in bottom sediments and around emissions of gases and thermal solutions.

In areas of hydrogen sulfide venting, the leading role in biogeochemical processes belongs to the bacteria that oxidise or reduce various forms of sulfur during primary production of organic matter (anoxygenic photosynthesis and chemosynthesis) or its decomposition. From the biogeochemical point of view, the relevant links in the sulfur cycle are groups of sulfur-reducing hyperthermophilic and extreme thermophilic bacteria (including new species of Archaebacteria) and mesothermophilic eubacteria. All participate in anaerobic destruction of organic matter and reduce sulfur to hydrogen sulfide. In hydrothermal zones, the sulfur may have a deep (endogenic) origin or may be formed as a result of biological and chemical oxidation of hydrogen sulfide.

Peptides and polysaccharides (starch, glycogen, pectin) are substrates for hyperthermophilic and extreme thermophilic bacteria. However, full breakdown to CO_2 of high-molecular-weight compounds does not occur during bacterial fermentation. Further breakdown of the products of fermentation produced by extreme thermophilic bacteria (acetate, formate etc.) is carried out by mesothermophilic eubacteria at lower temperatures ($<$50–60 °C) in the surface layers of the hydrothermal system, in the bottom sediments or in the bacterial mats. The data show that such groups of bacteria develop in all hydrogen sulfide venting areas and the rate of reduction of elemental sulfur are high. Such a pattern of anaerobic oxidation of organic substances is highly characteristic of shallow venting areas and has not been recorded previously in coastal ecosystems.

In zones of venting, where there is a low exchange of water with the open sea, as in bays, microalgae and bacteria form mats on the seabed. These mats contain bacteria of various physiological groups, microalgae, products of their metabolism and particles of sediments. Where hydrogen sulfide is emitted, the groups of bacteria oxidising or reducing sulfur compounds are dominant in the mats and in the bottom sediments. In the mats, the sulfur cycle is connected to the carbon cycle, to both production and breakdown of organic matter. Diatom mats develop in venting areas that do not contain hydrogen sulfide and elemental sulfur. Experiments on destruction or removal of parts of mats show that active hydrothermal flow and a temperature gradient are prerequisites for growth of the mats.

The thickness of the mats varies from tenths of a millimetre up to 20–30 cm, and they cover significant areas of the seabed. Nematodes and harpacticoids are dominant forms of meiobenthos in diatom mats; nematodes and ciliates dominate in bacterial and algobacterial mats, concurrently with settlement of sedentary polychaetes at high population density and biomass. Benthic communities of high population density and biomass develop in bacterial mats and diatom mats (or under them in sandy bottom sediments) in Kraternaya Bight and MacEwans Bight. Some species of macrozoobenthos use the mat bacteria and microalgae as their basic source of food. Those data and assessed rates of production of organic matter in various types of mats demonstrate that they are important biological components in the trophic chain in shallow-water venting areas. Particles and scraps of mats are transferred by vertical hot flows into the water column and distributed over a large area.

The primary organic matter formed during photosynthesis and chemosynthesis in diatom, algobacterial and some bacterial mats is a significant addition to the amount of organic matter synthesised in the water column. In Kraternaya Bight, the proportion of primary organic matter formed by the diatom and the algobacterial mats, concurrently with that of microphytobenthos on rocky and sandy bottom sediments, ranges from 10 to 30% of the values of primary production in the water column. In algobacterial mats of MacEwans Bight, production is of the same order as values of primary production in the water column. In Matupi Harbour, primary production by the mats considerably exceeds (several times) the rate of a photosynthetic and chemosynthetic production of cyanobacteria, diatoms and bacteria in the water column.

In bacterial mats with colourless sulfur bacteria *Thiothrix* and *Beggiatoa* and the "Thiodendron" bacterial association, chemotrophic metabolism dominates. The important role in such biogeochemical processes is the oxidation of sulfur compounds (hydrogen sulfide and thiosulfate) to elemental sulfur or to sulfates. As already noted, these mats can function as a biogeochemical barrier to hydrogen sulfide.

High productivity of pelagic and bottom communities in venting zones and aggregations of organisms on the bottom determine the high content of organic matter and need effective mechanisms to break it down. As mentioned earlier, the thermophilic bacteria break down organic matter in the mats or in bottom sediments located in areas of high temperature (50–90 °C). This process continues at a lower rate at lower temperatures and is apparently limited by lack of a suitable acceptor for surplus hydrogen. At the same time, aerobic and anaerobic saprophytes, cellulose-decomposing bacteria, sulfate-reducing, denitrifying and methane-oxidising bacteria (i.e., the common bacteria for usual seabed sediments) also take part in the breakdown of organic matter in most of the surveyed areas reviewed here. A distinctive aspect of breakdown processes is the high rate at all stages, which is related to the high levels of organic substrates. In all areas of shallow-water volcanism, an important role in the carbon cycle belongs to metals with variable valency. Quantitative estimation of bacterial reduction and oxidation of iron, manganese, zinc and copper is difficult. Nevertheless, the data on availability of such groups of bacteria in the water column and in bottom sediments of Kraternaya Bight (Namsaraev *et al.*, 1991) and on significant enrichment of water and bottom sediments with metals suggest that, like the sulfur-reducing and sulfide-oxidising groups of bacteria, the iron- and manganese-reducing and -oxidising microorganisms can transform valency forms of metals and take part in recycling carbon. Such processes are extremely important, as they considerably affect the biogeochemical condition of the bottom sediment in marine ecosystems subjected to external flow of reduced compounds of sulfur and heavy metals (Plate 11).

High rates of production, abundance of organic substrates in the water column and intense development of microflora on the bottom in venting zones allow the formation of a benthic fauna of high population density and biomass. From these data, we can distinguish a number of general aspects in the formation, structure and distribution of biota in zones of shallow-water gas-hydrothermal vents.

The macrozoobenthos of areas of shallow-water venting has low species diversity. A few taxonomic groups of animals dominate by both biomass and population density. The taxonomic structure of populations in areas of venting is determined by the geographical location (temperate and tropical latitudes), by the character of the seabed (hard and soft bottoms, rigid lava flows or hydrothermal constructions), by temperature of bottom sediments and volcanic fluids and by chemical composition of the vent fluids.

In most of the surveyed areas in the western Pacific, the fauna is mostly common species, widespread in the region or in the World Ocean, together with opportunistic species. The opportunists can also form high-density populations in eutrophic waters subjected to anthropogenic impact.

At hydrothermal vents in temperate latitudes of the Pacific (Kuriles, New Zealand) cerianthids, burrowing bivalves and sedentary polychaetes dominate by biomass. In Kraternaya Bight and MacEwans Bight, representatives of these taxa form communities of very high population density and biomass (some kilograms per square metre of bottom). Judging from density parameters of populations of these animals (>1,000 ind m^{-2} for cerianthids, up to 10^6 ind m^{-2} for *P. vulcanica* in Kraternaya Bight and >1,500 ind m^{-2} for *Tawera spissa* in MacEwans Bay. The extreme physicochemical conditions of the environment do not inhibit their growth and development. Population growth is determined to a great extent by interspecific competition for small areas of continuously high energy. The impact of predators cannot be excluded. For example, large predators are absent on the bottom of

Kraternaya Bight, resulting in numerous hermit crabs that dispense with protection. However, there are a large number of arroworms (Chaetognatha) that consume the planktonic larvae of bottom invertebrates, including cerianthids. This may be one aspect of population control of common animal species. The predatory gastropod *Cominnella adspersa* and burrowing starfish *Astropecten polyacanthus* may control the population of the bivalve *Tawera spissa* in MacEwans Bight.

In the tropical locations, common representatives of the fauna living directly in venting areas are the sponge *Oceanapia* sp. with ascidians, molluscs, spionid polychaetes and various species of crabs. The species structure of coral communities is considerably reduced, when compared with a typical coral reef of the Sea of Bismarck. Volcanic activity in Matupi Harbour is greater than in Kraternaya Bight or in MacEwans Bight. In Matupi Harbour, the vents are stronger and have higher temperatures, as do some areas of the seabed. Therefore, despite high values of photosynthetic production and bacterial production in these tropical areas, temperature is a key factor determining the low biomass and density of animal populations. Development of the sponge population on hydrothermal ring formations may be connected to the high content of silicate in volcanic fluids at the Rabalanakaia venting zone.

High sea bottom temperatures and intense water exchange limit the diversity and distribution of the benthic fauna in Volcanic Crater (Bay of Plenty). Mobile animals, such as crabs and amphipods, having minimal contact to the seabed are dominant.

Judging from the species diversity and abundance of the benthic animals living on a gypsum dome and in bottom sediments of the Calypso venting zone, it would seem that the biota have not been affected by the high concentrations of arsenic, antimony and mercury there (Sarano *et al.*, 1989).

The benthic communities in shallow-water venting zones have traits in common with communities in waters subjected to anthropogenic impact (thermal, residential or industrial pollution) or to other changes resulting in deterioration of the environment. In areas of such impact, the composition and trophic structure of the communities changes for the worse and the most sensitive species are eliminated. Species adaptable to a wide range of environmental factors and having powerful adaptive traits, such as resistance to temperature and salinity fluctuations, an ability to change their type of metabolism, a certain type of feeding, an ability to survive in conditions of low oxygen content or in the presence of sulfide, can gain a selective advantage under extreme environmental conditions. Opportunistic species commonly occupy such areas, and spionid and capitellid polychaetes are good examples of such species that flourish in extreme environments and have a high reproductive potential (Tulki, 1968; Fauchald and Jumars, 1979). The high tolerance of capitellid polychaetes to sulfide has been shown in zones of shallow-water hydrothermal vents of Milos, Aegean Sea (Gamenick *et al.*, 1998). As our data show, they are also abundant in regions of shallow-water volcanism. Cerianthids and *Macoma* spp. can also be regarded as opportunists.

Some biochemical changes, which might imply adaptations to venting, were observed in sea urchins, bivalves and gastropods (Muzyka and Tarasov, 1991, Tarasov *et al.*, 2003). In all surveyed areas, the activity of microsomal oxidation, cytochrome P_{450} activity, mitochondrion cytochromes and 5-aminolevulinic acid (the precursor for synthesis in the cell) were three to nine times higher than in the soft tissues of the same or a closely related species living outside the venting area. The data, especially the high rates of activity of microsomes and cytochrome P_{450}, suggest that in the environment and in cells of animals there are toxic substances that can be neutralised by these biochemical reactions. However, it remains unclear which compounds and elements initiate the biochemical changes.

Differences in the accumulation of heavy metals in soft tissues of animals have been observed in various species of bivalves in various regions of shallow-water venting. Two closely related species from Kraternaya Bight, *Macoma golikovi* and *M. calcarea*, both had high content of iron, manganese, zinc, copper, cadmium and nickel in the tissues, but concentrations of zinc and cadmium were, respectively, one order and 1.5–2 times higher in *M. golikovi* than in *M. calcarea* (Kamenev *et al.*, 2004). Near vents in Matupi Harbour, where there is a high content of dissolved and suspended forms of metals (Fe, Mn, Zn, Cu, Pb, Cd and Ni), only iron and manganese are highly accumulated in the tissues of the bivalves *Barbatia* sp. and *Septifer bilocularis*; the concentrations of other metals in their tissues were not elevated and were less than is normal in the general environment (Kavun, 1996). Comparable results have been obtained with bivalves from communities in zones of deep-water venting (Roesijadi *et al.*, 1985; Smith and Flegal, 1989) and remain unexplained.

Extreme environmental conditions in zones of shallow-water volcanism have produced morphological changes in the external and internal structure of the shell of the burrowing bivalve *M. golikovi*, in which developmental anomalies increase in the immediate proximity of vents (Kamenev, 1989, 1990, 1991a). Morphological disturbances have also been recorded in littoral fucoid algae (Khristoforova and Malinovskaya, 1991).

At deep-sea vents (Grassle, 1985, 1986; Hessler *et al.*, 1988; Galkin and Moskalev, 1990; Brooks and Wiley, 1988; Tunnicliffe, 1991; Tunnicliffe *et al.*, 1998; Van Dover, 2000; Galkin, 2002; Gebruk, 2002), more than half of all animal species in the community are vent obligates, not occurring outside vent area. Moreover, the biomass around deep-sea vents is dominated by several species that have a reduced or missing digestive system and obtain their energy from symbiotic chemosynthesising bacteria.

New species of nematodes, bivalves and polychaetes have been described from the shallow-water gas-hydrothermal venting area of Kraternaya Bight. Most of these are present in high biomass but have not been recorded from other parts of the of the Kurile Island chain. However, they can hardly be described as vent obligates, because the coastal waters of the Kurile archipelago have not yet been studied sufficiently. Pogonophores of the genus *Siboglinum* from zones of volcanic activity of the Bay of Plenty are a new species (Malakhov *et al.*, 1992), but they remain undescribed; all the described species of this genus are found in reducing sediments and are not vent obligates.

Thus, in contrast to the fauna of deep-water hydrothermal communities, obligate hydrothermal species have not yet been found among common animal species in areas of shallow-water venting in the west Pacific. This absence of obligate vent species from shallow-water vents and seeps has been considered and discussed by many authors (Davies and Spies, 1980; Powell *et al.*, 1983; Fricke *et al.*, 1989; Hovland and Thomsen, 1989; Dando *et al.*, 1991, 1994a, 1995; Dando and Hovland, 1992; Abbiati *et al.*, 1994; Thiermann *et al.*, 1994, 1997; Morri *et al.*, 1999; Gebruk, 2002).

Various animal species in which symbiotic bacteria provide the main nutrition have been recorded in the shallow venting areas studied. They include the bivalve *Axinopsida orbiculata orbiculata* from Kraternaya Bight, other bivalves of the family Thyasiridae and the pogonophore *Siboglinum* sp. However, these species are few and their role in the trophic structure of the communities is not significant. These data, as well as the data of other authors (Dando *et al.*, 1994b, 1995; Thiermann *et al.*, 1997), show that animals with chemosymbiotic nutrition have a negligible role in the macrobenthos of shallow-water vent areas, as discussed in Gebruk (2002). Attached suspension feeders, deposit feeders collecting detritus from bottom surface and, to a lesser extent, grazers dominate the trophic structure of such benthic communities.

The development of benthic communities in zones of shallow-water vents depends on the duration of the hydrothermal stage. In Matupi Harbour, the vents persist for ~50 years. Because of this short life and despite the high values of primary production normally found inshore in tropical latitudes, the macrobenthos of Matupi Harbour has a low population density and biomass. Apparently, the bottom communities are at an early stage of succession, compared with the fauna in Kraternaya Bight and the Bay of Plenty, where hydrothermal activity continues for some thousands of years.

The data on energy exchange in the abundant species of benthic animals in Kraternaya Bight imply that the contribution of the macrobenthos to total oxygenic metabolism of the bottom communities is small (Tarasov, 1991c, 1999).

In general, the ecosystems at shallow-water vents are highly productive areas of the ocean, where there are two sources of energy and a good supply of mineral substances. Most of the species are migrants from the surrounding waters or are opportunists. The proportion of the two patterns of synthesis of primary organic matter (photosynthesis and chemosynthesis) can vary, depending on the duration of the hydrothermal processes, the rates of water exchange and the composition of the vent fluid.

From their structure and functional characteristics, the pelagic and benthic communities that develop in zones of shallow-water venting may by regarded as natural systems that are transitional between the highly specific deep-water hydrothermal communities and the normal communities of shallow coastal areas.

ACKNOWLEDGEMENTS

I am grateful to Professors A. J. Southward and P. A. Tyler, as editors, for encouraging me to write this review and for their help in correcting the language, style and presentation. Thanks are due to Dr. L. Dolgov for the initial conversion from Russian to English; Professors A. Adrianov and V. Malakhov for unpublished data on meiobenthos; Professor M. Propp, A. Matochkin and A. Omelyanko for loan of colour slides and prints; and anonymous reviewers for their constructive comments. The work was supported by the Russian Federal Program "The World Ocean" project, "The Dynamics of Ecosystems, Productivity and Bioresources of the World Ocean," Ministry of Industry, Science and Technology of the Russian Federation (2003–2004) and by the Program of Fundamental Researches of the Presidium of the Russian Academy of Science "The Origin and Evolution of the Biosphere," section "Formation and Evolution of Extreme Marine Ecosystems in a Modern History of the Biosphere" (2004).

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Plate 1 (A) Kraternaya Bight. View from the northern circular ridge (Photo M. Propp); (B) Kraternaya Bight. Bacterial mats surrounding a sublittoral gas-hydrothermal vent in the southeastern part of the bight, depth 5 m (Photo M. Propp).

Plate 2 (A) Matupi Harbour. Rabalankaia hydrothermal zone in Blanche Bay, vapour arising from hot volcanic fluids; (B) Bay of Plenty. White Island seen from RV "Academician Alexander Nesmayanov", May, 1990.

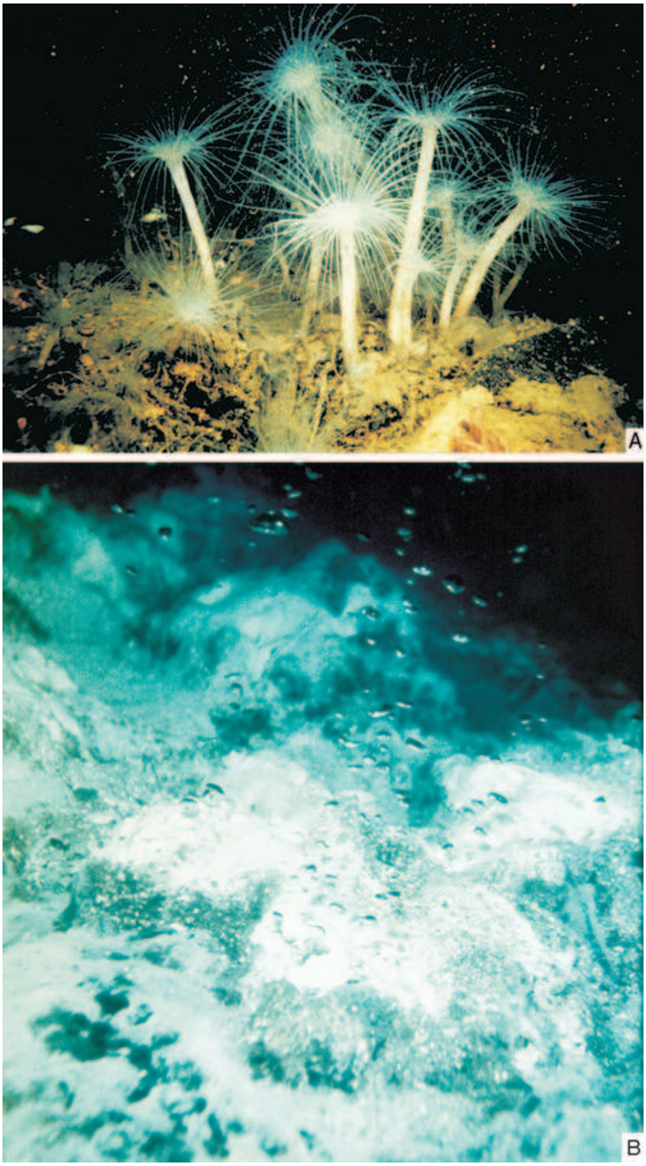

Plate 3 (A) Kraternaya Bight. *Cerianthus lloydii* (Anthozoa, Ceriantharia) in a diatom mat, north area vents (Photo A. Matochkin); (B) Kraternaya Bight. Bacterial mat at hydrogen sulfide venting, depth 20 m (Photo A. Matochkin).

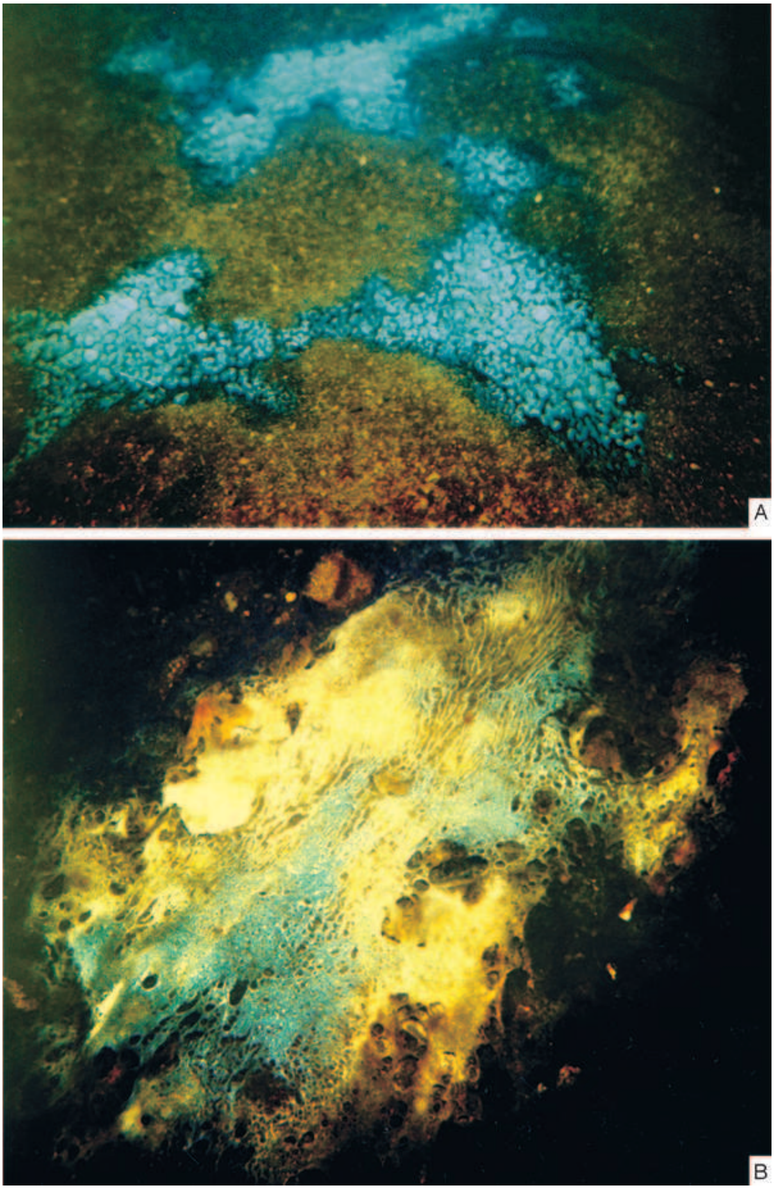

Plate 4 (A) Kraternjaya Bight. Bacterial mats of the "Thiodendron" association in the southwest part, depth 15 m (Photo A. Matochkin); (B) Kraternaya Bight. Algobacterial mats in an area of volcanic seepage, depth 3 m (Photo A. Matochkin).

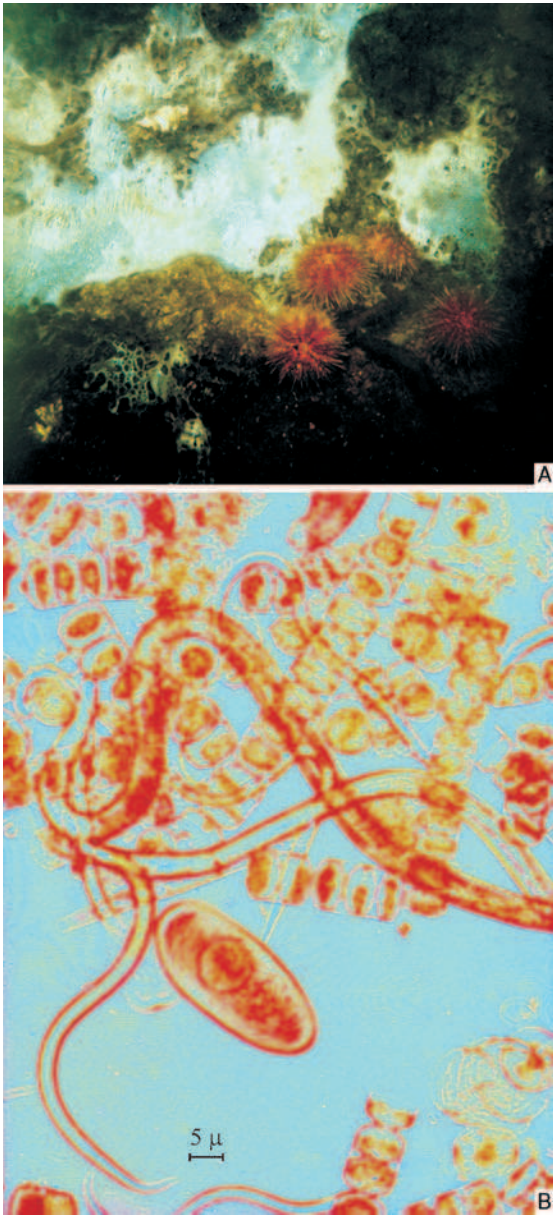

Plate 5 (A) Kraternaya Bight. Algobacterial mat and sea urchins, *Strongylocentrotus droebachiensis,* at a volcanic seep, depth 5 m (Photo A. Matochkin); (B) Kraternaya Bight. Nematodes, diatoms and ciliates from the algobacterial mat.

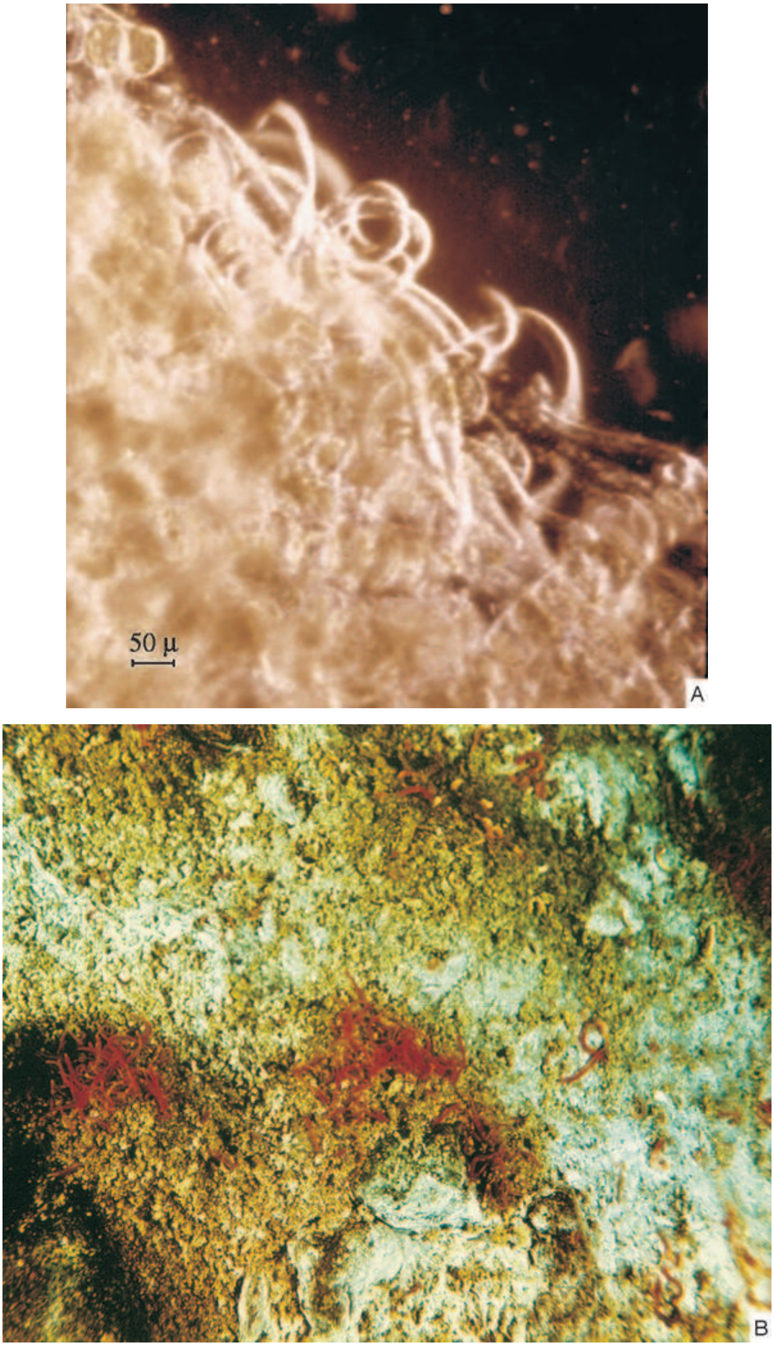

Plate 6 (A) Kraternaya Bight. Abundant nematodes on the surface of an algobacterial mat; (B) Matupi Harbour. Small polychaetes, *Polydora* sp., abundant in bacterial mats covering hot underwater sandy slopes through which gas and hydrothermal fluids seep; Tavurvur venting area 2, depth 3 m (Photo M. Propp).

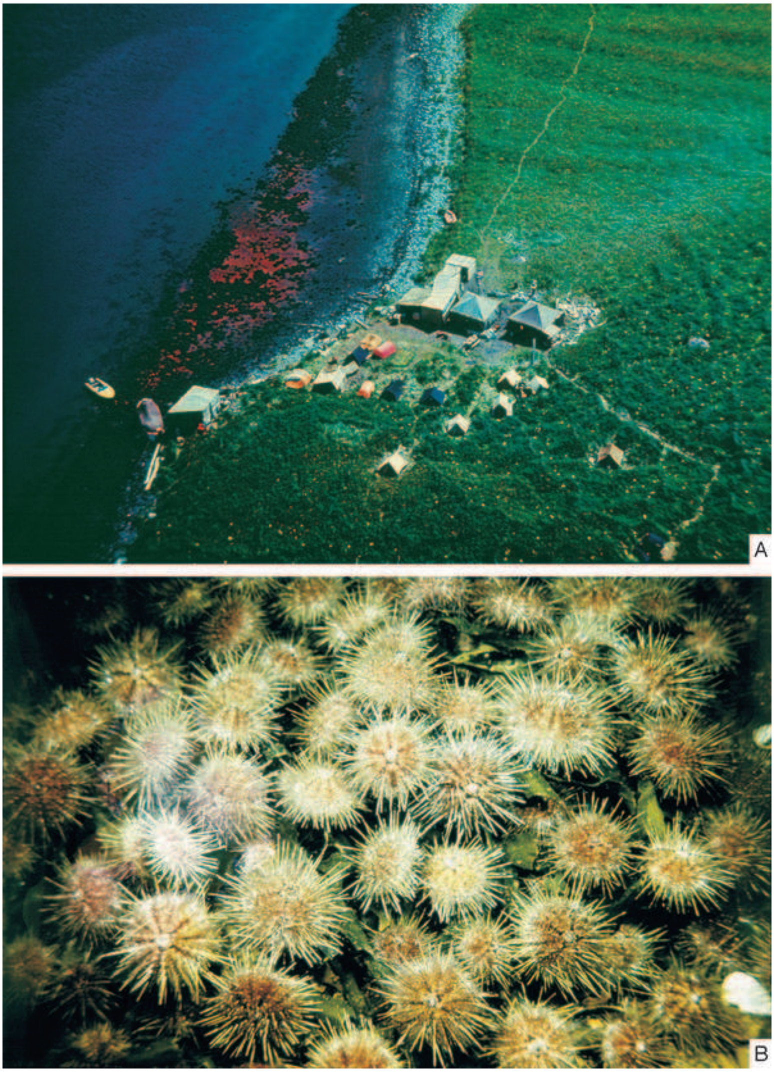

Plate 7 (A) Kraternaya Bight. Scientific base camp and littoral zone covered with iron-phosphoric deposit, seen from the top of volcanic rock, south coast of eastern basin; (B) Kraternaya Bight. Sea urchins, *Strongylocentrotus droebachiensis,* at a depth of 2 m (Photo A. Matochkin).

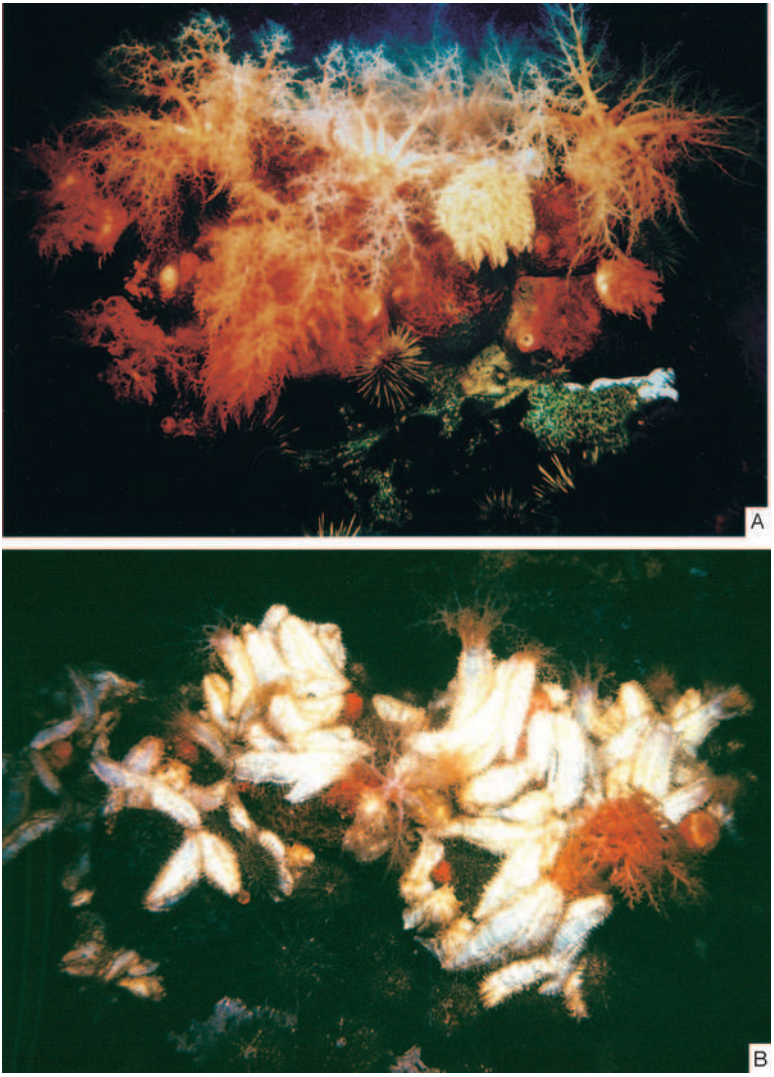

Plate 8 (A) Kraternaya Bight. Holothurians, *Psolus fabricii*, on boulders and stones, depth 15 m (Photo A. Matochkin); (B) Kraternaya Bight. Holothurians, *Eupentacta pseudoquinquesemita,* at high population density in 10 m to 15 m depth (Photo A. Matochkin).

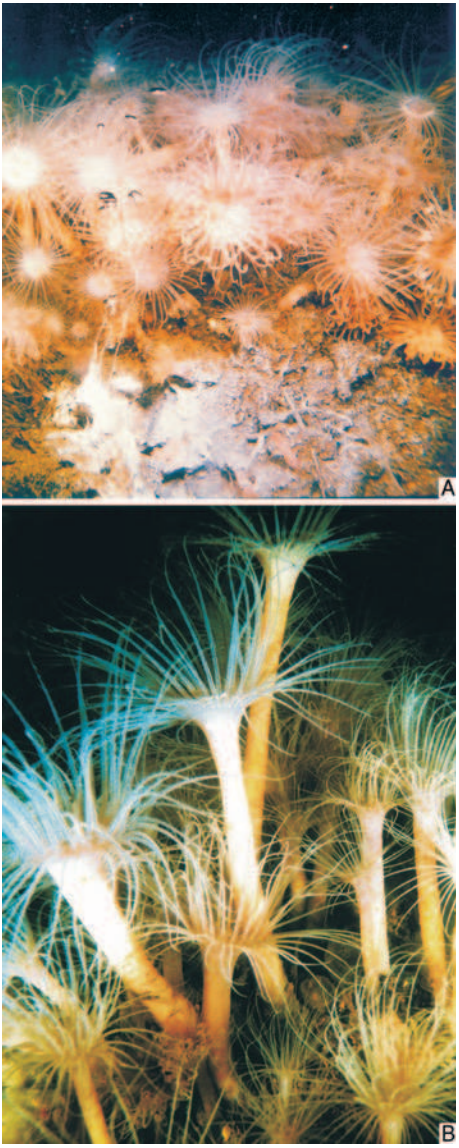

Plate 9 (A) Kraternaya Bight; *Cerianthus lloydii,* abundant in soft sediments around vents in the eastern basin, depth 22 m. (Photo A. Matochkin); (B) *Cerianthus lloydii* aggregation in the southwest part of the bight, depth 10 m (Photo M. Propp).

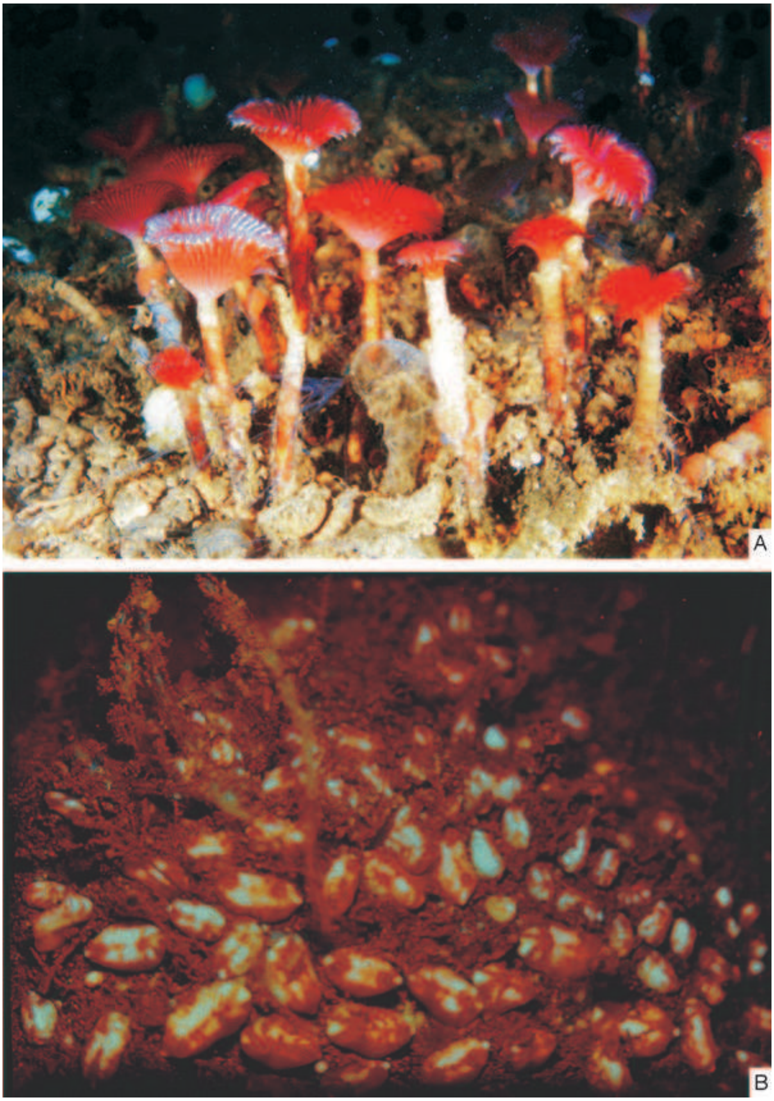

Plate 10 (A) Kraternaya Bight. Polychaetes, *Myxicola infundibulum,* in the north part of the Bight, depth 15 m (Photo M. Propp); (B) Matupi Harbour. Thyasirid bivalves coated with iron-oxide particles at a depth of 20 m in Tavurvur volcanic area 2, Blanche Bay (Photo A. Omelyanenko).

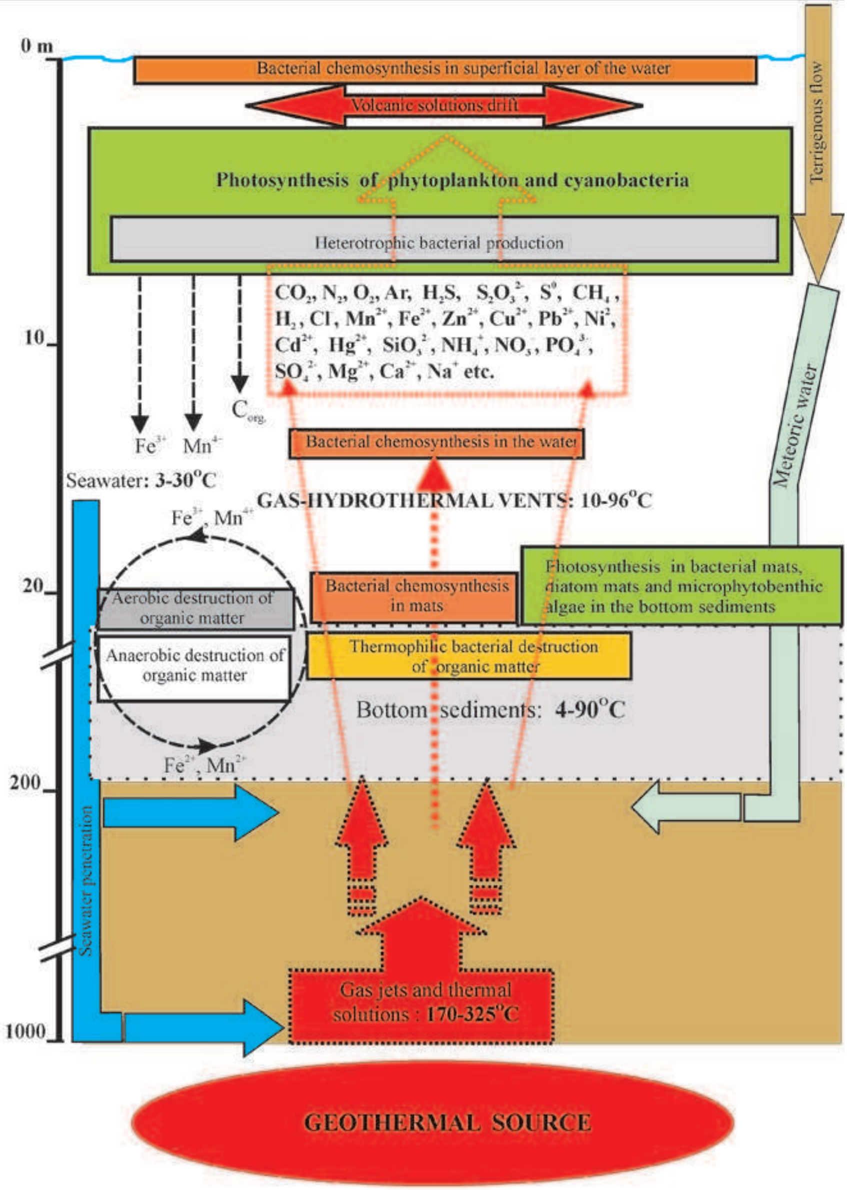

Plate 11 Major biological and geochemical processes in coastal marine ecosystems located in areas of shallow-water hydrothermal venting. The arrows show flows of volcanic solutions, elements and compounds, and water penetration through fractures in the volcanic structures, the bottoms of bays and through sediments. In rectangles; basic groups of microorganisms and major processes of synthesis and destruction of organic matter in shallow hydrothermal ecosystems.

TAXONOMIC INDEX

SUBJECT INDEX