

Ecology of Antarctic Marine Sponges: An Overview¹

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SYNOPSIS. Sponges are important components of marine benthic communities of Antarctica. Numbers of species are high, within the lower range for tropical latitudes, similar to those in the Arctic, and comparable or higher than those of temperate marine environments. Many have circumpolar distributions and in some habitats hexactinellids dominate benthic biomass. Antarctic sponge assemblages contribute considerable structural heterogeneity for colonizing epibionts. They also represent a significant source of nutrients to prospective predators, including a suite of spongivorous sea stars whose selective foraging behaviors have important ramifications upon community structure. The highly seasonal plankton blooms that typify the Antarctic continental shelf are paradoxical when considering the planktivorous diets of sponges. Throughout much of the year Antarctic sponges must either exploit alternate sources of nutrition such as dissolved organic carbon or be physiologically adapted to withstand resource constraints. In contrast to predictions that global patterns of predation should select for an inverse correlation between latitude and chemical defenses in marine sponges, such defenses are not uncommon in Antarctic sponges. Some species sequester their defensive metabolites in the outermost layers where they are optimally effective against sea star predation. Secondary metabolites have also been shown to short-circuit molting in sponge-feeding amphipods and prevent fouling by diatoms. Coloration in Antarctic sponges may be the result of relict pigments originally selected for aposematism or UV screens yet conserved because of their defensive properties. This hypothesis is supported by the bioactive properties of pigments examined to date in a suite of common Antarctic sponges.

HISTORICAL OVERVIEW

The Southern Oceans that surround Antarctica are immense, comprising about 10% of total world ocean area. Marine benthic invertebrate communities surrounding the continent are rich and diverse (Clarke, 1992; Crame and Clarke, 1997; Gray, 2001), traits that may be related to the continent's biogeographic isolation and great age (Dayton, 1990; Dayton *et al.*, 1994). The considerable age of this marine system has its roots in the separation of Antarctica from Gondwana in the Cretaceous about 140 million years ago (Tingey, 1991; Thompson *et al.*, 1991). During the early Tertiary, South America finally separated from West Antarctica and functional isolation was further demarcated by the establishment of deep sea conditions in the Drake Passage at the boundary of the Oligocene/Miocene (35 million years ago). These geological events facilitated the establishment of the clockwise Antarctic Circumpolar Current or West Wind Drift (Kennett, 1982; Foster, 1984; Thompson *et al.*, 1991). While a comparatively low velocity current (Foster, 1984), it is by volume the largest oceanic current in the world and has served to further isolate Antarctic benthic marine invertebrates from other oceanic regions (Dayton *et al.*, 1994).

DISTRIBUTION AND SPECIES RICHNESS

Because of the extensive temporal and biogeographic isolation from faunas of other southern hemisphere

seas it is perhaps not surprising that the sponge fauna of Antarctica is largely indigenous. Nonetheless, as with other groups of Antarctic marine invertebrates (Dayton *et al.*, 1994), there are also taxonomic affinities with eurybathic sponges from the deep sea (Koltun, 1970) and especially the Magellanic region of southern South America and the Falkland Islands (Sarà *et al.*, 1992). There is a remarkable degree of homogeneity among distributions of Antarctic sponges throughout continental Antarctica as well as surrounding islands extending even to the sub-Antarctic (*e.g.*, as far north as Kerguelen slightly to the north of the Antarctic Convergence in the Indian Ocean) (Sarà *et al.*, 1992). Indeed, the majority of species have circumpolar distributions (Koltun, 1969, 1970; Sarà *et al.*, 1992). The specific dispersal mechanisms which explain the ubiquity of such circumpolar distribution patterns, in spite of sections of continental shelf interrupted by abyssal sea floor, are intriguing given that both oviparous and viviparous sponges typically produce short-lived free-swimming lecithotrophic larvae (Hyman, 1940; Fell, 1974; Bergquist, 1978; Simpson, 1984; Maldonado and Bergquist, 2002). Nonetheless, tempos of larval development in Antarctic marine invertebrates can be orders of magnitude longer in duration than their temperate or tropical counterparts (reviewed by Pearse *et al.*, 1991). And even though brood protection (parental care during much of embryonic and larval development) appears to be relatively common in the small number of Antarctic sponges examined to date (Arnaud, 1974; Konecki and Targett, 1989), studies are needed to document larval development rates and their planktonic swimming durations

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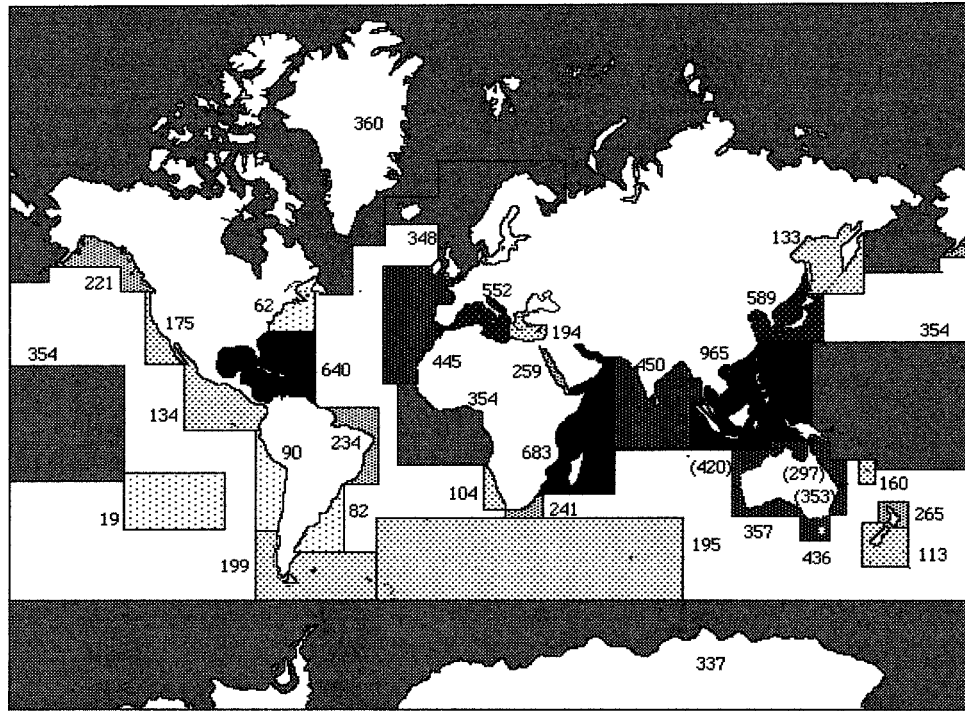


FIG 1. Map showing Demospongiae species richness of 35 marine biogeographic provinces and regions reproduced from van Soest (1994: as Fig. 2). Numbers of species found in each of the areas are printed either inside or immediately next to the schematic area delimitations. Shades indicate relative richness (darkest areas have highest numbers of species), white areas are land or deep sea bottoms lacking sufficient data. Antarctic richness (337, revised to 352 in the present paper) is similar to that of the Arctic region (360).

to evaluate the dispersal capabilities of lecithotrophic larvae of Antarctic sponges. Burton (1932) proposed that floating propagules (asexual buds or small sponge body fragments) might explain circumpolar distributions of Antarctic sponges. The likelihood of flotation in fragments of Antarctic sponges seems remote as fragments are negatively buoyant (J. B. McClintock, C. D. Amsler, B. J. Baker, unpublished data). However, in subantarctic marine environments macroalgal rafting has been observed to disperse benthic invertebrates (Helmuth *et al.*, 1994) and might play a role in dispersing some sponges along the Antarctic Peninsula. Finally, Sarà *et al.* (1992) have proposed that the apparent wide geographic ranges of sponge species in Antarctica might be due to complexes of cryptic species that are highly conserved morphologically but genetically distinct.

Sponges can dominate Antarctic benthos (Beliaev and Ushakov, 1957; Dayton *et al.*, 1970, 1974; Koltun, 1968, 1970; Voss, 1988; Gerdes *et al.*, 1992; Barthel and Gutt, 1992; Sarà *et al.*, 1992; Arntz *et al.*, 1997; Teixidó *et al.*, 2002). Estimates of species richness in the Antarctic vary between 300 and 352 (Koltun, 1970; Sarà *et al.*, 1992; van Soest, 1994; Arntz *et al.*, 1997) depending on precise delineation of the Antarctic region. A more recent estimate puts the total number of species at 436 “species” (352 Demospongiae, 49 Calcarea, 35 Hexactinellida) if trinomial taxa, subspecies and varieties are included (R. W. M. van Soest, unpublished data). The numbers of Antarctic sponge

species found in Southern Seas can be compared with patterns of species richness in temperate, tropical, and Arctic seas (Fig. 1; van Soest, 1994). Species richness patterns in some marine faunas have been suggested to show a latitudinal cline of decreasing species richness from the tropics to the poles (Thorson, 1957; Stehli *et al.*, 1967; Rex *et al.*, 1997). However, as for a number of other marine benthic taxa (Clarke and Crame, 1997; Crame and Clarke, 1997; Arntz and Rios, 1999; reviewed by Gray, 2001; Piepenburg *et al.*, 2002), this is not the case for sponges. Both northern and southern hemispheres show a pattern of generally high species richness of sponges in the tropics, a significant decline in numbers of species in temperate seas, and then an apparently increased species richness in polar seas. Antarctica has a similar demosponge species richness as the Arctic—352 versus 360 species, respectively (Fig. 1), and clearly more species than in several adjacent temperate waters. Starman and Gutt (2002) compared mega-epibenthic diversity between the Arctic (off northeast Greenland) and Antarctica (Weddell and Bellingshausen Seas) and concluded that while Antarctica housed more taxa, a generally assumed higher diversity of Antarctic assemblages was an over-generalization. High species richness in the Antarctic is likely related to its geographic isolation, great age, pronounced structural heterogeneity (particularly epibiotic communities), and large geographic area (Brey *et al.*, 1994; Gray, 2001; Starman and Gutt, 2002).

TABLE 1. *Antarctic Demospongiae*.*

Order	Number of species
Homosclerophorida	5
Spirophorida	11
Astrophorida	15
Hadromerida	39
Halichondrida	16
Poecilosclerida	194
Haplosclerida	60
Dictyoceratida	4
Dendroceratida	4
Halisarcida	3
Verongida	1
TOTAL	352

* Compiled by R.W. M. van Soest.

DEMOSPONGIAE

Eighty-one percent of Antarctic sponges belong to the Demospongiae; they represent 11 orders (Table 1). Approximately half (55%) of the Antarctic demospo- ges belong to the order Poecilosclerida, followed by Haplosclerida (17%) and Hadromerida (11%). Keratose or horny sponges (Dictyoceratida, Dendrocerati- da, Verongida) are scarce; the species in these three orders comprise only 2.5% of Antarctic demospo- ges. This contrasts with temperate and especially sub-tropi- cal and tropical latitudes where keratose sponges can be common. Keratose sponges have a high ratio of organic to inorganic mass, with skeletons comprised exclusively of spongin fibers (Hyman, 1940). A simi- larly depauperate keratose sponge fauna characterizes the Arctic (Hentschel, 1929). The basis for the rela- tionship between polar seas and the paucity of keratose species is unknown. In the Southern Ocean one pos- sibility is that seasonal constraints on the availability of plankton in continental shelf waters constitute a sig- nificant resource constraint that selects for sponges with low ratios of organic to inorganic mass and thus reduced energy demands. In further support of this hy- pothesis, Barthel (1995) found low contents of meta- bolically active tissue in a broad suite (31 species) of Antarctic demospo- ges.

The bathymetric distributions of demospo- ges can be summarized by arbitrarily dividing depths into four discrete intervals and delineating those species that span or fall exclusively within a given depth range (Table 2). From these patterns it is clear that steno- bathy is unusual among Antarctic demospo- ges, but occurs most commonly in the 100–500 m depth inter- val. Stenobathy is also evident among the small num- ber of demospo- ges that occur at depths greater than 1,000 m, where 7 of the 9 species in this grouping occur only below this depth. Thus there is a small but distinct complement of deep-sea species among Ant- arctic demospo- ges. In contrast, eurybathy is common among the Antarctic demospo- ges, with the majority of the species occurring across more than one depth interval (Table 2).

Fewer demospo- ges occur in shallow water in Ant- arctica than in temperate or tropical regions, where

TABLE 2. *Bathymetry of Antarctic Demospo- ges*.

Depth interval (meters)	Percent of total species in interval	
	(Not exclusively)	(Exclusively)
0–100	53	9
100–500	76	23
500–1000	23	2
>1000	9	7

they far outnumber those of greater depths (Vacelet, 1988). This pattern is also apparent in the Arctic where the numbers of demospo- ges shallower than 100 m are substantially lower than those found in the 100– 600 m depth interval (Hentschel, 1929; Vacelet, 1988). In the Antarctic it is possible that some of this bias is attributable to sampling artifacts, as the majority of identifications of sponges have come from dredged collections often taken at great depths. Nonetheless, two additional factors, ice scour and anchor ice, clearly play key roles in preventing recruitment and eliminat- ing established populations of all types of sponges in near-shore environments. Ice scour is a major struc- turing force in nearshore marine benthic Antarctic communities (reviewed by Gutt, 2001). Grounded ice- bergs are capable of scouring down to depths of even 600 m, while the seasonal break up of the annual sea ice and its subsequent compaction against shorelines leads to shallower (10–25 m depth), but more frequent and broad-based, scouring events (Gutt, 2001). Anchor ice (submerged ice attached or anchored to the sea floor) forms around substrates and sessile marine in- vertebrates including sponges down to depths of about 33 m (Dayton *et al.*, 1969, 1970; Gutt, 2001). As an- chor ice has a lower density than sea water, once it reaches a critical mass it floats to the surface taking the substrate and attached organisms to the surface, where they are either frozen into the sea ice or pushed by currents to the shore. In either case, mortality is almost certain. Anchor ice has profound effects on zo- nation patterns in shallow benthic marine invertebrate communities of Antarctica (Dayton *et al.*, 1969, 1970, 1974).

CALCAREA

Compared to the demospo- ges, the numbers of cal- careous sponge species in Antarctica are low (Table 3) and limited to two orders, Clathrinida (6 species in 3 genera) and Leucosolenida (48 species in 11 genera) (Table 3). Three genera of Leucosolenida, *Achramor- pha*, *Dermatetron*, and *Jenkina*, are endemics. Two other genera in this order, *Breitfussia* and *Megapogon*, occur exclusively in the Antarctic, Arctic or deep sea. Both *Achramorpha* and *Megapogon* belong to the fam- ily Achramorphidae, known only from cold environ- ments (R. W. M. van Soest, unpublished data). Ant- arctic calcareous sponges occur more shallowly than the demospo- ges, with all 49 species collected be- tween depths of 25 and 385 m (R. W. M. van Soest, unpublished data). Although the biogeographic distri-

TABLE 3. *Antarctic Calcarea*.*

Subclass Calcinea	Number of species
Order Clathrinida	
<i>Clathrina</i>	2
<i>Leucetta</i>	3
<i>Leucettusa</i>	1
Subclass Calcaronea	
Order Leucosolenida	
<i>Leucosolenia</i>	8
<i>Sycetta</i>	2
<i>Sycon</i>	2
<i>Sycantha</i>	1
<i>Grantia</i>	4
<i>Leucandra</i>	12
<i>Dermatetron</i>	2
<i>Jenkina</i>	2
<i>Achramorpha</i>	4
<i>Breitfussia</i>	2
<i>Megapogon</i>	4

* Compiled by R.W. M. van Soest.

butional patterns of Antarctic calcareous sponges are poorly known, little evidence suggests that they have local distributions, and they are most likely circum-polar.

HEXACTINELLIDA

Similarly depauperate in terms of species richness are the hexactinellid sponges. Barthel and Tendal (1994) recognize only 28 species within three orders. Including sub-species and varieties, the number increases to 35 "species" (R. W. M. van Soest, unpublished data, Table 4). The Antarctic hexactinellids are striking in their population dominance and ecological relevance (Barthel, 1992a, b). This is particularly striking given the fact that about two thirds of the hexactinellid species occur only below 1,000 m depth, and half of these even deeper than 2,000 m. For example the large glass sponges *Anoxycalyx* (*Scolymastra*) and *Rossella* are very common at scuba diving depths (30–40 meters) in McMurdo Sound, Antarctica (Fig. 2). These large sponges are subject to predation by spongivorous and omnivorous sea stars (Dayton *et al.*, 1974) and harbor a commensal fauna that is richer than that in demosponges (Barthel and Tendal, 1994). Importantly, siliceous spicules form "spicule mats" that can be several meters deep (Koltun, 1968). Such spicule mats provide a three-dimensional habitat that serves as a valuable refuge for a wide variety of marine invertebrates (Barthel, 1992b; Barthel and Gutt, 1992).

The growth rates of hexactinellid sponges are very low. For example, *Anoxycalyx* (*Scolymastra*) *joubini* and *Rossella nuda* showed no measurable growth during a ten-year observation period (Dayton, 1979). Growth rate models based on oxygen consumption rates predicted extremely low productivity values for three Antarctic sponges (Gatti, 2002). Future studies may reveal that slow growth rates may be common in Antarctic sponges. However, a notable exception is the

TABLE 4. *Antarctic Hexactinellida*.*

Subclass Amphidiscophora	Numbers of species
Order Amphidiscophora	
Family Hyalonematidae	
<i>Hyalonema</i>	2*
Subclass Hexasterophora	
Order Hexactinosida	
Family Farreidae	
<i>Farrea</i>	1
Family Euretidae	
<i>Pararete</i>	1
<i>Chonelasma</i>	1
<i>Bathyxiphus</i>	1*
Order Aulocalycoidea	
Family Aulocalycidae	
<i>Aulocalyx</i>	1
Aulocalycidae indet.	1
Order Lyssacinosa	
Family Euplectellidae	
<i>Holascus</i>	2*
<i>Malacosaccus</i>	2*
<i>Acoelocalyx</i>	1*
<i>Docosaccus</i>	1*
<i>Saccocalyx</i>	1*
Family Rossellidae	
<i>Caulophacus</i>	4*
<i>Rossella</i>	9
<i>Bathydorus</i>	1
<i>Calycosoma</i>	1
<i>Anoxycalyx</i>	2
<i>Acanthascus</i>	1
<i>Lophocalyx</i>	1
<i>Sympagella</i>	1

* Compiled by R.W. M. van Soest. Asterisks indicate deep sea species (>2000 m depth).

rapid growth rates measured in the opportunistic Antarctic demosponges, *Mycale acerata* and *Homaxinella balfourensis* (Dayton *et al.*, 1974; Dayton, 1989). That several Antarctic sponges are capable of rapid growth suggests that low temperature is not necessarily a barrier to molecular or cellular growth processes, but rather differential growth rates in sponges may be integral species-specific life history traits.

COMMUNITY STRUCTURE

Because sponges are dominant components of the Antarctic benthos they play a key role in community dynamics (Dayton *et al.*, 1974; McClintock, 1987; Dayton, 1989; Cerrano *et al.*, 2000a; Cattaneo-Vietti *et al.*, 1999). The seminal ecological studies of Dayton *et al.* (1974) in McMurdo Sound exemplify this most notably. Here the rich sponge community below a depth of about 33 m (Fig. 2) comprises very large hexactinellids (*Anoxycalyx* (*Scolymastra*) *joubini*, *Rossella racovitzae*, and *R. nuda*), along with a suite of demosponges, other sessile and sluggish marine invertebrates, and numerous predators including the spongivorous sea stars *Perknaster fuscus* and *Acodontaster conspicuus*, the omnivorous sea stars *Odontaster validus* and *O. meridionalis*, and a sponge feeding nudi-

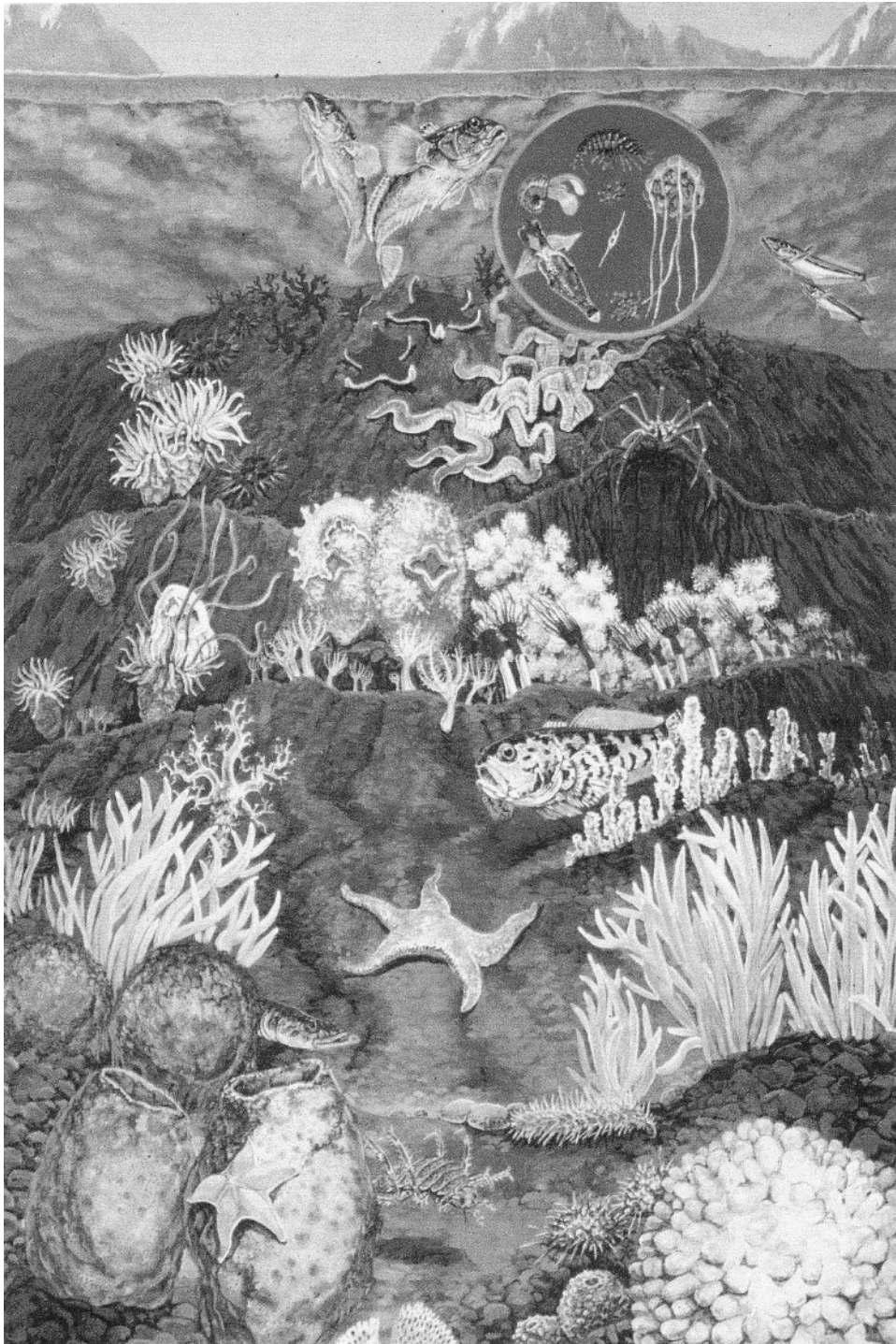


FIG 2. Painting of the sponge-dominated benthos of McMurdo Sound, Antarctica (from McClintock and Baker, 1998; Painting by D. W. Miller). Note the large hexactinellid vase sponge *Anoxycaalyx* (*Scolymastra*) *joubini* (bottom left hand corner), the large knobby-shaped hexactinellid *Rossella nuda* (bottom right corner), the bush-shaped demosponge *Homaxinella balfourensis* (left and right), and the worm-shaped demosponge *Isodictya erinacea* (lower center). The shallower zone (<33 m depth) conspicuously lacks sponges.

branch, *Doris kerguelenensis* (formerly *Austrodoris mcmurdensis* and *A. kerguelenensis*).

The dietary specializations of these sponge predators have important ramifications on benthic community dynamics. For example, *P. fuscus* specializes on

the rapidly growing, space-dominating demosponge *Mycale acerata*, regulating its populations and thus maintaining higher community species diversity. *A. conspicuus* and *D. kerguelenensis* consume mainly the three rossellids, and the unique filter feeding behavior

of the abundant omnivorous sea star *O. validus*, in a keystone role in the community, regulates larval recruitment of spongivorous sea stars, with the net result of indirectly mediating sponge biomass (Dayton *et al.*, 1974). While reduced spongivory has been suggested in some areas of Antarctica such as the eastern Weddell Sea shelf (Barthel, 1995), the circumpolar distributions of sponges, spongivorous sea stars and nudibranchs as well as omnivorous sea stars that include sponges in their diets (Dearborn, 1977; Dayton, 1989; reviewed by McClintock, 1994; Cerrano *et al.*, 2000a) argues that these predator-prey interactions are likely important determinants of benthic community structure on a broad biogeographic scale.

Additional biotic factors, although poorly studied to date, that may influence the structure of sponge communities include interspecific competition and patterns of recruitment (Arntz *et al.*, 1994; Clarke, 1996). Moreover, a host of abiotic factors including ice scouring, anchor ice, depth, substratum quality, currents and sedimentation are also important determinants of sponge community structure (Dayton *et al.*, 1970, 1994; Gallardo, 1987; Teixidó *et al.*, 2002).

Antarctic sponges also provide important habitat for a community of associated organisms (Gutt and Schickan, 1998). Bacteria and benthic diatoms frequently colonize outer surfaces as well as the interstices of ostia and oscula (Hamilton *et al.*, 1997; Cerrano *et al.*, 2000b; Amsler *et al.*, 2000a), while isopods, amphipods, gastropods, bivalves, polychaetes and other invertebrates occur within and upon sponges, especially hexactinellids (Barthel and Tendal, 1994). Some invertebrates associated with Antarctic sponges appear to have life histories integrally tied to their sponge host. For example, size-frequency analysis of the amphipod *Seba antarctica* in the hexactinellid *Anoxycalyx (Scolymastra) joubini* revealed two distinct size classes of individuals within the sponge, suggesting an obligate sponge-associated life cycle (Barthel and Tendal, 1994). Sponges may also provide a means of improving exposure to water currents. Antarctic ctenoids and holothuroids often perch on sponges (*e.g.*, the oscular rim of large hexactinellids) presumably to increase the efficiency of their own feeding (Barthel *et al.*, 1991; Dearborn, 1977; Gutt, 1988; Barthel and Tendal, 1994).

TROPHIC CONSTRAINTS

Benthic suspension feeders on the continental shelf of Antarctica occur in seas generally characterized as plankton-depauperate. Eppley and Peterson (1979) characterize Antarctic plankton communities as existing primarily in states of "regeneration," rather than exhibiting large phytoplankton or zooplankton blooms. When blooms do occur they can be intense, but they are usually short. This presents a paradox for Antarctic sponges. How do these remarkably abundant benthic suspension feeders sustain themselves in light of an apparent lack of plankton as a source of nutrients and energy? Gili *et al.* (2001) review this intriguing ques-

tion and suggest that the answer probably lies in a complex of factors including an ability to exploit microplankton (pico- and nano-plankton comprised mainly of flagellates), mechanisms to exploit resuspended detrital material, and adaptations to ensure low maintenance energy requirements through low renewal and growth rates. Mechanisms to further exploit nutrient resources may include bacterivory as has been demonstrated in some tropical sponges (Reiswig, 1971) and use of dissolved organic carbon as seen in Antarctic filter feeding bivalves (Chiantore *et al.*, 1998).

The enhanced repertoire of feeding behaviors of Antarctic benthic suspension feeders is elegantly exemplified by the colonial soft coral *Gersemia antarctica* (Slattery *et al.*, 1997). Colonies of this tree-shaped soft coral bend over and lay prostrate on the fine sediments, then pivot 360°, rolling on their trunks and using their polyp-bearing branches to capture and consume organic detrital material on the sediment surface. From an expanded prone position, colonies eventually free their "substrate anchor" from the sediment through a series of contractions localized in its basal region. Once free, the colony inflates its hydrostatic skeleton extending its distal mass away from the site of origin. Water expulsion and contraction results in a net forward inch worm-like movement of the entire colony (Slattery *et al.*, 1997). Once relocated, colonies repeat this novel detrital feeding process. Sponges of course lack the ability to exploit such tactics, although at least one tropical species has been observed to climb the walls of aquaria over a period of several days (A. Kohn, personal communication). Nonetheless, the discovery of a carnivorous sponge (*Asbestopluma hypogea*) living in a low nutrient-resource cave environment demonstrates a remarkable flexibility in feeding adaptation. This sponge has completely lost its aquiferous system and feeding cells (choanocytes). Instead it captures small crustaceans with hook-like spicules located on outside body filaments (Vacelet and Boury-Esnault, 1995). Once crustacean prey is captured, they are engulfed and digested by specialized migrating cells. Significantly, more than 10 species belonging to the same family as *Asbestopluma* have been recorded from Antarctic waters, among which there is at least one living in shallow-water. This discovery suggests that future studies of Antarctic sponges may yet reveal novel adaptations to exploiting nutrients in a resource constrained environment.

CHEMICAL DEFENSES AND ROLE OF PIGMENTS

Earlier studies hypothesized that the incidence of chemical defenses in marine sponges correlates inversely with latitude (Bakus and Green, 1974; Green 1977). This hypothesis was based on a perceived decline of sponge predation and thus reduced selection for chemical defenses in higher latitudes. While Antarctic sponges are indeed subject to little, if any, fish predation, they are heavily preyed on by sea stars and nudibranchs. Thus not surprisingly chemical defenses

are now known to be relatively common in Antarctic sponges (reviewed by McClintock and Baker, 1997, 1998; Amsler *et al.*, 2000b, 2001a, b) and little evidence supports a latitudinal cline in sponge chemical defenses (Amsler *et al.*, 2000b; also see Becerro *et al.*, 2003). Chemicals defend Antarctic sponges against predators as well as fouling bacteria and diatoms.

The Antarctic demosponge *Latrunculia apicalis* sequesters 90% of its defensive discorhabdins in the outermost surface layer (0–4 mm depth) where they are maximally effective against predatory sea stars, a pattern indicating optimal resource allocation (Furrow *et al.*, 2003). Antarctic sponge metabolites are similar chemically to those found in temperate and tropical sponges, generally belonging to the alkaloid and terpene classes (Amsler *et al.*, 2001a, b). Nonetheless, one of the potentially unique “Antarctic” stories about sponge chemical defenses may revolve around their pigments.

Some primary predators of marine sponges in temperate and tropical latitudes are visual predators, including many fish species and sea turtles (Chanas and Pawlik, 1995; Pawlik *et al.*, 1995). In contrast, Antarctic sponges have existed for many millions of years in the absence of visual vertebrate predators yet have been under strong predator pressure from invertebrates, primarily sea stars (Dayton *et al.*, 1974; Dearborn, 1977; McClintock, 1994). Hypothesized forces selecting for coloration in sponges include aposematism (warning coloration), as has been shown in a variety of marine and terrestrial organisms (Harrison and Cowden, 1976; Guilford, 1988; but see Pawlik *et al.*, 1995), and photoprotection (Harrison and Cowden, 1976; Bergquist, 1978).

Antarctic sponges generally occur in low light levels below the zone of ice scour and anchor ice (>33 meters depth) (Dayton *et al.*, 1974). Using dosimetry studies, Karentz and Lutze (1990) have demonstrated that the biological effects of ultraviolet radiation (UVA and UVB) in coastal Antarctic waters are only detectable above 20 m depths and usually much shallower. Moreover, seasonal sea ice cover and lack of sunlight during polar winter months as well as the factors cited above all contribute to making it unlikely that pigments in Antarctic sponges play a role in photoprotection. With no obvious role in aposematism or photoprotection we hypothesize that brightly pigmented Antarctic sponges represent a sub-set of sponges that had evolved pigments for such purposes long ago, yet have retained their coloration because the pigments themselves possess defensive properties.

Chemical investigations of a suite of common conspicuously colored antarctic sponges have revealed that in all cases their pigments are responsible for their defensive properties. Examples (Fig. 3 A–D) include the alkaloids variolin A and discorhabdin G, pigments of the red and green sponges *Kirkpatrickia variolosa* and *Latrunculia apicalis* (Figs. 3A, B), both of which cause strong feeding deterrence in spongivorous sea stars (Yang *et al.*, 1995; Amsler *et al.*, 2001b). The

bright yellow cactus sponge *Dendrilla membranosa* (Fig. 3C) possesses an isoquinoline pigment (Baker *et al.*, 1995) that inhibits growth of marine bacteria, likely defending against the establishment of biofilms and successional fouling (Amsler *et al.*, 2001b). Finally, the conspicuous polychaete sponge *Isodictya erinacea* (Fig. 3D) produces the yellow pigment eribusinone, a tryptophan catabolite similar to catabolites regulating crustacean molting (Moon *et al.*, 2000). We have shown that eribusinone causes molt inhibition and enhanced mortality in co-occurring spongivorous amphipods (Moon *et al.*, 2000). To the best of our knowledge this is the first known example in the marine realm of an animal using chemical mimicry to inhibit molting in an arthropod (terrestrial plants are well known to mimic insect molt hormones to select against grazing). Collectively, these findings support P. K. Dayton’s speculation over 25 years ago (quoted in Harrison and Cowden, 1976) that Antarctic sponge pigments might possess deterrent properties.

In summary, Antarctic sponge genera with an ancestry of pigmentation may have lost their coloration over long periods of biogeographic isolation, as selective pressures for pigmentation in Antarctica were insufficient to sustain this trait. In contrast, those Antarctic sponges that employ their pigments as chemical defenses per se retained their pigmentation. Moreover, our studies bring to light that animal pigments, classically considered as photoprotectants or as agents of adaptive coloration in reproduction, camouflage, mimicry, or aposematism (Harrison and Cowden, 1976; Bergquist, 1978; Owen, 1982), can also play important roles as chemical defenses.

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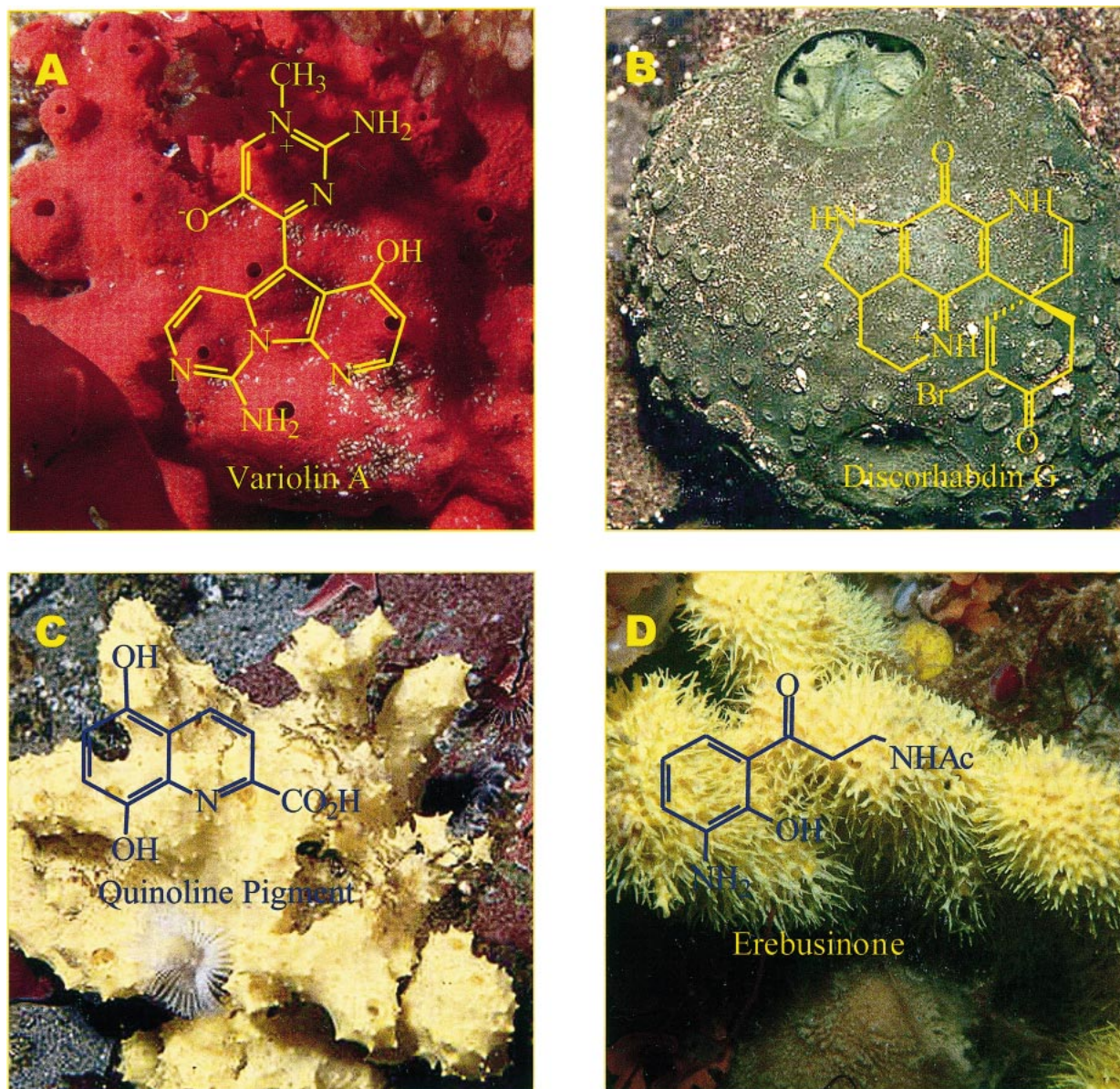


FIG 3. Brightly colored Antarctic marine sponges employ pigments as defensive agents. A, B: Variolin and discorhabdin pigments in the red sponge *Kirkpatrickia variolosa* (A) and the green sponge *Latrunculia apicalis* (B) deter spongivorous sea stars. C: quinoline pigment in the cactus sponge *Dendrilla membranosa* defends against fouling by marine bacteria. D: erebusinone pigment in the polychaete sponge *Isodictya erinacea* causes molt inhibition and mortality in spongivorous amphipods. Photographs by B. J. Baker.

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