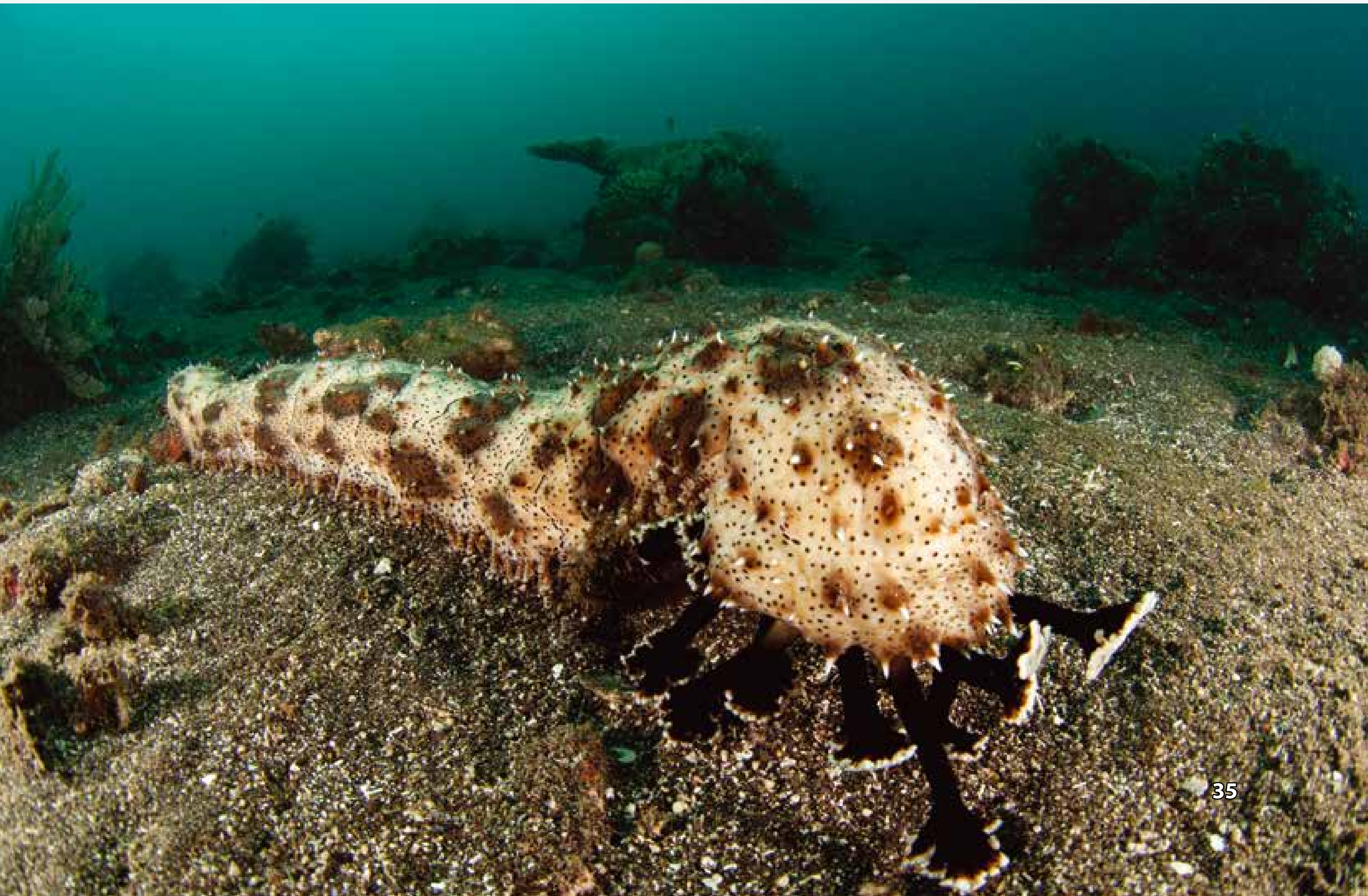
Locomotion

Locomotion is accomplished in echinoderms by structures including arms, tube feet, spines and the body wall. The approach differs among the various classes. Asteroids that inhabit hard substrates have suckered tube feet (**Fig. 1.22A**), and they move efficiently across the seafloor. In contrast, burrowing asteroids have pointed, suckerless tube feet that are used to excavate sediments. Sea urchins move about by means of their spines and tube feet. The spines articulate with a ball and socket joint and can move freely. Sediment-dwelling echinoids use their spines in a rowing motion to move through the sediment anterior-end forward; their small tube feet are not used in locomotion (**Fig. 2.36**). Rocky burrow-dwelling echinoids are relatively sedentary with some, such as the tropical Australian *Echinostrephus*, becoming incarcerated as the opening of the burrow is closed due to the growth of calcareous algae (**Fig. 1.27**).

Ophiuroids move over the substratum by a sinusoidal rowing motion of their arms, propelled by muscles working the joints between arm segments (**Fig. 1.6A**). Ophiuroid tube feet rarely play a major role in locomotion, although some species can climb vertical surfaces using their sticky tube feet. Burrowing ophiuroids use their tube feet to displace sediment as they plough into the substratum. Basket stars and

Figure 1.28 Motile sea cucumbers like the aspidochirotid sea cucumber ***Pearsonothuria graeffei*** (Holothuriidae) crawl across the sediment using the three rows of suckered tube feet on the underside. They are deposit feeders and use their peltate tentacles to collect sediment which is then passed to the mouth.

[J.Freund]



snake stars can spend prolonged periods with their arms coiled around corals, sponges or rocks (**Fig. 9.1; Box 9.1**), although they can also use their arms to crawl about. Some ophiuroids can swim over short distances, sometimes with the aid of specialised arm spines (Hendler & Miller 1991; **Box 1.5**).

Locomotion in holothuroids is often related to their feeding habit. Suspension feeders are often sedentary, while deposit feeders can be highly mobile, moving over or through sediments (**Figs 1.28, 2.38**). Locomotion is achieved by the tube feet working with the body wall musculature, or by undulating contractions of the body in species that lack tube feet. The medusa-like, deepsea holothuroids (elasipods) are remarkable for their spectacular swimming and sailing modes of locomotion propelled by contraction of the body wall muscles (**Box 1.5**). These are the only truly pelagic echinoderms (**Figs 11.15, 11.17**).

Crinoids move using their arms and, to a certain extent, their cirri and stalk. When disturbed, feather stars exhibit a spectacular swimming response, moving alternate sets of arms in balletic fashion (see **Box 1.5**).

2: Ecology and Behaviour

Timothy D. O'Hara and Maria Byrne

Echinoderm habitats

Echinoderms are exclusively marine and are probably among the most stenohaline of marine invertebrates (Stickle & Diehl 1987; Barker & Russell 2008; Russell 2013). There are no freshwater or terrestrial species, however a few species can survive in brackish water (8–30‰), such as in the fjords of New Zealand, and the Baltic and Black seas, or in estuaries with fluctuating salinities (Stickle & Diehl 1987; Barker & Russell 2008; Russell 2013). Only crinoids have never been found in low salinity environments (Stickle & Diehl 1987). In general, echinoderms cannot prevent the accumulation of fluids in the coelom in low salinity environments.

Echinoderms occur in all marine benthic habitats from the splash zone of the intertidal to the depths of the oceanic trenches. The ophiuroid, *Perlophiura profundissima*, was reported from 8,135 m in the Bougainville Trench (Belyaev & Litvinova 1972) and a holothuroid from 10,710 m (Zenkevitch 1963). Some holothuroids (Pelagothuriidae) are even pelagic (**Fig. 11.17; Box 1.4**), swimming in herds above the muddy floors of the deep sea.

Some species (or complexes of species) have been reported to have vast bathymetric ranges — among ophiuroids *Ophiura irrorata* ranges from 72 to

Figure 2.1 Intertidal pools of Australia's southern rocky shoreline provide a home for hardy echinoderms. Here you will commonly find seastars and sea urchins that are able to cope with the harsh and constantly changing environment of temperature and salinity fluctuations together with powerful wave action, exposure to the sun and the threat of predators. [J.Mallefet]

Figure 2.2 ***Meridiastra calcar*** (Asterinidae), commonly called the carpet seastar, is one of the most widespread seastars of intertidal rock pools in southern Australia. These multi-armed seastars grow to about 50 mm in diameter, and have a highly variable colour pattern, usually with a grey-green background with splashes of orange, yellow or red.

[M.Spencer]

5,830 m, *Asteronyx loveni* from 100 to almost 5,000 m (**Fig. 9.7A**), and *Amphipholis squamata* (**Box 9.2**) from the intertidal zone to 1,350 m (T.D.O'Hara, personal observation). There are no gas pockets in the body of echinoderms and, consequently, pressure is not a direct barrier to their distribution (Fell & Pawson 1966a). Temperature is a more potent barrier: polar, temperate and tropical regions have distinctive echinoderm communities (see **Chapter 5**).

Intertidal rock platforms

Relatively few echinoderms have adapted to the extreme environmental variability of the intertidal zone, where species must endure periods of desiccation, high temperatures and high salinities (**Fig. 2.1**). Across southern and eastern Australia asteroids of the asterinid genera *Parvulastra* and *Meridiastra* (cushion stars) can be numerous on intertidal rock platforms (McElroy *et al*. 2012; Nguyen *et al*. 2012; Nguyen & Byrne 2014; Martinez *et al*. 2016; **Figs 1.9, 2.2**). The viviparous

A

B

Figure 2.3 In tropical and subtropical waters of the Indo-Pacific and Red Sea the brittlestar ***Ophiocoma scolopendrina*** (Ophiocomidae) is a dominant inhabitant of intertidal reef flats, living in small crevices in reef and coral rubble or dense vegetation. This species displays a distinctive feeding behaviour know as 'surface-film feeding':

A, from its crevice on an intertidal flat ***Ophiocoma scolopendrina*** stretches out its arms at low tide, ready to feed.

B, ***Ophiocoma scolopendrina*** engaged in 'surface-film feeding'. At low tide individuals stretch arms up to the water-air interface and vigorously sweep the interface with the oral surface of the arms, gathering nutrient-rich particulate matter which is then ingested. This method of feeding ends when the water column becomes too deep for the arms to reach the surface; deposit feeding and suspension feeding may then be employed.

[M.Byrne]

asterinid seastars (**Boxes 3.1, 4.5**) are among the most tolerant echinoderms with respect to living high on the shore where they are exposed to extremes of temperature and salinity (Byrne 1996a; Byrne & Walker 2007). In eastern Australia the echinometrid sea urchin *Heliocidaris erythrogramma* (**Fig. 4.5A–E**) is common in low intertidal rock pools where it forms burrows in the substrate and catches drifting algae (Keesing 2013).

In tropical Australia, two other echinoderms are ubiquitous under intertidal rocks — the small, black holothuroid *Afrocucumis africana* (**Fig. 11.8**) and the locally super-abundant ophiuroid *Ophiocoma scolopendrina* (Byrne 2008). *Ophiocoma scolopendrina* can be readily observed scooping up the scum left behind by the retreating tide (Oak & Scheibling 2006; **Fig. 2.3**). This species is also abundant under boulders and coral rubble in the Great Barrier Reef where it can occur in very high densities (~100–200 per m^2) (M.Byrne, personal observation). Turfing coralline algae, *Corallina*, and the green alga, *Halimeda*, in intertidal rocky areas in temperate and tropical areas, respectively, provide habitat for many echinoderms. They are important recruitment and nursery areas for many species with planktonic larvae and provide a living environment for a number of diminutive species including the two ophiuroids *Ophiactis resiliens* and *Amphiura constricta* (Falkner & Byrne 2006).

Embayments

The muddy and sandy seafloors of Australia's sheltered bays and inlets support many echinoderms. The most common groups are the filter-feeding amphiurid ophiuroids (**Figs 1.11A, 9.20**), which project their long arms into the water column, and deposit-feeding holothuroids, heart urchins and sand dollars that digest organic particles from the sediment. In Port Phillip Bay, Victoria, some of the most abundant invertebrates are the brittlestars *Amphiura elandiformis* and *A. parviscutata*; the synaptulid sea cucumber *Rowedota allani*; and the heart urchin *Echinocardium cordatum* (**Fig. 2.36; Box 10.6**). Other groups include scavenging ophiuroids, such as *Ophiura kinbergi* and *Ophiomusium* species (**Fig. 9.9**), that skate along the seafloor seeking carrion and prey; and carnivorous asteroids, such as species of *Astropecten* and *Coscinasterias*, (**Fig. 1.8B,C**), that favour bivalves. In the tropics, large asteroids including species of *Anthenea*, *Archaster* and *Protoreaster* (**Figs 2.4, 8.16, 8.29, 8.30**) and holothuroids, such as *Holothuria*, can be numerous in sheltered waters (**Fig. 11.1**).

Faunal diversity is generally higher within seagrass meadows, as they include niches not available in muddy and sandy habitats (Waycott *et al.* 2007). Few species eat the unpalatable seagrass fronds, but the ubiquitous

Figure 2.4 Seagrass meadows provide a rich habitat for many marine animals including a variety of echinoderms like these chocolate chip seastars, ***Protoreaster nodosus*** (Oreasteridae), which commonly form aggregations.
[D.Harasti]

Figure 2.5 The temnopleurid sea urchin ***Amblypneustes pallidus*** is found usually attached to seagrass and algal holds in the temperate waters of southern Western Australia and South Australia (see also **Box 10.2**).

[G.Bell]

algal epiphytes as well as seagrass detritus are consumed by herbivorous echinoids (species of *Holopneustes* and *Amblypneustes*; **Figs 2.5, 2.17**) and omnivorous asteroids, such as *Meridiastra gunnii* and *M. calcar* (**Fig. 2.2**). Ophiuroids and crinoids use the seagrass fronds as perches from which to feed on plankton carried by tidal currents, and deposit-feeding holothuroids feed on the organically enriched sediments present around the seagrass rhizomes (Wolkenhauer *et al.* 2010). The presence of the sea cucumber *Holothuria scabra* (**Fig. 4.3A**) in the subtropical seagrass beds of Moreton Bay can enhance growth of the seagrass, presumably due to enhanced nutrient cycling when this species is present (Wolkenhauer *et al.* 2010). More importantly, seagrasses provide an important nursery resource for juveniles for a number of echinoderms including the sea urchin, *Tripneustes gratilla*, and several commercially important species such as the the sea cucumbers — sandfish, *H. scabra* and the black teatfish, *H. whitmaei* (Koike *et al.* 1987; Hamel *et al.* 2001; Vaïtilingon *et al.* 2003; Byrne *et al.* 2004b; **Fig. 4.3B**).

In channels in the embayments, 'mini-reefs' formed from clusters of ascidians and sponges provide shelter and food for echinoderms. Around much of southern Australia, the solitary ascidian *Pyura stolonifera* forms the basis of these clusters, anchored into the sediment by a long rhizome. Sponges, hydroids and bryozoans then colonise these ascidian thickets. Brittle stars, such as ophiotrichids (*Ophiothrix caespitosa* and *Macrophiothrix spongicola*; **Fig. 1.1B**) and ophiactids (*Ophiactis savignyi*; **Fig. 9.21D**) associate with sponges on these 'mini-reefs'. The brittle stars can take advantage of the currents created by the sponges to facilitate their own feeding, and, remarkably, *Ophiothrix* species have been seen to clean the surface of their host, clearing particles that obstruct the flow (Hendler 1984a). The larvae of *O. fragilis* in European waters settle preferentially on sponges (Turon *et al.* 2000) and on the surface of adult *O. fragilis* (Morgan & Jangoux 2004). Australian species such as the ophiuroids *Ophionereis schayeri* and *Ophiomyxa australis*, asteroids, *Coscinasterias muricata* and the holothuroid, *Australostichopus mollis,* use these 'mini-reefs' as shelter (**Fig. 2.6**). In the tropics, the ophiuroid *Ophiactis savignyi* can be endozoic, living within the canal system of certain sponges (Caspers 1985).

Shallow-water mangrove habitats also support many echinoderms and are important nursery areas for juvenile asteroids, including *Archaster typicus* (Bos *et al.* 2011; **Fig. 8.16**).

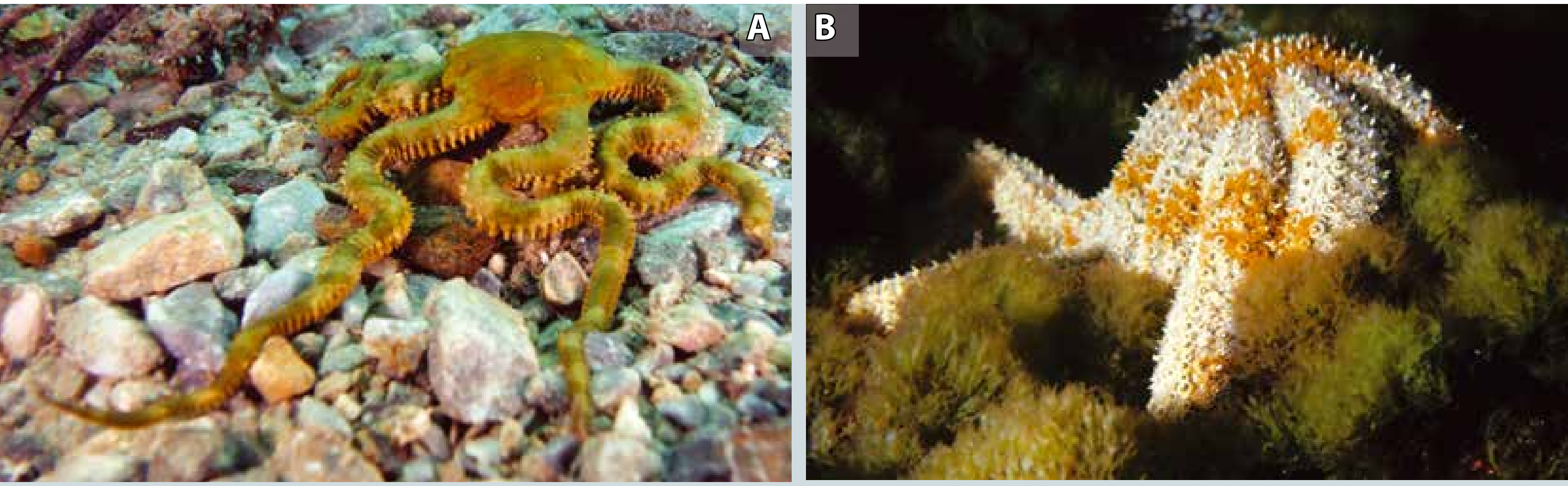


Figure 2.6 In broad coastal bays, small reefs, predominantly covered with sponges and ascidians, provide a safe refuge for a number of echinoderms. **A**, the brittlestar ***Ophiomyxa australis*** (Ophiodermatidae) frequents both shallow and deep reefs to about 400 m around most of Australia's shores and the Indo-West Pacific. **B**, the large eleven-armed seastar, ***Coscinasterias muricata*** (Asteriidae), is common in the temperate waters of southern Australia and New Zealand where it inhabits rocky and sandy areas, under rocks and in the open, to a depth of 150 m.

[A, R.Paton; B, G.Bell]

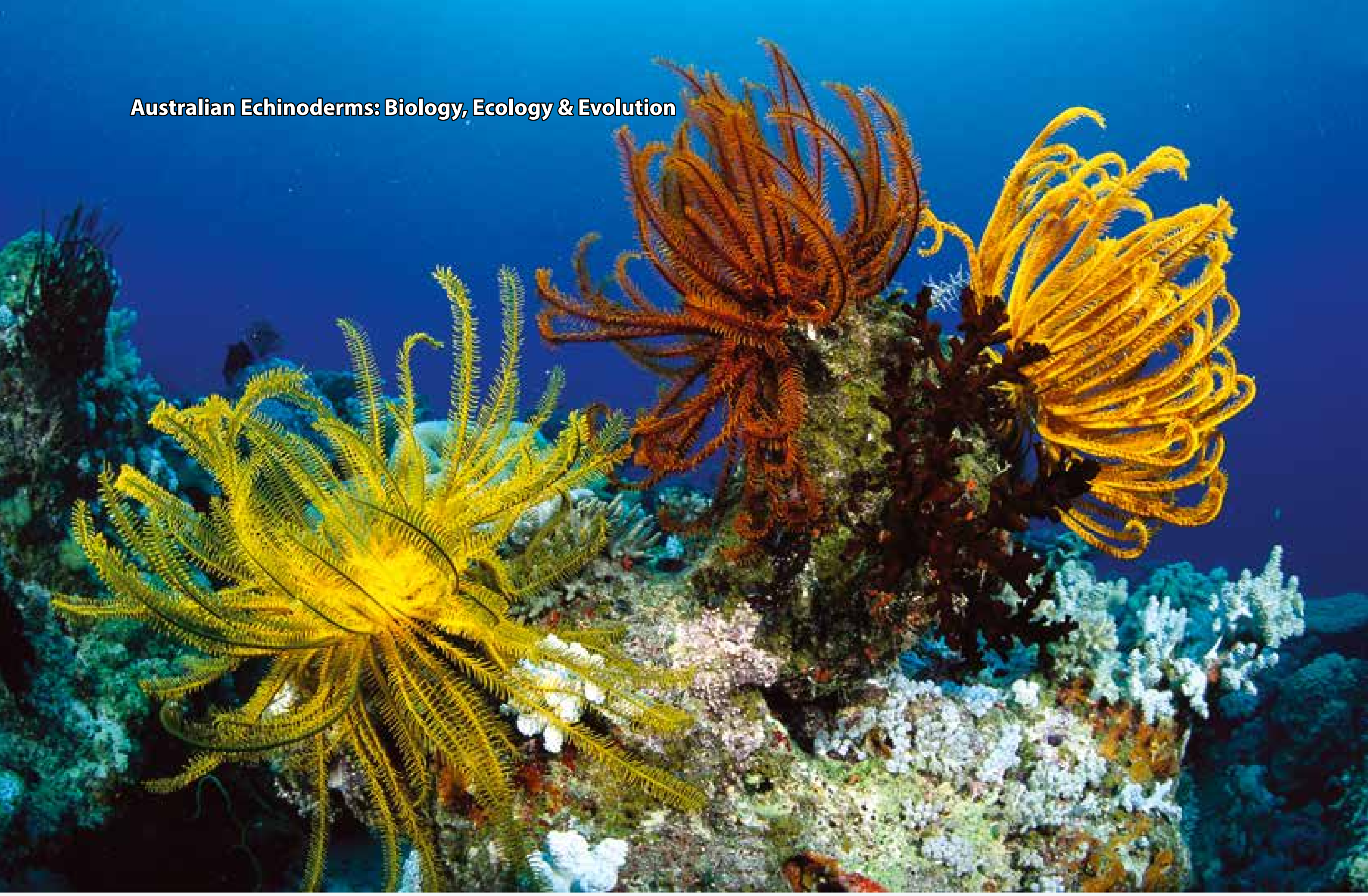


Figure 2.7 The rich marine environments of tropical coral reefs support an extraordinary number of colourful echinoderms such as these conspicuous feather stars ***Anneissia bennetti*** (formely ***Oxycomanthus bennetti;*** Comatulidae). Attached atop a coral bommie, with arms extended, they feed in the strong currents.

[F.Bavendam]

Reefs

Large numbers of filter-feeding echinoderms make use of habitats with high water movement around subtidal rocky and coral reefs; these currents provide a rich source of planktonic food (**Fig. 2.7**). Most notably, these echinoderms tend to be crinoids, basket stars and cucumariid holothuroids (**Figs 1.16A, 9.1**). In southern Australia, kelp holdfasts often contain many ophiuroids (*Ophiactis resiliens*, *Ophiothrix caespitosa*) and holothuroids (*Plesiocolochirus ignavus*). Larger species, such as the ophiuroids *Ophionereis schayeri* and *Clarkcoma canaliculata*, and the crinoid *Cenolia trichoptera*, are found under rocks and in crevices. Sea urchins play a major ecological role grazing algae from rocks and in determining benthic habitat type. *Centrostephanus rodgersii* forms 'barrens', areas completely cleared of foliose algae (Byrne & Andrew 2013; Keesing 2013; **Box 2.1**). This diadematid sea urchin tends to live in crevices during the day emerging at night to graze on algae, thus forming macroalgal free areas around its burrow. In south-eastern and southern Australia *Heliocidaris erythrogramma* also forms barrens (Keesing 2013). The temnopleurid sea urchin *Holopneustes purpurascens* is unusual in being a canopy dweller living wrapped in kelp (**Box 10.2**). Some asteroids, such as *Uniophora granifera* and *Coscinasterias muricata*, (**Figs 1.8B, 8.39**), are important predators of molluscs on temperate rocky reefs, whereas others, including species of *Pentagonaster*, *Petricia, Fromia* and *Nectria* (**Figs 2.8, 8.19, 8.22D-H**), feed on colonial invertebrates.

Echinoderms are a conspicuous and ecologically important component of coral reef communities (Birkeland 1989a; Byrne *et al.* 2004b; Byrne 2008; Pearse

2009). Crinoids are particularly diverse and abundant on coral reefs (see **Chapter 11**), taking advantage of the many elevated perches to spread out their arms and feed (**Fig. 2.7**). The most famous echinoderm, however, is the asteroid *Acanthaster planci* (the crown-of-thorns seastar), a predator of coral polyps (**Figs 2.12, 8.15; Box 4.4**). When populations of this species build to large numbers (called outbreaks; see **Chapter 4**) they can consume large quantities of coral polyps on a reef, leaving behind white coral skeletons (**Fig. 4.9B**). Among other large asteroids in tropical regions is the pin-cushion star, *Culcita novaeguineae* (**Fig. 8.28**), which also eats coral polyps, as well as algae and detritus. Most coral reef seastars belong to the family Ophidiasteridae, which includes the large blue seastar, *Linckia laevigata*, and multicoloured *Fromia*, *Nardoa* and *Tamaria* species (**Fig. 8.25A–F**). These species graze on the surface, eating encrusting sponges and other animals.

Ophiuroids are also diverse on coral reefs, particularly species in the family Ophiocomidae (**Fig. 9.12**). The black *Ophiocoma erinaceus* and various *Ophiomastix* species inhabit coral heads, and a range of other species live under coral rubble and in clumps of the green alga *Halimeda*. Ophiotrichids are also common. Among these, *Macrophiothrix* species (**Fig. 9.22B–D**) extend their long arms from burrows under rocks, and *Ophiothrix* and *Ophiopteron* species can be found at night, wound around tubular soft corals.

Sea urchins are important members of the grazing guild on coral reefs and play a key ecological role in preventing algae from overgrowing coral. Diadematid needle-spined urchins (*Diadema*, *Echinothrix*) typically live in crevices in the coral reef during the day and emerge at night to feed (McClanahan & Muthiga 2013; Muthiga & McClanahan 2013). *Echinometra*, a complex of species across the tropical Indo-Pacific, are major bioeroders of reef substrate, chewing through coral rubble (**Fig. 2.9**). They are often common in very shallow water. In Ningaloo Reef, Western Australia, *Echinometra* species are superabundant in reef habitat where they form extensive burrows in dead coral, habitat generated by the scraping activity of their teeth (**Box 10.3**). In contrast, on the Great Barrier Reef *Echinometra* species are far less abundant (M.Byrne, personal observation).

Coral reefs also support a high diverstity of holothuroids from the families Holothuriidae (for example, *Holothuria*, *Bohadschia*, *Actinopyga*), Stichopodidae (*Stichopus*, *Thelenota*) and Synaptidae (*Synapta*, *Opheodesoma*) (see **Chapter 11**). Many of the large tropical species are commercially important and are harvested in Australia and elsewhere for Bêche-de-mer (see **Chapter 4**).

Figure 2.8 The eight species of the endemic genus ***Nectria*** (Goniasteridae) are among the most colourful sea stars found in Australia's southern temperate waters. Living mostly in habitats associated with rocky reefs and shorelines, and sometimes seagrass meadows, from the mid-west of Western Australian to mid-east of New South Wales and Tasmania they feed primarily on sponges, ascidians, bryozoans and algae. One of the most vibrant sea stars, the ocellate seastar, ***Nectria ocellata***, grows to 260 mm; here it crawls amongst a field of sea pens, ***Sarcoptilus grandis*** (Cnidaria: Pennatulacea), in search of food in the waters of Port Davey, Tasmania.

[F.Bavendam]

Figure 2.9 Members of the sea urchin genus ***Echinometra*** (Echinometridae) are capable of significant bioerosion across the tropical Indo-Pacific. In Australia, ***Echinometra*** species can abrade large quanitities of reef rock/coral while feeding and excavating burrows. Feeding activity is greatest at night. This genus is in need of taxonomic revision and at least four species occur in tropical Australia (see **Box 10.3**).

[C.Bryce]

Numerous closely related species often co-occur on the same reef, especially at tropical latitudes (Byrne *et al.* 2004b). Careful study of these animals has indicated that they have slightly different habitat, feeding or reproductive biology and that they may not be in direct competition with each other (Sides & Woodley 1983). One of the best known examples of this phenomenon is among *Ophiocoma* brittle stars that dominate shallow tropical reefs. Six to seven species can often be found on reefs across the Indo-West Pacific, including the Great Barrier Reef in the north-east and Ashmore Reef off Western Australia (**Fig. 9.12B,C**). Close examination of some of these indicated the presence of cryptic species and, consequently, even greater diversity than currently appreciated (O'Hara *et al.* 2004). These species inhabit the reef infrastructure or rubble and are often very abundant in rubble areas shoreward of the reef crest (Byrne *et al.* 2004a). On Indian Ocean and Pacific Ocean reefs, including Hawaiian reefs, these animals have been found to have similar feeding strategies, but markedly different microhabitat specialisations. For example, *O. scolopendrina* prefers the high intertidal (**Fig. 2.3**), *O. pica* inhabits live coral heads, and *O. brevipes* lives in sand under rocks (Chartock 1972; Sloan *et al.* 1979).

On deeper reefs, a range of epizoic ophiuroids and crinoids occur on foliose black corals, sea fans and sea whips. Ophiuroids include the basket stars (*Euryale*, *Astroboa*; **Figs 1.12A, 9.1**), the serpent stars (*Astrobrachion*; **Box 9.1**), the colourful Ophiotrichidae, and the small Ophiactidae and Ophiacanthidae species. Crinoids are very abundant on deeper reefs in tropical regions, including the striking multi-armed *Anneissia* species (**Fig. 7.1**).

Continental shelf and slope

Below the influence of wave action, the continental shelf shares many species with sheltered embayments. Members of the families Amphiuridae and Ophiuridae dominate the ophiuroid fauna on soft sediments, with species of Ophiotrichidae, Ophiomyxidae and Ophiactidae common amongst sponges and other colonial invertebrates. Echinoids include pencil urchins such as *Goniocidaris* (**Fig. 10.8C**) and a range of heart urchins including *Brissus* (**Fig. 10.41**).

An important change in faunal composition takes place between the continental shelf (<200 m) and the continental slope. Numerically, ophiuroids and holothuroids dominate echinoderm slope faunas. The Ophiacanthidae and Ophiuridae are the most diverse ophiuroid families, providing almost two-thirds of the species from the continental slope off south-eastern Australia (T.D.O'Hara, personal observation). Typically, the Ophiacanthidae are filter-feeders, with many species epizoic on cold water corals and sponges. The Ophiuridae generally inhabit the sediments and are deposit feeders or active carnivores.

Deepsea holothuroid families include the Elpidiidae, Synallactidae, Gephyrothuriidae (Aspidochirotida), Laetmogonidae, Deimatidae, Psychropotidae (Elasipodida) and Molpadiidae (Molpadida). Numerous species from these families are known from the east coast of Australia (O'Loughlin 1998a, 1998b), including the elpidiids, which are able to walk across the seafloor on their large tube feet (Pawson 1982a).

Crinoids, asteroids and echinoids are less common, but often attain a larger size and sometimes cluster. Meadows of stalked crinoids of the family Isselicrinidae occur along rocky ridges and the deepsea asteroids of the families Goniopectinidae, Ctenodiscididae, Porcellanasteridae, Pterasteridae, Benthopectinidae, Brisingidae and Zoroasteridae tend to inhabit soft sediments.

Seamounts, vents and the abyssal plain

The seamounts south of Tasmania were surveyed extensively in 1997 and 2007 before and after the establishment of a deepsea marine protected area (**Fig. 2.10; Box 4.6**). The deeper seamounts with intact *Solenosmilia* coral cover were found to support a diverse and abundant ophiuroid fauna with Subantarctic affinities (Koslow & Gowlett-Holmes 1998; O'Hara *et al.* 2008). Most are filter feeders, including numerous members of the Ophiacanthidae. Several stalked crinoids were found that had never been reported previously from Australia (Améziane & Roux 2011). The asteroids included several species of multi-armed Brisingidae such as *Novodinia australis* (**Figs 2.10, 8.43**) and *Brisingella distincta* that lift their arms into the currents to feed. Seamounts affected by trawling were covered with the elongate orange sea urchin, *Dermechinus horridus* (**Fig. 10.22E,F; Box 4.6**). Holothuroids were rare. The 2003 NORFANZ expedition discovered a rich echinoderm fauna on seamounts across the Lord Howe Rise and Norfolk Ridge (Williams *et al.* 2006).

The only collections reported from the abyssal plain (>4,000 m depth) around Australia are four trawls taken by the research ship *Galathea* in the Tasman Sea as part of the Danish Deep Sea Expedition 1950–1952.

Figure 2.10 The deepsea benthic communities of the Tasmanian seamounts are diverse and unique. At depths above 1,400 m the benthic floor is mostly dominated by the coral ***Solenosmilia variabilis*** which provides a sheltered environment for a variety of animals such as crabs, fish, sea spiders, brittle stars and seastars like ***Novodinia australis*** (Brisingidae).

[CSIRO]

Box 2.1 Urchin barrens and abalone

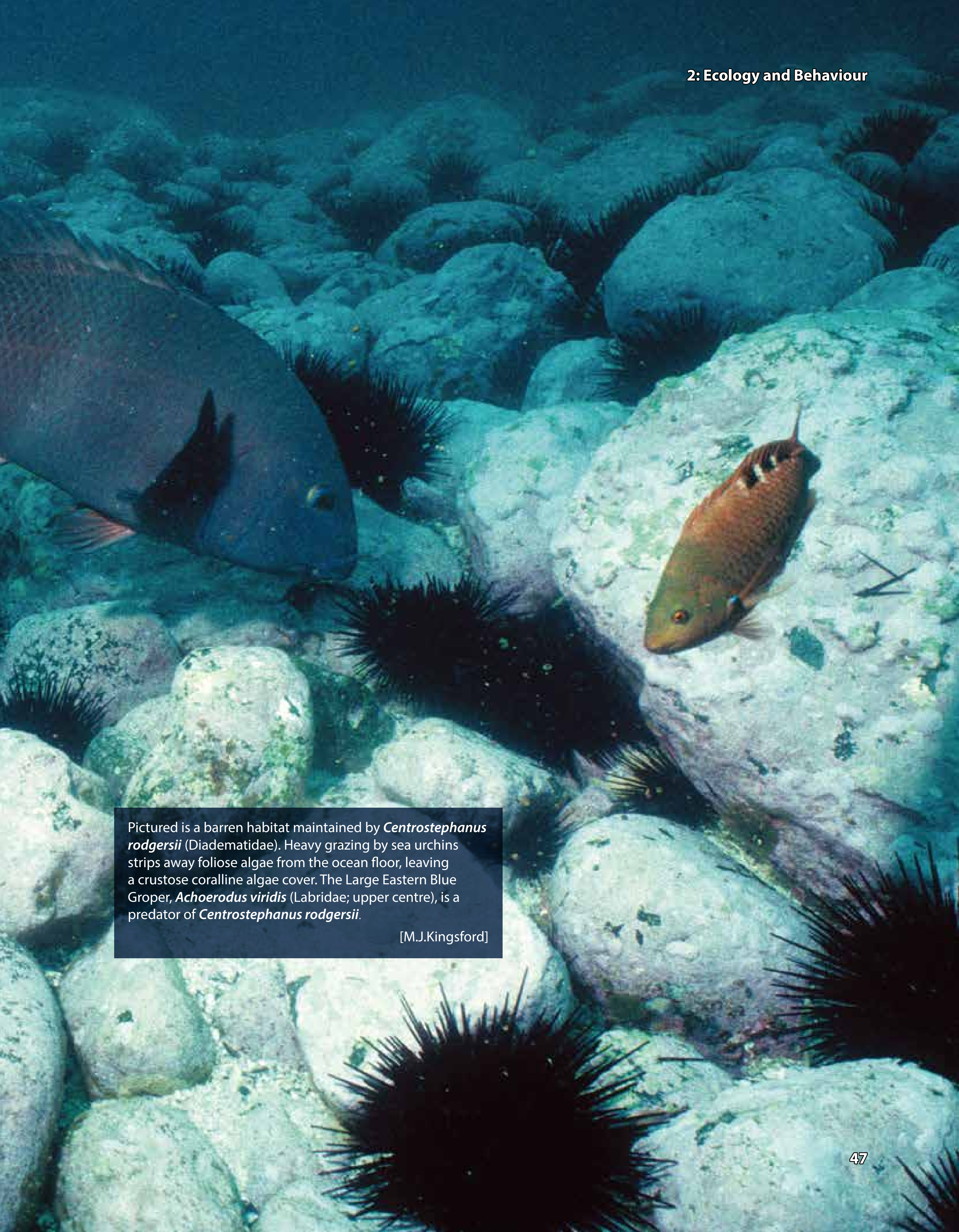
In many temperate regions of the world, large sea urchins and abalone co-occur and utilise strikingly similar macroalgal food and habitat resources. Abalone and sea urchins also have the same predators, including humans, they have similar life histories with dispersive larvae, and their juveniles recruit to crustose coralline algal habitats near the adults. The ecological overlap and potentially competitive relationship between these fishery species have prompted a number of studies into their ecological interactions.

Abalone and sea urchins are major grazers of macroalgae. Sea urchins have a profound influence on the balance between the presence of kelp and barren ground habitats. Along the east coast of Australia grazing by the sea urchin *Centrostephanus rodgersii* creates a mosaic of these two habitat types. In areas where urchins are numerous and the physical environment allows them to graze away from shelter, the seafloor is devoid of kelp and is covered by encrusting pink coralline algae. Under these conditions urchins are sustained by drift kelp and can maintain this environment; their resilient physiology adjusts body and gonad growth to food availability. In other regions, where urchin foraging is constrained by lower population density or environmental conditions, lush beds of the kelp *Ecklonia radiata* dominate the seafloor. This is so striking that on clear days with good visibility the mosaic of habitats of fringe and barrens can be seen during aerial surveys of the New South Wales coast. The recent spread of *C. rodgersii* to Tasmania has seen the creation of extensive barrens, this invasion having been facilitated by the southerly transport of larvae in the East Australian Current, the circulation of which is being altered by climate change. Interestingly, the Western Australia species *C. tenuispinus* is not known to exert a similar influence on habitat.

With its ability to influence the local availability of food and shelter, *C. rodgersii* can have a profound impact on abalone populations. This appears to be so in New South Wales where abalone are rare in the barrens habitat, and although the interaction in extreme barrens seems to result in direct competitive exclusion of abalone, the relationship is more complex than meets the eye. A similar competive interaction between abalone and *C. rodgersii* is evident in Tasmania following the southern range extension of this urchin from New South Wales.

In some regions, urchins and abalone can have a mutually beneficial interaction, because, by their grazing, urchins maintain patches of encrusting coralline algae, the preferred settlement substrate for abalone larvae. Juvenile abalone also shelter under the spine canopy of urchins, and in South Africa, the protection of juvenile abalone from predators such as fish and lobster is essential for sustaining abalone populations. Furthermore, given their ability to ensnare drift kelp, sea urchins provide food for the abalone. The recruitment and early juvenile success of abalone along the west coast of North America appears to be dependent on the grazing and shelter provided by sea urchins.

Further reading Andrew 1993; Andrew *et al*. 1998; Mayfield & Branch 2000; Ridgway 2007; Ling *et al*. 2008, 2009a, 2009b; Strain & Johnson 2009; Byrne & Andrew 2013



Pictured is a barren habitat maintained by ***Centrostephanus rodgersii*** (Diadematidae). Heavy grazing by sea urchins strips away foliose algae from the ocean floor, leaving a crustose coralline algae cover. The Large Eastern Blue Groper, ***Achoerodus viridis*** (Labridae; upper centre), is a predator of ***Centrostephanus rodgersii***.

[M.J.Kingsford]

Only the holothuroids have been identified, and these included six species of elasipods (Hansen 1975), many of which also occur on the lower continental slope (O'Loughlin 1998a). However, studies elsewhere in the world have reported small paedomorphic ophiuroids from the family Ophiuridae on the abyssal plain and in the oceanic trenches (Belyaev & Litvinova 1972). No hydrothermal vent or cold hydrocarbon seep faunas have been described from Australia, although several vent-specialist ophiuroids are known from the Atlantic and eastern Pacific oceanic ridges (Tyler *et al.* 1995a; Stöhr & Segonzac 2006).

Interactions

Feeding

Echinoderms exhibit a wide range of feeding strategies reflecting the diverse morphologies and evolutionary histories of the various groups (Jangoux & Lawrence 1982; Lawrence 2007, 2013a, 2013c; Martinez *et al.* 2017). The more important of these strategies are discussed in **Chapter 1** and are further described **Chapters 7–11**.

Predators

Many echinoderms are predatory, but these, in turn, are consumed by a range of predators. Predation is so important that many specialists believe that it has driven much of the evolution of echinoderms. The diversification of fish in the Mesozoic has been implicated in the elimination of the large aggregations of ophiuroids and stalked crinoids that characterised Palaeozoic seas (Aronson 1987). The decline of the holasteroid and cassiduloid heart urchins in Australia corresponds with the arrival of predatory cassid molluscs (McNamara 1994b). The spiny nature and nocturnal habits of many echinoderms are adaptations

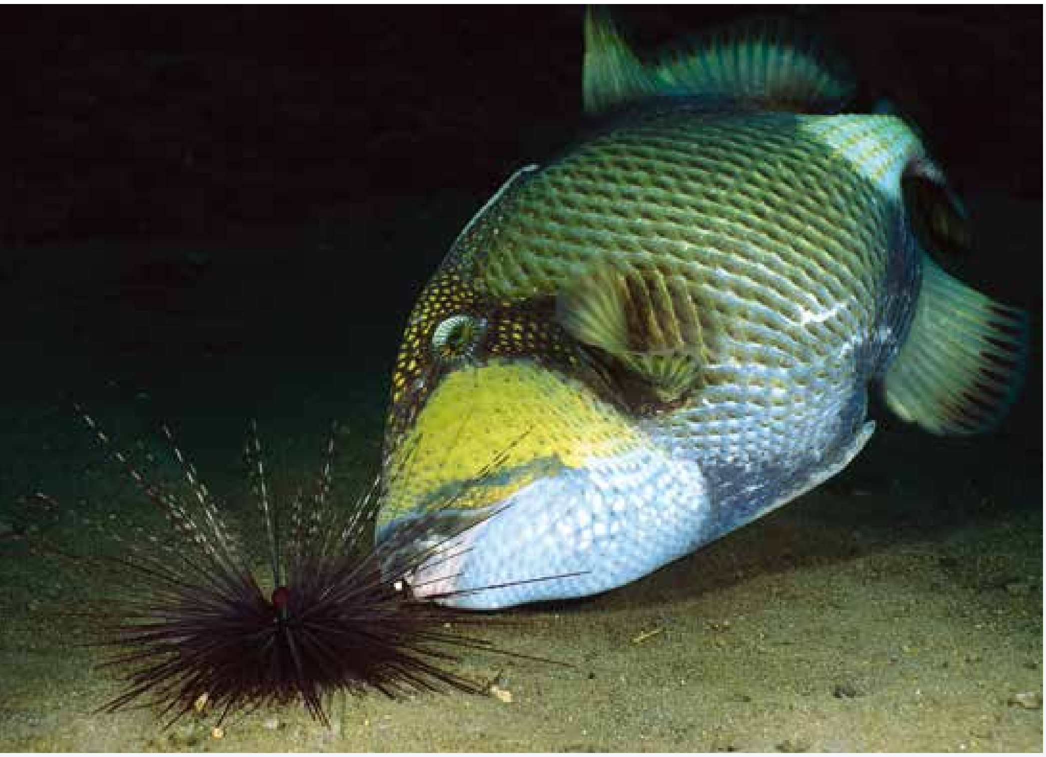
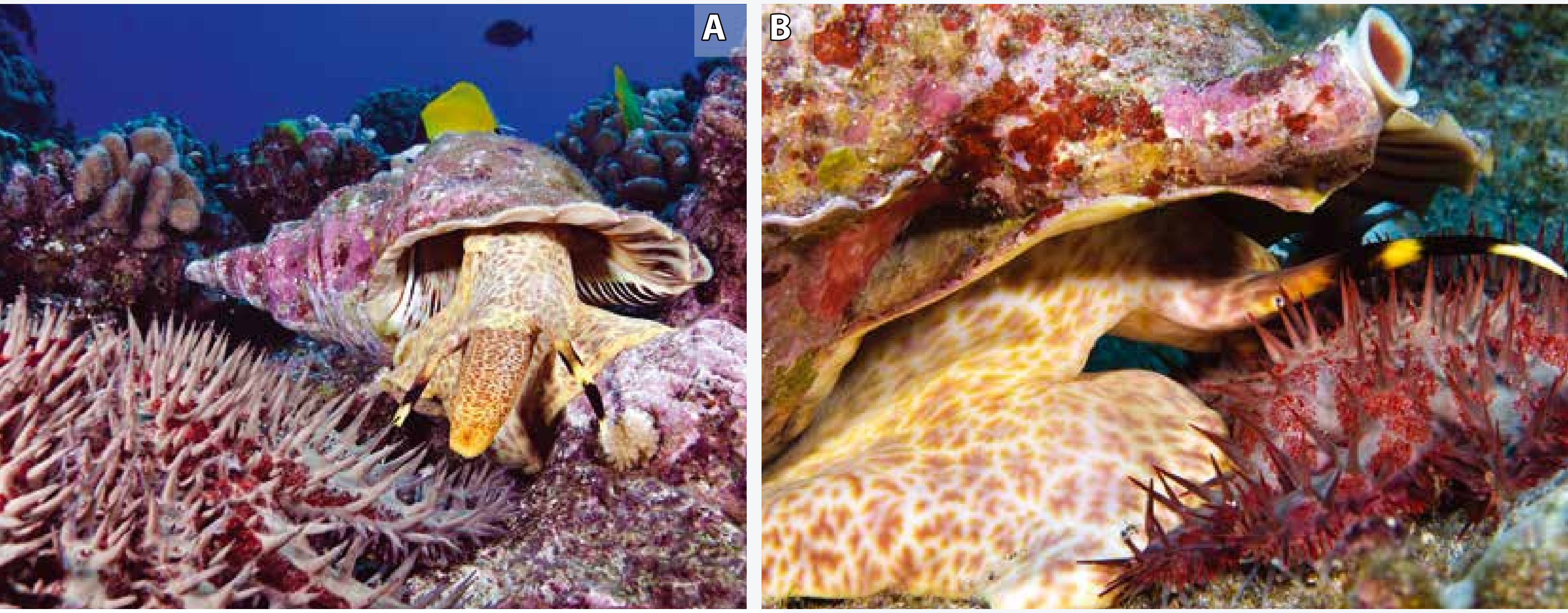


Figure 2.11 A Titan Triggerfish, ***Balistoides viridescens*** (Balistidae), attacks a long-spined sea urchin, ***Diadema setosum*** (Diadematidae), it has dislodged from between rocks. Titan Triggerfish use their strong jaws and prominent chisel-like teeth to flip over sea urchins and crack the tests on the aboral surface where there are fewer spines; they also feed on corals, crabs, molluscs and tube worms. Titan Triggerfish are also territorial and have been seen to remove ***Linckia*** seastars from their province; the Triggerfish picks up the seastar in its mouth and drops it some distance away (M.Byrne, personal observation). [F.Bavendam]



affording defence against predation (Keesing & Halford 1992a, 1992b). Many echinoderms also occupy chemically rich habitats such as those which include sponges and algae that are unpalatable to fishes; this may be another predator avoidance mechanism for echinoderms (Hendler & Littman 1986; Falkner & Byrne 2006).

Fish, gastropods, octopus, crabs and lobsters are the major predators of adult echinoderms in many environments (**Figs 2.11, 2.12, 10.5**). Two of the best known molluscan predators are the giant triton (*Charonia tritonis*) which preys on the crown-of-thorns (*Acanthaster planci*; **Fig. 2.12**) and the pin-cushion seastar (*Culcita novaeguineae*) and the helmet shell (*Cassis cornuta*) that preys on urchins (**Fig. 10.5**). At the other extreme are coral polyps that can capture small echinoderms (Hendler & Littman 1986). Asteroids and cidaroid urchins also prey on other echinoderms. For example, the asteroid *Mediaster australiensis* has been recorded as a significant predator of the ophiuroid *Ophiacantha fidelis* on the continental slope of eastern Tasmania (Blaber *et al.* 1987), and the deepsea cidaroid sea urchins can attack and consume stalked crinoids (Baumiller *et al.* 2001, 2008). On temperate rocky shores *Parvulastra exigua* (**Fig. 1.9**) is preyed on by *Meridiastra calcar* (**Figs 2.2, 8.17F**), and this may be a factor in the separation of these two species into the mid and low intertidal zones, respectively (Stevenson 1992).

Figure 2.12 The giant triton, ***Charonia tritonis*** (Ranellidae), is one of the few predators of the crown-of-thorns seastar, ***Acanthaster planci*** (Acanthasteridae); see also **Box 4.4**.

[G.Bell]

Figure 2.13 The sea urchin ***Heliocidaris erythrogramma*** (Echinometridae) with bald spot disease. Lesions, most likely caused by a bacterial infection, develop on the test causing necrosis and loss of spines. This can result in the death of the individual.

[B.Mos]

Diseases

Echinoderms are host to a range of diseases caused by microorganisms (Jangoux 1987a), often seen as bald or darkened patches on the body. These diseases are caused by bacteria. Bald spot disease of sea urchins, where necrotic lesions of tissue develop on the test, is common in Australian species and many other species around the world (**Fig. 2.13**). This disease is lethal and appears to be caused by pathogenic bacteria (*Vibrio*) (Gilles & Pearse 1986; Becker *et al*. 2007; Girard *et al*. 2012; Wang *et al*. 2013; Sweet *et al*. 2016; Brothers *et al*. in press). The test looses its spines at the 'spot' and weakens as necrosis develops. In the terminal stages of the disease the bald spots may develop a green colour as the naked test patch is colonised by algae. Sea urchin bald spot disease appears to be on the increase due to climate driven increases in sea temperature (Girard *et al*. 2012; Sweet *et al*. 2016; Brothers *et al*. in press). In New South Wales increased incidence of bald spot disease in *Heliocidaris erythrogramma* and *Holopneustes purpurascens* is correlated with increasing sea temperatures (Sweet *et al*. 2016).

Mass mortalities of urchins have occurred in the North Pacific (*Strongylocentrotus purpuratus*), North Atlantic (*Strongylocentrotus droebachiensis*) and the Caribbean (*Diadema antillarum*) in the 1980s (Gilles & Pearse 1986; Scheibling & Hennigar 1997; Lessios 2005; Muthiga & McClanahan 2013; Scheibling & Hatcher 2013). The disease in the North Atlantic was caused by an amoeboid agent, whereas an unknown organism was responsible for the Caribbean event. The die-off of *Diadema* was catastrophic: the sea urchin disappeared from most of the region which resulted in an ecological shift from coral reefs to algal reefs. Thirty years later the *Diadema* populations are only present in patches and they seem unlikely to recover to previous densities due to low spawner density preventing successful reproduction (Levitan *et al*. 2014). Mass mortalities of *Strongylocentrotus purpuratus* and *Paracentrotus lividus* (Atlantic and Mediterranean) were due to bald spot disease (Gilles & Pearse 1986; Girard *et al*. 2012). As sea urchins are considered to be the most important group of consumers living in shallow water these mass mortalities have major ecological implications (Steneck 2013).

Microbial infections of crown-of-thorns seastars have been described from juveniles, but do not appear to influence the population size of this seastar. The most recent echinoderm disease-driven mass mortality is from the seastar wasting disease. This has resulted in the death of thousands of asteroids along the west coast of North America (Hewson *et al*. 2014). The disease attacks many species causing the seastars to degenerate and then fall apart; a number of asteroid species have disappeared from extensive areas of coastline. The disease is transmissible and the disease-causing agent appears to be a virus (Hewson *et al*. 2014).

Figure 2.14 ***Thromidia catalai*** (Mithrodidae), sometimes called the giant seastar, can reach a span of 600–650 mm and weigh up to 6 kg. It is found across the Indo-Pacific and in Australia it lives in the tropical waters of Queensland and Western Australia.

[G.Bell]