



Part II: Species and species groups

Chapter 11

Vulnerability of benthic invertebrates of the
Great Barrier Reef to climate change

Pat Hutchings, Shane Ahyong, Maria Byrne,
Rachel Przeslawski and Gert Wörheide

11.1 Introduction

This chapter deals with benthic invertebrates inhabiting the extensive inter-reef soft bottom habitats and those occurring on the reef, excluding corals. For the remainder of the chapter, the term 'benthic invertebrate' refers to all invertebrates excluding corals. An assessment of the impacts of climate change on non-coral benthic invertebrates poses particular challenges: i) benthic invertebrates include an extraordinary diversity of marine organisms, including many microscopic, infaunal, boring or ephemeral species that can be difficult to sample and are poorly known taxonomically; ii) benthic invertebrates employ a diversity of reproductive strategies, broadly including planktotrophy (development through feeding larvae), lecithotrophy (development through non-feeding larvae) and direct development (release of post-metamorphic juveniles), as well as asexual reproduction, making broad generalisations of dispersal capabilities difficult; iii) factors determining species distributions are poorly known for most species; iv) benthic invertebrates exhibit a tremendous variety of lifestyles and forms, including colonial, sedentary and errant species; v) many species include either a pelagic larval or adult stage, so effects of climate change may vary during their lives (see McKinnon et al. chapter 6 for comments on planktonic forms); and, vi) research on the biogeography of benthic invertebrates on the Great Barrier Reef (GBR) is strongly biased towards commercial or destructive species.

Owing to the general lack of data on marine invertebrates on the GBR, much of our comparative information will be taken from examples based on other coral reef areas. In some cases, this will include studies from temperate areas, information from the fossil record, and data from closely related species that occur elsewhere.

This chapter will focus on representatives of the most conspicuous groups: sponges, echinoderms, molluscs and crustaceans, with comments on other groups wherever possible.

No attempt has been made to include meiofauna in this review, which, while being abundant and diverse on the GBR, have been poorly studied. Many of the generalisations made about the macrofauna, however, would also be applicable to this component of the fauna. While mention is made of intertidal habitats, this will be more fully covered in the coastal and estuarine chapter (Sheaves et al. chapter 19). Similarly, species living in estuarine habitats will be covered in more detail in the mangrove chapter (Lovelock and Ellison, Chapter 9).

11.1.1 Benthic invertebrates of the GBR

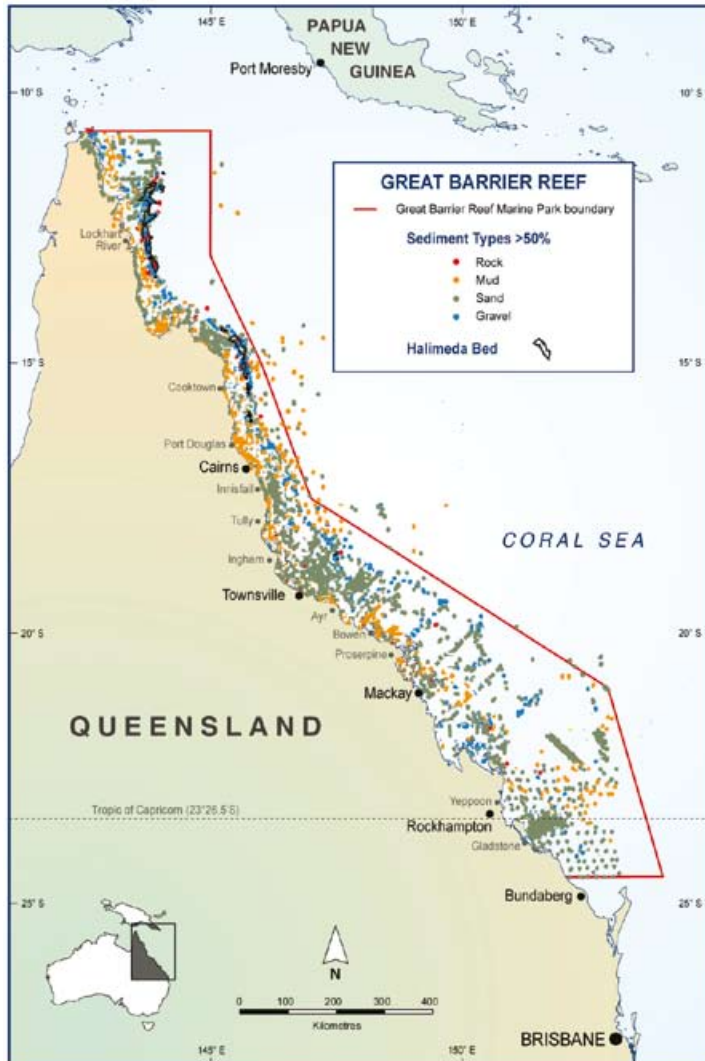
Benthic invertebrates are diverse and abundant both on reefs and in inter-reef areas. Most, if not all, marine phyla are represented²⁵⁷, ranging in size from microscopic to macroscopic (up to 1.5 metres in length for *Tridacna gigas*). Our knowledge of the fauna is patchy and biased towards larger animals, especially those living on coral substrate, and those associated with commercial harvesting, shell collecting, or aquaculture²¹¹. Ponder et al.²¹¹ summarise what is known about all the macro invertebrates found on the GBR, and Hutchings et al.¹⁴⁴ provide a synopsis of the benthic invertebrate diversity.

11.1.1.1 Soft-bottom communities

The GBR includes soft-bottom communities that extend from the coast to beyond the outer barrier reefs, from shallow intertidal zones to depths of 200 metres. Most of these communities occur within the Great Barrier Reef lagoon. Some areas are vegetated; the boundaries of some seagrass beds are well

defined (Waycott et al. chapter 8) and extensive meadows of *Halimeda* occur in deep water (50 to 96 metres) along much of the GBR⁷³. Sediments range from fine mud at the mouth of rivers to calcareous sands^{151,251} (Figure 11.1) that largely determine species composition¹⁴¹. Sediment type is often used as a surrogate for biodiversity in defining the bioregions in inter-reef habitats of the GBR^{a,68}, though latitudinal variation may be masked by the distribution and availability of suitable sediments.

Figure 11.1 Distribution of sediments in the GBR



Prepared using data from the GBRMPA and Australian Institute of Marine Science.

a For further information, see www.gbrmpa.gov.au/corp_site/key_issues/conservation/rep_areas

The Great Barrier Reef Seabed Biodiversity Project coordinated by the Australian Institute of Marine Science is attempting to map and document sessile epibenthic fauna^b. This report, due for completion in mid 2007, records many new species and new occurrences of species across the GBR (P Doherty pers comm). Nevertheless, this extensive spatial survey has collected only the larger epibenthic fauna and some of the larger infaunal organisms, because dredges and videos were employed rather than grabs. Complete documentation of GBR biodiversity will take years, if not decades, to complete. No comprehensive infaunal survey has been undertaken. Although Birtles and Arnold^{24,25} did complete several infaunal cross-shelf transects in the 1970s and 1980s, sorting of the samples has not been completed. Elsewhere, infaunal lagoon sediments have been found to have very high species richness and diversity^{5,157,92}.

11.1.1.2 Coral reef communities

More than 2900 coral reefs are present throughout the GBR region, varying greatly in size and position, from shallow inshore waters to the outer barrier reef. This includes fringing reefs around more than 900 islands, shallow and deep isolated reefs, and those forming extensive reef ecosystems^{133,134}.

While the corals of the GBR are well documented and exhibit considerable across-shelf and latitudinal variation²⁸⁰, patterns for associated fauna are far less well known. Benthic invertebrates occur both on the surface of the reef, and deep within the coral substrate as borers (eg molluscs, polychaetes, sponges) or as cryptofauna (eg molluscs, polychaetes, bryozoans, brachiopods) living in burrows or crevices sometimes created by the borers^{138,227,172}. Knowledge of the diversity of borers and cryptofauna of coral substrates is limited to a few localised studies^{103,138}. Hutchings¹³⁷ and Peyrot-Clausade et al.²⁰⁸ showed that the composition of the boring community is largely determined by substrate type (ie coral species) and the time since coral death, with the community changing as the substrate is bioeroded²⁰².

11.1.2 Current understanding of bioregionalisation

11.1.2.1 Sponges

Major trends from biodiversity analyses of Australian tropical fauna at smaller 'intra-regional' spatial scales indicate that sponges frequently form spatially heterogeneous assemblages with patchy distributions¹²⁹, sometimes with as little as 15 percent similarity in species composition between geographically adjacent reef sites¹²⁶. Several environmental variables are known to contribute to community heterogeneity: light, depth, substrate quality and nature, availability of specialised niches, water quality and flow regimes, food particle size availability, and larval recruitment and survival^{288,127,229}. At larger landscape scales (ie scale diversity, definition from Hooper et al.¹³²), latitudinal gradients of species richness are absent, moving from eastern temperate to tropical coastal and shelf faunas^{131,132}. However, significant differences in species composition are evident between the major Australian marine coastal and shelf bioregions, the Coral Sea and sub-Antarctic territories¹³⁰. Those differences might be the result of glacial sea-level changes that have impacted current systems and the resulting connectivity among regions.

b www.reef.crc.org.au/resprogram/programC/seabed/index.htm

One of the three biodiversity ‘hot spots’ around tropical Australia, each containing more than 600 species of sponges, is restricted to the mid- and outer reefs on the GBR, including the Coral Sea Reefs and the Marion Plateau¹³². Lizard Island and the Capricorn Bunker Group in the southern GBR (more than 250 species each) were found to have exceptionally rich faunas.

Although clear bioregionalisation of sponge distributions was not evident, between 5 and 15 percent of regional faunas (New Caledonian fauna¹³⁰, Sahul Shelf fauna¹²⁷) appeared to have wide Indo–Pacific ranges. More recently, however, molecular evidence disputed the existence of these so-called widely distributed species (eg *Astrosclera willeyana*²⁹⁶, *Chondrilla* spp.²⁷³), suggesting that they may instead consist of several cryptic sibling species, each with high genetic diversity that is not clearly manifested morphologically. However, determining acceptable, definable or practical spatial scales for these cryptic species boundaries still remains unclear.

11.1.2.2 Echinoderms

Echinoderms are a conspicuous and diverse component of the invertebrate fauna of the GBR^{57, 76, 55, 99, 235, 22, 39}. The 630 species of echinoderms recorded from the GBR are divided as follows: sea stars (Asteroidea), 137 species; brittle stars (Ophiuroidea), 166 species; sea urchins (Echinoidea), 110 species; sea cucumbers (Holothuroidea), 127 species; and feather stars (Crinoidea), 90 species. Although a detailed bioregionalisation survey has not been carried out on echinoderms of the GBR, the recent Great Barrier Reef Seabed Biodiversity Project is likely to significantly expand our knowledge of the group. For the most part, echinoderms from tropical Australia are non-endemics with a broad distribution in the Indo–Pacific Ocean^{76, 56, 71, 236, 235, 109, 237}. Some currently recognised echinoderm species may prove to be complexes of species, some of which may be discerned by life history traits and subtle morphological differences^{62, 196}. For example, several sea star species in the genera *Cryptasterina* and *Aquilonastra* have been shown to each comprise a species complex^{62, 197}, and some of these species could be endemic to the GBR³⁷. The *Cryptasterina* group includes both free-spawning species with a planktonic larva and viviparous brooders that give rise to crawl-away juveniles^{62, 35}. Molecular analyses have been key to discovery of this previously undetected species diversity. Similarly, several studies of sea stars indicate genetic differences within populations on either side of the Indo–West Pacific break^{292, 18, 293}. Some of these genetic differences in the crown-of-thorns starfish (*Acanthaster planci*) and the cobalt-blue starfish (*Linckia laevigata*) may have been influenced by recent past (Pleistocene) changes in climate and sea level¹⁸. Both of these are free spawners with a dispersive larva^{21, 292}. This indicates strong potential for modification of the genetic structure of marine invertebrate populations as a result of climate change.

Sea cucumbers and brittle stars are the most abundant echinoderms in most parts of the GBR, though species of *Echinometra* and feather stars, living in the open, are perhaps more conspicuous in subtidal areas^{7, 25, 22, 78, 39}. Although diverse, sea stars are not abundant, with the exception of spectacular outbreaks of *Acanthaster planci* (crown-of-thorns starfish). Sea urchins, too, are generally not abundant on the GBR compared with other areas^{13, 221}, although species of *Echinometra* and *Diadema* can be locally abundant.

Sea cucumbers form a diverse and conspicuous assemblage of species throughout the GBR. They live in a variety of habitats, from exposed reefs (eg *Actinopyga mauritiana*) to intertidal and deep lagoons (eg *Holothuria*, *Actinopyga*, *Stichopus* species)^{110, 109, 274, 39}. Sea cucumber genera include commercial

species that comprise the bêche-de-mer fishery. A recent genetic study of the commercial sea cucumber (Holothuroidea) known as the black teat fish, *Holothuria nobilis*, revealed that the fishery was composed of at least two species separated at the Indo–West Pacific break: *H. nobilis* from the Indian Ocean and *H. whitmaei* from the Pacific²⁷⁷. The taxonomy of several other commercially important sea cucumber species and species complexes on the GBR is currently being investigated³⁶.

The species richness of brittle stars on the GBR is impressive, with species in the families Ophiocomidae, Ophiotrichidae and Ophiodermatidae being well represented. Brittle stars are often common under slabs of coral rubble and in crevices shoreward of live coral habitats^{252,40}.

The echinoderm fauna of the northern GBR is more diverse than the fauna along the southern margin in the Capricorn Bunker group (Byrne, unpublished data). For example, brittle stars are particularly diverse in the northern GBR where they utilise rubble and boulder habitat and can be very abundant in shallow water and intertidal areas³⁹. While this habitat exists elsewhere, such as One Tree Reef on the southern GBR, a similar diversity and abundance of tropical brittle stars is not evident (Byrne, unpublished data). The reason is not known, but may be related to larval supply. In contrast, holothuroids are prevalent throughout the GBR and are abundant and diverse in the southern GBR^{112,113, 114,39}.

11.1.2.3 Molluscs

Molluscs pose a unique challenge in regard to examination of their distribution patterns on the GBR. Gosliner et al.¹⁰² estimated that molluscs encompassed 60 percent of all marine invertebrate species in the Indo–West Pacific, and the phylum is one of the largest and most diverse in the marine environment. Thus, Mollusca are rarely examined in their entirety in biogeographical studies. Rather, a particular class or smaller taxonomic or ecological group is typically surveyed. Moreover, molluscan surveys on tropical reefs are usually biased towards macromolluscs, do not account for parasitic or commensal species, and do not adequately consider spatial heterogeneity, thus greatly underestimating overall molluscan diversity²⁷. There is also a much larger emphasis on shelled species compared to sacoglossans, nudibranchs and other unshelled molluscs. Thirty percent of the estimated 3400 Indo–West Pacific opisthobranch species are probably undescribed¹⁰¹. Intensive surveys in New Caledonia revealed 2738 species of molluscs, an order of magnitude larger than previously reported for this region²⁷ and likely similar to GBR molluscan diversity. Single specimens represented 20 percent of these species, and 28.5 percent of species were represented only by empty shells, suggesting that the current number of molluscan species recorded in the tropical Indo–West Pacific considerably underestimates actual diversity²⁷. This same survey identified molluscs ranging in size from 0.4 to 450 mm, with most species (33.5%) having an adult size smaller than 4.1 mm. In contrast, ‘seashell’ species (larger than 41 mm) accounted for only eight percent of total species²⁷, but research and surveys often focus on these larger species (eg Catterall et al.⁴⁶), particularly those of commercial importance.

The large area and discontinuous habitat of the GBR makes spatial heterogeneity particularly important to quantifying molluscan diversity. Molluscan diversity and abundance in a given community are influenced by many abiotic factors. Substrate is one of the most important factors to influence molluscan assemblages^{11,302}, with great variation among hard- and soft-bottom assemblages. Small, herbivorous gastropods with low species diversity often dominate in seagrass beds¹⁷³, while larger predatory macromolluscs are more common on hard substrates, particularly coral reefs. A survey of a drowned reef off the Venezuelan coast revealed that only 21 percent of macromollusc species

were found in both soft- and hard-bottom areas³³. Great variation in molluscan assemblages also exists within hard- and soft-bottom communities. On hard substrates, coral-associated molluscs are prevalent on coral reefs, and encrusting and crevice-dwelling bivalves dominate non-coral substrates³⁰². The quality of hard substrates seems to particularly influence the abundance of predatory gastropods, with more neogastropods on hard substrates with refuges than on flat hard surfaces¹⁶¹. Both infaunal bivalves and gastropods are found in sandy substrates, and these assemblages may directly correlate with grain size. Molluscan assemblages in soft sediments show continuous variation related to environmental gradients⁶⁹.

Similar to other phyla (eg echinoderms, crustaceans), molluscs on the GBR include a comparatively large proportion of species with a broad Indo–West Pacific range. In a study of molluscs on Elizabeth and Middleton reefs immediately south of the GBR, 89 percent of molluscan species sampled occurred throughout the Indo–West Pacific and only 3.1 percent of these species were endemic¹⁶⁹. Despite their low richness, endemic species may be the most abundant on some reefs¹⁶⁹. Surveys of benthic invertebrates indicate that volutes have the highest degree of endemism, and overall endemism occurs most frequently on the GBR with shared components between New South Wales and southern Queensland¹⁷¹.

Some species with a high level of genetic differentiation between archipelagos elsewhere in the Indo–West Pacific show little genetic variation on the GBR, such as the turbinid *Astraliium*¹⁸³. Similarly, the giant clam *Tridacna maxima* shows significant genetic variation between archipelagos in French Polynesia, but even with its high dispersal capabilities¹⁶⁶, shows little differentiation on the GBR¹⁹. Within the GBR, genetic diversity may show latitudinal gradients. Two tropical trochids with similar lecithotrophic life histories (including the commercially harvested *Trochus niloticus*) show increasing genetic differentiation from northern to southern GBR populations²⁶. Reasons for these patterns remain unknown but suggest that distance alone does not control marine speciation¹⁸³.

11.1.2.4 Crustaceans

Crustaceans are speciose and abundant throughout the GBR with around 1300 species so far recorded from the area. The most conspicuous are the comparatively large decapods (crabs, shrimps and lobsters) and stomatopods (mantis shrimps), and other small-bodied but speciose groups such as peracarids, ostracods and copepods. Nevertheless, little information is presently available on the bioregionalisation of Crustacea on the GBR. Many of the commercial decapods in Queensland waters exhibit heterogeneous latitudinal and longitudinal distributions. For instance, northern, central and southern prawn fisheries are dominated by Endeavour (*Metapenaeus* spp.) and tiger prawns (several species of *Penaeus*), banana (*Fenneropenaeus merguensis*) and red-spot king prawns (*Melicertus longistylus*), and bay (*Metapenaeus* spp.) and eastern king prawns (*Melicertus plebejus*), respectively²⁹¹. The red-spot king prawn is a largely reef or inter-reef species favouring calcareous sediments, whereas banana and giant tiger prawns favour muddy inshore turbid waters on muddy substrates. Though juveniles of many species of commercial prawns use the same nursery habitats (namely coastal seagrass), adults have different substrate preferences^{60,260,106}. Similarly, commercial crabs and crayfish are not uniformly distributed throughout eastern Queensland. The blue swimming crab (*Portunus pelagicus*), though ranging along the entire Queensland coast including inter-reef areas, appears in greatest numbers in southern coastal waters. The mud crab (*Scylla serrata*), also ranging widely in

Great Barrier Reef waters, is most common coastally where its favoured mangrove habitat is principally located. Similarly, tropical spiny lobsters (eg *Panulirus ornatus* and *P. bispinosus*) are most prevalent in the northern GBR, although they range further south into New South Wales^{70,63}.

Assemblages of coral-associated crustacean cryptofauna exhibit highest abundance and species richness on back-reef sites on mid-shelf reefs^{214,215}. Whereas copepods dominate mid-shelf cryptofaunal assemblages, the proportions of ostracods and peracarids are significantly higher on inner-shelf reefs, despite lower overall richness. Factors that might account for the observed patterns are scale-dependent, with primary production variation at the cross-shelf scale and microhabitat features at the replicate level. Similarly, the highest diversity and density of pelagic copepods on an inter-reef transect of the central GBR occurs in mid-shelf waters²⁸⁹.

Similar patterns have also been observed for Indonesian coral-dwelling Stomatopoda, with highest species richness on mid-shelf reefs⁷⁷. However, composition of inshore, mid-shelf and outer-reef stomatopod 'communities' was significantly different. Distribution patterns of stomatopod species in the lagoons of New Caledonia and the Chesterfield Islands indicate patchy and discontinuous distributions that are highly correlated to environmental variables such as sediment type, terrigenous input and hydrodynamics²²⁵. On the GBR, distribution patterns of Stomatopoda remain to be thoroughly examined. Nevertheless, based on data derived from Ahyong², 50 percent of GBR stomatopods are shared with New Caledonia and the Chesterfield Islands, and 34 percent are shared with the Spermonde Reefs, Indonesia^{2,3}. Distributions of stomatopods on the GBR often appear to be highly correlated with substrate, terrigenous input and hydrodynamics^{77,225}. Though latitudinal gradients have not been analysed in detail, increasing species richness of both inter-reef and coral-dwelling stomatopods generally follows a northward trend, and this appears to also hold for most decapods.

11.1.2.5 Other groups

Information on the distribution and abundance of other benthic invertebrates is patchy. For example, polychaetes are abundant in both sediments and in reef habitats throughout the GBR. Detailed taxonomic studies exist for some families (eg Terebellidae, Nereididae). Polychaete species exhibit a range of biogeographical patterns, from occurring throughout the reef to narrow-range endemics (Hutchings unpublished data), and it is likely that these patterns will hold for many polychaete families. Whereas some species have been reported with broad Indo–Pacific distributions, closer examination usually shows this is rarely valid¹⁴². Soft corals on the GBR exhibit greatest diversity on mid-shelf reefs, although cover is relatively low (often less than 5%)⁸¹. Inshore and offshore species also occur on these mid-shelf reefs, though some species are restricted to these reefs.

Bryozoans are well represented on the GBR by more than 300 species, though this number is probably a significant underestimate¹⁰⁰. Many of the ascidians found on the GBR range widely throughout the Indo–Pacific; particularly common are large mats of diademnids with algal symbionts¹⁸¹.

11.1.3 Geographical range summary

In summary, benthic marine invertebrates on the GBR include widely distributed Indo–Pacific species, as well as species with a distinct northern or southern distribution. In each group, species with discrete distributions (narrow-range endemics) also occur. Some species occur in inshore waters

and can tolerate a wide range of environmental conditions, while others seem to be limited to specific environments⁸². For example, some corals and other benthic invertebrates in the Daintree region show a remarkable tolerance for extreme turbidity and sediment load after heavy rains. Similarly, several coral reef stomatopods, such as *Gonodactylaceus falcatus*, *G. graphurus* and *Pseudosquilla ciliata* tolerate the varying salinity, turbidity and sedimentation prevalent on coastal or nearshore reefs. Other reef stomatopods, such as members of the Takuidae, occur only on reefs under a more 'oceanic' influence⁷⁷ (Ahyong unpublished data). Some sponges are well adapted to live in more turbid environments (eg mangroves⁷⁴) and are generally more abundant and diverse in back-reef areas on the GBR (Wörheide pers obs). Similar patterns were obtained for other invertebrate groups, with species more abundant in, or restricted to, inshore muddy environments, and some infauna favouring inshore turbid environments¹⁹⁹. As already indicated the distribution of infauna is heavily dependent upon sediment type and organic content, the distribution of which is related to factors such as river plumes for terrestrial-derived sediments, wave patterns, and ocean currents.

The GBR consists of a mosaic of habitats and, because the distribution of the benthos is largely driven by the availability of suitable habitat, much of the fauna consists of isolated populations. Interconnectivity of benthic invertebrate populations has not been examined on the GBR, with only a few exceptions. Populations of giant clams and crown-of-thorns starfish are genetically continuous, as would be expected from species with pelagic larvae^{26,18}. Similarly, considerable gene flow exists between populations of coral species with pelagic larvae¹³⁶. Populations of tiger prawns (several *Penaeus* spp.) in Queensland, though exhibiting a degree of sub-structuring, are also genetically continuous¹⁰⁶. It is noteworthy, however, that some mollusc populations with little genetic variation on the GBR exhibit a high level of genetic differentiation between archipelagos elsewhere in the Indo–West Pacific¹⁸³, and genetic diversity may follow latitudinal gradients²⁶.

The origin of the GBR and its subsequent geological history are well documented (eg Davies and Hopley⁶⁷, Davies⁶⁵). The present-day GBR is young (approximately 9000 years old), and is built on the foundations of previous GBRs (over a period of approximately 600,000 years since the mid-Pleistocene²²²). Reef growth initiated on the Marion Plateau post–early Miocene (23 million years ago) (Davies⁶⁶ and literature cited therein) and successive GBR ecosystems are not necessarily identical owing to the great differences in pathways and processes that influence connectivity between the biota over geological time (eg Cappo and Kelley⁴³ and literature cited therein). Certainly, the cyclical rise and fall of sea level after the glacial low stand 18,000 years before present (Larcombe et al.¹⁶⁴ and literature cited therein) had major impacts on connectivity and distribution of marine biota on the GBR by leaving large areas of the GBR exposed, dry and unsuitable for marine organisms. A comparison of drill-core data from around Lizard Island with sea-level curves for northeast Australia indicated rapid reef initiation (within 500 years) at Lizard Island after flooding of the granite basement about 6700 years before present²²².

11.1.4 The role of benthic invertebrates on the GBR

Benthic marine invertebrates play a variety of roles in the GBR. Macrofaunal activity in sediments is important in global nutrient cycling and transport, transport of sediments, processing of pollutants, and secondary production including commercial species²⁵⁷, though these roles are rarely quantified. The macrofauna, as already mentioned, encompasses a tremendous diversity of phyla.

The component species exhibit a range of feeding and reproductive cycles, and are important food sources for groups at higher trophic levels, including fish, many commercial species of crustaceans and intertidal wading birds.

Inter-reef areas are rarely a homogenous habitat of sediment. Rather, they are a mosaic of sediments and isolates of sponge, gorgonians and molluscs that provide substrate for many mobile species, including fish. Only in areas that have been subjected to heavy trawling will such important habitats be absent¹⁴⁰.

Sponges are an important component of macrobenthic communities on hard substrates, as well as small isolates on soft substrates. They continuously filter water, removing bacteria and dissolved organic and particulate organic matter. However, recent studies clearly show that these cryptic communities are pivotal in nutrient and carbon cycling on the reef^{224,226}. In addition, recent initiatives to establish viable aquaculture of commercial bath sponges in the Torres Straits, in collaboration with local indigenous people, highlight their socio-economic importance. Sponges also provide shelter and microhabitats for other fish and invertebrates^{c,120}.

Echinoderms also play important roles in the GBR, particularly as bioturbators and predators. Aspidochirotid holothurians are benthic deposit feeders and are prominent members of the soft-sediment benthos^{275,276}. Burrowing species are particularly important in bioturbation and oxygenation of the nutrient-poor carbonate sediments that dominate much of the GBR^{274,275,276}. Loss of these holothurians from lagoon and inter-reef areas therefore, is likely to affect sediment–ecosystem processes^{275,276}. The influence of crown-of-thorns starfish on the ecology of macrobenthic communities on the GBR is probably one of the most important among the invertebrates^{185,61,149}.

Molluscs act at all trophic levels: as prey, predators (including carnivorous, herbivorous, deposit-feeding, filter-feeding and verminivorous species), parasites, and hosts (for symbiotic or parasitic organisms). Like some echinoderms and crustaceans, infaunal molluscs are important bioturbators, such as *Cerithideopsis cingulata* in subtropical mudflats¹⁵². Bivalves may be particularly important to some reef or inter-reef communities because many are filter feeders able to improve water quality. For example, giant clams from Tonga weighing 850 grams, can filter up to 600 ml of water per minute¹⁶⁰. Since filtration rates largely depend on body size¹⁶⁰, *Tridacna maxima* and *T. squamosa*, the species of giant clam most common on the GBR, can be expected to filter water at a similar rate based on their similar size. Gastropods and bivalves include some of the engineers of the reef, acting as builders through the remains of their calcified shells²⁹⁹, as architects through their boring behaviour that provides habitat for cryptofauna¹⁸⁶, and as demolishers through boring behaviour or predation that can weaken coral attachment^{58,232}. Several GBR species of molluscs are also aquacultured or commercially harvested for food (eg *Trochus* sp., scallops, squid)^{290,301}, nacre (eg *Trochus niloticus*)³⁰¹, or whole shells (eg *Strombus* sp., *Conus* sp., *Volute* sp.) (see Weis et al.²⁸⁵ for comprehensive list of species collected for their shells in Queensland). The most popular species in the Australian specimen shell trade are by far those in the Cypraeidae, followed by the Volutidae and Haliotidae²¹⁰.

Crustaceans are also important at all trophic and ecosystem levels. For example, copepods are important grazers and a major food source for larval and adult fish¹¹¹. Burrowing decapods, particularly thalassinideans and alpheid shrimps are significant bioturbators¹⁸⁹. Peracarids and other

c <http://www.crctorres.com/research/T1-6.html>

micro crustaceans are significant for their scavenging, detrital recycling and low trophic position^{155,154}. Decapods and stomatopods are commercially harvested from inter-reef areas throughout the GBR. Some of the most important commercial decapods (namely crabs and prawns) are opportunistic feeders, being both predatory and facultative scavengers²⁸⁴. Stomatopods and many decapods can be high-level predators in all habitats², and are in turn preyed upon by pelagic fish (as larvae) and demersal fish (as adults).

Loss of marine invertebrates will have major socio-economic consequences in terms of commercial and recreational fisheries and tourism with many divers and photographers fascinated by marine invertebrates, especially nudibranchs⁴ and flat worms¹⁹¹.

Many benthic invertebrates are also a rich source of bioactive compounds with various medicinal, industrial and commercial applications. Sponges, bryozoans and ascidians are the major source of toxic secondary metabolites in the sea¹⁸⁸ and therefore have been the prime target for research⁸⁴. Other marine invertebrates, such as nudibranchs, have the ability to sequester and modify compounds obtained from dietary sources, thus providing even more potential for useful bioactive compounds from benthic invertebrates^{53,204}. Some evidence indicates that bioactive compounds of certain invertebrates may vary according to region and even reef⁶³. These compounds are likely dependent on food sources, changes to microbial faunas across small environmental gradients, or seasonally changing habitat conditions.

11.2 Vulnerability of benthic invertebrates to climate change

Whereas individual components of climate change are discussed below, in reality, benthic invertebrates will be subjected to several concurrent stressors that may exacerbate the effect of other stressors (see section 11.3.2). For example, a species that is already stressed by rising temperatures will probably be far more susceptible to other stressors, such as ultraviolet radiation (UVR) and salinity extremes^{125,218}. In many cases, the extreme events will have greatest impact on individuals. Lough (Chapter 2) provides ranges of predicted changes, and much greater changes may occur at particular sites with impacts varying during the year and their effects varying according to the life stage of the organism. In addition, the speed of change is important for all the factors considered, and detailed predictions are not available generally, let alone for particular sites. These factors make assessing the vulnerability of the tremendous diversity of marine invertebrates on the GBR extremely difficult and imprecise.

11.2.1 Exposure

11.2.1.1 Ocean circulation

Currently, there is no consensus on whether the direction or strength of currents within the GBR will change, although it seems highly likely. The GBR is presently dominated by two large-scale global circulation systems: the south-easterly trade wind circulation, and the Australian summer monsoon westerly circulation. These effectively divide the year into the warm summer wet season (October to March) and the cooler winter dry season (April to September). Any changes to these circulations have the potential for major impacts on the recruitment of benthic invertebrates, many of which have pelagic larvae. If established current variations²⁶⁵ occur earlier or later in the year, larval dispersal may

be affected as well as food availability for pelagic larvae. Changes in water currents may also impact food availability for many of the filter-feeding organisms in benthic communities (McKinnon et al. chapter 6) in terms of abundance and quality of available food, shifting water masses of different temperatures and the influence of increased runoff.

11.2.1.2 Water temperature

Sea surface temperatures (SSTs) have increased on the GBR, although not uniformly, with the degree of increase being greater in winter than summer and greater in the central and southern regions than the northern GBR. Projected rises are 1 to 3°C and it seems likely that SST extremes will change and follow air temperature extremes. Certainly, increased incidences of coral bleaching are evident, often leading to the death of corals and associated fauna, thereby modifying coral reef communities. While effects will be greatest in shallow waters, increased temperatures will be transmitted through the water column with effects decreasing with depth.

In addition to increasing SSTs, the number of days with temperature extremes is also on the rise. The GBR is already experiencing a greater number of more extreme hot days and nights, and fewer cold days and nights with respect to air temperature (Lough chapter 2). Coastal air temperatures are predicted to rise by 4 to 5°C by 2070, although not uniformly along the GBR. For example, at the offshore Myrmidon Reef automatic weather station, average daily SSTs ranged from a minimum of 24°C in the last week of August to a maximum of 29°C in the first week of February (4.8°C range)^d. However, the difference between the minimum and maximum observed daily SSTs is 9.5°C, so local extremes are likely to have significant effects on intertidal and shallow water species²¹⁷ with effects varying along the coast.

11.2.1.3 Light spectra

Changes in water temperature and storm events may affect dissolved organic carbon and particulate matter, which will in turn modify the attenuation of light and UVR in a given region²⁴⁴. Recent analyses suggest that turbidity accounted for 74 to 79 percent of variation in light irradiance in a shallow subtidal coral reef, with increasing attenuation at depths⁹. In addition, recent evidence suggests that climate change may delay recovery of the ozone layer²⁴⁵, and ozone depletion may be linked to more rapid climate change¹¹⁷, thereby exposing intertidal and shallow-water organisms to longer periods of human-increased UVR.

Species living in intertidal and shallow water will be most vulnerable to changes in light attenuation and UVR exposure, especially those with symbiotic algae such as giant clams⁷⁵, sponges¹²², anemones^{278,75} and those spawning in intertidal habitats exposed to full sun²¹⁸.

11.2.1.4 Physical disturbance (tropical storms)

In the past 30 years the number of cyclones affecting the GBR may have declined, but those that do occur are more intense¹⁹² (Lough chapter 2). Predicted enhanced greenhouse conditions include both warmer SSTs and changes in the atmospheric temperature profile with a 5 to 12 percent increase in wind speeds and higher rainfall. It is unclear, however, whether there will be changes in location

d For further information, see <http://www.aims.gov.au/pages/facilities/weather-stations/weather-index.html>

and frequency of tropical storms and to what extent they will be modulated by El Niño–Southern Oscillation (ENSO) events. Increased intensity of storm events will disturb or destroy reef habitats, especially in shallow and coastal waters. Associated increases in storm surge will also impact on shallow coastal communities. These impacts will be compounded by rising sea level (see 11.2.1.5).

Although it is unclear how rainfall patterns will change along the GBR coast, rainfall patterns and river flows are projected to exhibit greater variation between wet and dry years than in the past, with spatial and inter-annual variability modulated by ENSO and Pacific Decadal Oscillation (PDO) (Lough chapter 2).

The most vulnerable groups of organisms during storm activities, with associated increased river flow and sedimentation, are sessile species or egg masses in the intertidal or shallow subtidal which are physically torn from the substrate or buried, and infaunal organisms that are physically dislodged by wave action that erodes the habitat. Both groups have difficulties in reattaching themselves or reburrowing into the sediment before being washed out to sea, onto unsuitable habitats or stranded on beaches²⁹⁴. A general trend of shifting community structure with increasing sedimentation or resuspension has been observed for sponges^{16,44}. Similarly, fluctuations in sediment load were partly responsible for changes in the structure and composition of sponge assemblages on tropical rocky shores in the Bay of Mazatlan (Pacific Ocean, Mexico)⁴⁴, and in a New Zealand study, sediment levels of more than 0.5 cm precluded settlement. Re-settlement success appears to be inversely correlated with sediment depth¹⁶. For the temperate reef sponge *Cymbastella concentrica*, increased siltation led to a reduction in weight and a lower reproductive activity²³⁰. It has also been shown for Caribbean sponges that strong storms (hurricanes) have a dramatic impact on sponge communities, with loss of nearly half of the individuals and biomass in San Blas (Panama) during Hurricane Joan in 1988²⁹⁸.

11.2.1.5 Ocean acidification and sea level rise

The oceans are becoming more acidic owing to absorption of anthropogenic carbon dioxide from the atmosphere^{175,198,238,159}. The long term natural variability of oceanic pH is unknown, but can be inferred through study of coral skeletons²⁰⁶. A recent study of boron isotopes in coral from the southwestern Pacific provided evidence that large variations in pH have occurred over approximately 50 year cycles and that these natural pH cycles can modulate the impact of ocean acidification on coral reef ecosystems^{206,180}. In addition, efficient lagoon flushing is required for reef water to achieve pH equilibrium with the open ocean²⁰⁶. Thus, effects of predicted progressive acidification of the ocean on coral reef communities will differ among reefs depending on natural cycles and degree of reef flushing.

It is expected that ocean acidification will have a major impact on organisms such as molluscs and echinoderms that use calcium carbonate for skeletal support of their bodies^{162,250}. Other groups likely to be affected are foraminifera, soft corals and sea fans, as they also incorporate calcium carbonate into their skeletons. Calcification rates are depressed at lower pH and are influenced by temperature¹⁶². Conversely, some speculate that sea warming might stimulate increased calcification through enhancement of the physiological processes involved, potentially ameliorating the effect of acidification^{176,158,159}. The predicted impact of ocean acidification on coral reef invertebrates is controversial and a consensus is unlikely to be reached in the short term^{176,158,206,159,180}. Any changes to structure or density of coral skeletons, however, could impact the infaunal communities associated with either living or dead coral¹³⁸.

If the presently observed rate of sea level rise continues to 2100 then global sea level would be 310 ± 30 mm higher than in 1990, and this rate may accelerate over time⁵². Certainly, there will be regional variations along the GBR as the coastal topography and islands will determine the influence of tides and extent of inundation, in addition to modulation by ENSO events. The regional projection for sea level rise is 0.1 to 0.9 metres by 2100 (Lough chapter 2). The communities most vulnerable to sea level rise will be intertidal, seagrass and mangrove communities (Waycott et al. chapter 8, Lovelock and Ellison chapter 9 and Sheaves et al. chapter 19). Benthic invertebrates associated with live corals in shallow water are potentially vulnerable if these coral colonies fail to keep up with rising sea level.

11.2.2. Sensitivity

11.2.2.1 Ocean circulation

Changes in ocean circulation have the potential to disperse larvae over unsuitable habitats for settlement. The process of settlement is critical for many invertebrates, especially for sedentary or sessile species, and a clear correlation has been observed between the time propagules spend in the water column and dispersal distance^{246,247}. If larvae are dispersed over unsuitable habitat, they will fail to metamorphose and settle. Even if they can delay settlement, this is only an option for a limited time²⁰⁵. Species with short larval periods are most likely to be directly affected by changing ocean currents through dispersal to unfavourable sites or areas with a lower concentration of larvae, while those with longer larval periods or direct development may be more tolerant to changing currents because they will presumably be able to delay settlement until they arrive at a suitable habitat. For example, *Littorina saxatilis*, which releases brooded juveniles, is more widespread than the planktotroph *L. littorea*. This supports the hypothesis that species with long-lived larvae may be vulnerable to problems associated with current mediated dispersal, including a settling population too low to be viable (Johannesson¹⁴⁸ and literature cited therein). Filter-feeding organisms may also be affected by changes in current patterns, as the quality or abundance of their food supply in the water column may change.

11.2.2.2 Water temperature

Rising water temperatures will certainly impact on benthic invertebrates, but the degree of impact will vary between species and range from little impact to death. We have little precise information on lethal threshold temperatures, but we do know that water temperature affects metabolic rate and the timing of reproduction for some groups, including sponges^{89,90}, ascidians^{15,163}, molluscs²⁶⁸, and polychaetes⁹⁸. Increased temperature, in concert with other stressors like sedimentation, increased nutrients and physical damage will contribute to an increased abundance of certain sponge groups (eg boring sponges) and has been found to be responsible for decreases in live coral cover on a reef studied in Belize (Caribbean Sea²³⁹). However, no relationship between warm water incursions and bleaching of the sponge *Xestospongia muta* has been observed (J Pawlik pers comm).

It is predicted that extremes in water temperature will increase, which are likely to have significant effects both on survival of larvae and adults, as well as affecting growth and reproduction. The sensitivity of a species to thermal changes will probably vary geographically. Changes are predicted to be greatest in the central and southern part of the GBR, so species occurring in these areas are most likely to be impacted.

Development and growth rates of marine invertebrates are strongly and positively correlated to temperature^{93,200,150}. The strength of this relationship will depend on life history characteristics that will determine exposure to thermal fluctuations and extremes. For example, developmental rates of species that spawn in exposed habitats, during low tides, or daytime may be more affected by temperature changes and extremes than species that spawn in sheltered habitats, during high tides, or at night²¹⁶.

Development of larvae influences the thermal history of the population and spawning season^{93,150}. Increased temperature may reduce dispersal potential by accelerating growth rates and reducing time spent in the water column, thereby potentially limiting or reducing gene flow between otherwise connected populations¹⁹⁵. Isolation of populations could render them more susceptible to localised extinction.

11.2.2.3 Ocean acidification

All marine biota that have calcareous skeletons are sensitive to ocean acidification because carbonate saturation, which is related to pH, has a major effect on calcification rates^{157,159}. The predicted decrease in ocean pH by 0.4 to 0.5 pH units by 2100 may impact on the ability of invertebrates to secrete protective skeletons⁸⁵. The biota most sensitive to ocean acidification includes a broad suite of calcifying organisms including molluscs¹⁸⁴, echinoderms, crustaceans, bryozoans, serpulid polychaetes, foraminifera¹¹⁹ and some species of sponges, particularly at ocean conditions with pH lower than 7.5^{184,119}. These organisms have evolved the protective use of a shell or calcareous skeleton. Predicted changes in ocean pH will negatively affect shell and skeleton formation, development and strength, thereby affecting their primary function, as protection from physical damage, including predation. Indeed, recent modeling suggests that molluscs evolved optimal shell morphologies in response to predators¹⁴⁵, so any weakening of the shell may increase risk of predation. Calcification studies of gastropods and sea urchins indicated that a 200 parts per million increase in carbon dioxide (CO₂) in sea water adversely affected growth²⁵⁰.

11.2.2.4 Light spectra

Spectral changes associated with increased turbidity, sedimentation, and storm frequency will impact benthic invertebrates that obtain at least part of their nutrition from photosynthetic symbionts (eg giant clams⁷⁵ and anemones²⁷⁸). Sensitivity to turbid conditions will likely be species-specific, with some species able to switch to heterotrophy for long periods, thereby adapting to turbidity and increased light attenuation⁸.

Sponge-zooxanthellae associations appear to be more stable than coral-zooxanthellae associations, at least in some hadromerid sponges¹²². Although sponges bleach less frequently than adjacent corals²⁸¹, completely bleached individuals ultimately die⁹¹. A recent study of bleaching of *Xestospongia muta* in the Caribbean, however, suggests that cycles of bleaching are not necessarily deleterious (J Pawlik pers comm).

Increased UVR exposure may also negatively affect species without adequate or adaptive behavioural or chemical protection. Sessile organisms (such as didemnid ascidians) or those unable to detect UVR will be more vulnerable than species able to move away from damaging UVR. Marine animals obtain chemical sunscreens called mycosporine-like amino acids (MAAs) from symbioses or diet²⁴⁹.

In the latter case, photoprotective function cannot be intrinsically induced. Therefore, animals that rely heavily on MAAs for protective function, but obtain these solely through their diet, may be particularly vulnerable to increased UVR exposure.

11.2.2.5 Sea level rise

Rising sea level has the potential to inundate obligate intertidal species and shallow seagrass beds and adjacent mangroves (Waycott et al. chapter 8, Lovelock and Ellison chapter 9), which are home to diverse benthic marine invertebrate communities. Impacts will depend on the magnitude and rate of such changes. If the rate of change is slow, then seagrass communities and associated benthic communities have the potential to expand into shallower water. Conversely, loss of deep seagrass and conversion to a sandy or muddy substrate will drastically change invertebrate community composition.

Sea level rise may also affect benthic communities that are relatively isolated by geographical barriers by facilitating larval dispersal. The effect of geographical barriers could be reduced with heightened sea level, resulting in recruitment of invader species to a formerly isolated area¹⁷. Alternatively, increased larval dispersal between previously semi-isolated intraspecific populations could also help to maintain genetic continuity.

Coral communities (Hoegh-Guldberg et al. chapter 10) will be affected by sea level rise, which in turn will alter available substrate and affect other dependent benthic invertebrates¹¹. Bioeroders, such as boring sponges²²⁸, have further potential to destabilize the reef framework, making it more vulnerable to fatal storm damage.

11.2.2.6 Physical disturbance

Sessile organisms are vulnerable to detachment via physical disturbance. The magnitude of these effects will depend on their ability to reattach or withstand periods of detachment (eg Wilson²⁹⁴).

11.2.2.7 Rainfall and river flood plumes

Marine benthic invertebrates can be highly sensitive to changes in salinity (eg encapsulated molluscs²¹⁶) and many species have, at best, a limited ability to osmoregulate in the presence of freshwater¹⁹⁴. Different life stages usually have varying sensitivities with newly settled recruits the most vulnerable (see Webster and Hill chapter 5). Some species may be able to avoid this stressor by burrowing deeper into the sediment where salinity changes are reduced, and others can close their shells to exclude fresh water, but these reactions can only be sustained for short periods during which no feeding can occur. Reactions to flooding and salinity changes are likely to be species-specific within most groups. For example, recent studies show that two colonial ascidians with similar life histories show different tolerances to low salinities (E Westerman pers comm). Sponges also seem to be affected by salinity changes, with evidence of decreased growth rates and lower reproductive activity²³⁰. In addition, the size of the banana prawn harvest in the Gulf of Carpentaria and eastern Queensland strongly correlates with rainfall²⁶³, while reproduction and activity of the blue swimming crab is negatively affected by low salinity^{209,212}. Echinoderms are probably the most stenohaline of the benthic groups, with limited tolerance to decreases in salinity, particularly amongst the larvae¹⁸². In summary, the timing and duration of salinity reductions will be critical and effects will vary among taxa.

11.2.3 Impacts

11.2.3.1 Ocean circulation

Changes in ocean circulation can affect food availability to suspension feeders²⁸⁷, larval supply and upwelling. Food availability is an important factor controlling reproduction in some marine invertebrates (eg egg production in the ascidian *Botrullus schlosseri*¹⁰⁸, so changes in ocean circulation may have significant impacts on reproduction, larval survival and species ranges.

If larvae are dispersed to unsuitable habitats, and adults subjected to suboptimal current patterns, present species ranges could be significantly altered. Changes in circulation and upwelling, with downstream effects on primary productivity, will not only have implications for larval survival and recruitment, but also food availability for filter feeding animals such as crinoids, sponges, ascidians and many epifaunal bivalves.

Certain groups of molluscs may be more resistant to extinction as a result of changes in ocean circulation pattern. Examination of the distribution of narrow-aperture rock-dwelling gastropods, based on museum collections, has revealed that they are not significantly affected by deep-sea barriers in the Indo–West Pacific, a finding consistent with the resistance to extinction and high level of recent speciation of this group²⁷⁹.

11.2.3.2 Water temperature

Although little data exist on current geographic range changes in the GBR for most benthic invertebrates, the fossil record of molluscs indicates that water temperature has indeed played a major role in migrations and extinctions of many species, particularly in conjunction with sea level changes¹²¹. Some species have extended their range during warmer periods (eg Australian species introductions to New Zealand during the Pleistocene¹⁷, northward extension of *Venericardia procera* in the southwestern Atlantic during the late Quaternary¹. Other species presumably were unable to adapt to climate change and became locally extinct (eg the extinction of *Tegula atra* in the southwestern Atlantic during the late Quaternary¹ or completely extinct (eg many molluscs in the southern hemisphere during the Cretaceous-Tertiary extinction event and associated climate change²⁶⁴. In contrast, Jackson and Sheldon¹⁴⁷ suggest that temperature fluctuations and sea level change have had little impact on species composition of molluscs and corals in the fossil record throughout tropical America. They suggest that there is no correlation between the magnitude of environmental change and the subsequent ecological and evolutionary response, although the speed of change was much slower than what we are currently observing. While fossil coral communities have been studied in detail in the GBR²⁰¹, associated benthic invertebrates have not. Jackson and Johnson¹⁴⁶ point out that the excellent marine fossil record and the similarity between ancient and current species provides a great opportunity to investigate effects of environmental change on communities and ecosystems, but ‘unfortunately, this potential has not been fully exploited because of lack of well-sampled time series and adequate statistical analysis’. As ecological communities were profoundly altered by human activity long before modern ecological studies began, Jackson and Johnson¹⁴⁶ suggest that data from the Holocene should be considered the only standard for ‘pristine’ communities prior to human impact.

The wide variety of reproductive strategies in many benthic invertebrates makes generalisations on timing of reproduction difficult. For some species, such as the broadcast spawning sponges

Xestospongia bergquistia and *X. testudinaria*, spawning was observed during periods of warm water just prior to water temperature reaching its maximum⁹⁰. However, larval release in other species is not predictable, as in the viviparous sponge *Leucetta chagosensis* (Wörheide pers obs), or occurs year-round, as in the brooding shallow water sponge *Amphimedon queenslandica* (formerly referred to as *Reniera* sp.¹⁶⁸. Similarly, molluscan reproductive patterns are often unpredictable or species-specific, with no obvious relationships with taxonomy or avoidance of thermal stress²¹⁹. Most echinoderm species appear to spawn in summer and can be induced to spawn in response to temperature fluctuation^{220,54}. Some species with benthic development, including a new species of *Aquilonastra* from One Tree Island, lays its eggs in masses on intertidal rubble in winter, potentially as an adaptation to avoid the effects of high temperature on embryonic development, similar to that exhibited by closely related non-tropical species³⁴. Many of the most abundant aspidochirotid sea cucumbers on the GBR including *Holothuria* species and *Stichopus chloronotus* have distinct summer and winter patterns of sexual and asexual reproduction. They spawn gametes in summer and exhibit a peak in clonal reproduction by fission (splitting in half) in the winter^{113,167}.

Rising water temperature will almost certainly lead to species spawning earlier or for longer periods (eg ascidians, E Westerman pers comm) and may affect larval recruitment success. In the case of species producing planktotrophic larvae, this may not necessarily coincide with phytoplankton availability. This temporal separation of zooplankton and the phytoplanktonic food source is reported in the Atlantic and attributed to climate change¹¹⁸. In addition, species requiring other benthic organisms to provide cues for metamorphosis or food for juveniles may also fail to spawn at an optimal time. For example, some nudibranchs are specialised feeders on a single species of sponge, ascidian or bryozoan. Changes in spawning behaviour may therefore negatively affect larval metamorphosis or juvenile feeding if these substrates are not readily available.

Rising water temperature and associated factors are likely to affect larvae more than adults. Though not a tropical ecosystem, increased ocean temperatures correlate with zooplankton decline in the California Current²³³. Meroplankton (species in plankton for only part of its life cycle) seem to be more vulnerable to warming water than holozooplankton (species in plankton permanently)¹¹⁸, providing support to the hypothesis that larvae of marine invertebrates are more vulnerable to changing temperatures than adults. Any impact studies should therefore account for larval stages (McKinnon et al. chapter 6).

On temperate shores, Fitzhenry and Podolsky⁸⁷ found that increasing temperatures impacted negatively on reproductive success of the barnacle *Chthamalus fragilis*. Populations of species at the boundary of their temperature tolerances will either die due to elevated temperatures, fail to breed, or in some way modify their physiological processes such as respiration, growth and reproduction to adapt to the new conditions (eg molluscs¹). Temperature also affects key metabolic enzymes in littorinid molluscs, with variations found in populations at different latitudes and shore levels²⁵⁹ and similarly in the bivalve *Mytilus edulis*⁴⁹.

Species that only occur in far northern regions of the GBR may extend their populations further south with rising temperature. Range extensions into warmer waters have been documented in the northern hemisphere both through the fossil record (eg Aguirre et al.¹) and through research on current populations (eg Hiscock et al.¹²³). Obviously, migration of species is only feasible for mobile

organisms, but the pelagic larvae of sedentary or sessile species may settle further south or in deeper water and change distribution ranges. While boundary changes are yet to be documented for any Australian reef species, Barry et al.¹⁴ and Sagarin et al.²⁴⁰ found climate-related long-term faunal changes for Californian rocky intertidal communities after only a 0.75°C increase in water temperature and a 2.2°C increase in air temperature. Similarly, the dramatic decline in mussel beds along the California coast is attributed to warming waters. Note, however, that a recent comparison of late Pliocene and present-day molluscan assemblages from Cornwall in the United Kingdom suggests that climate change will not affect overall richness in this region, although species composition will change²⁸³. No similar comparisons have been made with the molluscan fossil record in the Indo–West Pacific. In other temperate areas there is also good evidence of intertidal communities changing with increases in both air and sea temperature²⁴³.

If water temperature increases persist for only a short time (eg a few days), some benthic burrowing species may avoid unfavorable conditions by burrowing deeper where temperature changes are lower (eg amphipods²⁷²), and others by reducing their metabolism (eg ascidians¹⁵). Their continuing survival, however, will depend on the frequency and timing of warming events, especially in relation to life cycles, with certain stages more vulnerable.

Recent research also suggests that ocean warming can facilitate the establishment and spread of invasive species. Stachowicz et al.²⁶² compared distribution patterns of ascidians with ocean temperature over 12 years and found that introduced species recruited earlier in warmer years, while native species showed no such relationship. Laboratory studies revealed that two invasive ascidian species grew faster than native species, but only at the warmest summer temperatures, suggesting that community changes due to climate change are primarily the result of changing temperature extremes, rather than annual mean changes²⁶². The order of species recruitment has a huge effect on community structure. Warmer water temperatures can facilitate earlier colonisation by invaders and associated community shifts to dominance by invaders²⁶².

11.2.3.3. Ocean acidification

The impact of ocean acidification on marine invertebrates will depend on the rate of change of seawater pH, relative to its natural variability²⁰⁶. It is expected that the impacts of ocean acidification will be greatest in surface and shallow water⁴¹. Current knowledge of the biology of skeleton formation indicates that the predicted changes in ocean pH by 0.4 to 0.5 units by 2100 may impact the ability of marine invertebrates to secrete protective skeletons. Existing skeletons may be weakened, providing less protection from predators and physical damage from trawling and storm activity, and less resistance to other physical factors, such as desiccation in the intertidal^{238,162}. Impaired skeletogenesis is expected to compromise survivorship of both planktonic and benthic life stages of coral reef invertebrates¹⁶². The larval skeleton of gastropods, sea urchins and other benthic invertebrates are particularly fragile and may not be produced under acidic conditions¹⁶². This may result in complete recruitment failure of a whole suite of benthic invertebrates. In addition, some organisms may also show indirect effects of ocean acidification by diverting resources from their shells towards improving physiological function. For example, the bivalve *Mytilus galloprovincialis* dissolves its calcium carbonate shell during periods of prolonged hypercapnia in order to increase haemolymph bicarbonate and limit acidosis¹⁸⁴.

Increased carbon dioxide in surface waters has also been shown to lower metabolic rate in benthic invertebrates¹⁸⁴. This may impact populations by affecting feeding, growth and reproduction.

11.2.3.4 Light spectra

Increases in light attenuation associated with increased turbidity and sedimentation will negatively affect organisms with photosynthetic symbionts. For example, turbid conditions with reduced light availability are known to impair the physiology of the giant clam *T. gigas*⁷⁵. The relationship between turbidity, heterotrophy and autotrophy is well studied among corals and their photosymbionts^{8,79}, but the effects of turbidity on most non-coral photosymbionts remain unknown. Under turbid conditions and sedimentation, the effects on corals can result in a switch to heterotrophy⁸, reduced growth³⁰⁰, or even expulsion of zooxanthellae²⁸⁶. The latter case may have serious consequences for the host, including death^{256,286}. Increased turbidity on coral reefs may also result in shifts in the bioeroding communities from sponges to bivalves and polychaetes¹⁷⁷.

11.2.3.5 Sea level rise

Sea level rise may affect current coral reefs by shifting coral recruitment to 'new' shallow waters. This will affect distributions of other benthic invertebrates associated with corals.

Data derived from the mid to late Holocene record of a southeastern Australian lagoon indicates that sea level fluctuations and associated changes in sedimentation caused community change in estuarine and intertidal environments, with a shift from dominance by molluscs and foraminifera to charophytes, associated with a sea level drop and closure of the lagoon⁹⁴. It is currently unknown how community dominance will shift on the GBR with sea level rise but, as mentioned previously, the biggest impacts will most likely occur in shallow, intertidal, and estuarine zones.

In addition, recruitment of benthic invertebrates to localised areas may be impacted if current geographic barriers to larval dispersal are bridged by sea level rise. Ben¹⁷ found evidence of this phenomenon on a much larger and dramatic scale with the Pleistocene extinction of 29 species of molluscs and the introduction of warmer water species in New Zealand after the breach of the Auckland isthmus caused by rising sea levels¹⁷. Obviously, no such similar formidable geographic barrier exists on the GBR, but sea level rise may breach smaller barriers to facilitate dispersal of larvae currently isolated from areas. This could result in local introductions of species and possibly competition-mediated extinctions, but could also help maintain genetic continuity between previously semi-isolated intraspecific populations.

Although global climate change is usually discussed only in terms of its negative effects, sea level rise may have a positive effect on the benthic invertebrates of coral reefs. Sea level has remained relatively static for the past several thousand years, and coral reefs have therefore reached an elevation where continued upward growth is constrained by sea level²⁵⁶. As sea level rises, this constraint is removed, ultimately increasing the availability of coral substrate for benthic invertebrates. As a result, invertebrate diversity in some lagoon environments may increase. Whereas current conditions ensure lagoon communities are limited by stressors associated with ocean circulation (eg salinity extremes or nutrient depletion), sea level rise may affect water circulation in these environments such that conditions more closely represent the open ocean²⁵⁶.

11.2.3.6 Physical disturbance

Increased storm activity will also indirectly impact inshore communities through more frequent mass flooding and increased runoff. These storm events may temporarily or permanently increase localised turbidity and freshwater input. In addition, direct impact of storms and higher sea levels may fragment fringing reefs, reducing their wave-breaking ability, leading to changes on island or mainland beaches²⁴⁸. With increased storm intensity, it is predicted that flood plumes will be larger and extend further offshore (see section 11.2.3.7). Sediment distribution, critical for many benthic infaunal organisms¹⁴¹, may be altered in the short term by storm events, especially in shallow water, and in the long term by altered hydrographic regimes. The amount of change will depend on the nature of the sediment, with fine sediments most easily disturbed and resuspended leading to increased turbidity. Changes in turbidity will affect certain specialist faunas such as phototrophic sponges, which are sensitive to light and turbidity changes²⁸⁸ (see section 11.2.3.4). Octocorals are susceptible to abrasion, dislodgement by storm waves, movement of sand and rubble⁸⁰, and during extreme events communities can be decimated.

11.2.3.7 Rainfall and river flood plumes

Freshwater plumes can be lethal to marine invertebrates, depending on the duration and resulting salinity. Increased monsoon activity on the northern GBR could well result in decreased seasonal salinity. Reduced salinity can be lethal to octocorals and other invertebrates on reef flats emersed at low tide during heavy rain or in freshwater lenses of river plumes⁸⁰. Community changes among colonial ascidian communities along the eastern United States have been with reduced salinity. After heavy flooding, sessile assemblages were dominated by the tolerant *Botryllus schlosseri*, in contrast to the normal mixed communities of *B. schlosseri* and *Botryllouides violaceus* (E Westerman pers comm). Even more concerning is the fact that *B. violaceus* is a recent invader and seems better adapted to changing and extreme environmental conditions than native species or less recent arrivals. The GBR may be similarly vulnerable to sessile invasive species with greater salinity tolerances.

Benthic organisms may also be indirectly affected by rainfall and river flood plumes in terms of food availability. Effects of rainfall on plankton will affect food availability for pelagic larvae, filter feeders and deposit feeders, as well as organisms higher up the food chain. Indeed, freshwater influx can negatively affect plankton abundance. For example, around Pulau Seribu, Indonesia, zooplankton composition showed significant seasonal differences¹⁰, and zooplankton volume decreased during the wet season²¹³.

Increased levels of sedimentation can negatively affect rates of photosynthesis in octocorals²²³ due to light absorption by particles deposited on the colonies or suspended in the water column. In the Caribbean, mass mortality of gorgonians was recorded after large river floods importing high sediment loads⁹⁵ and in some cases the fungus *Aspergillus* was exported from the land to the inshore waters. Mass mortality of *Gorgonia ventalina* and *G. flabellum* has been observed^{253,190}. On the GBR, flood plumes often contain nutrients, top soil and pesticides, which impact negatively on octocorals, making them more susceptible to fungal infections, colonisation by algae, barnacles, bryozoans or anemones. Often high levels of partial mortality occur in colonies⁸⁰. It seems likely that other colonial organisms or sessile invertebrates will be similarly affected.

11.2.4 Adaptive capacity

11.2.4.1 Water temperature

Analyses of the fossil record have revealed broad patterns indicating the adaptive capacities of molluscan groups to broad-scale change. During the Cretaceous-Tertiary extinction event, molluscan deposit feeders in the Southern Hemisphere were the group most resilient to changing environmental conditions, but this depended on life history characteristics and habitat²⁶⁴. Suspension-feeding molluscs, on the other hand, exhibited the highest extinction rate²⁶⁴. Of all molluscan groups, bivalves from genera with large horizontal and vertical ranges had the highest survival rate, while carnivorous gastropods with planktotrophic development showed the highest rate of speciation²⁶⁴. Responses of these taxa to water temperature and currents may be paralleled by GBR species, based on similar feeding mechanisms, developmental mode and phylogeny.

Species can move into colder and deeper water or into cooler waters of higher latitudes (eg the bivalve *Venericardia procera*¹), but this is an option only for species with planktonic larvae or mobile adults, and where suitable habitat is available. Sessile or colonial animals that rely largely on asexual reproduction will be severely hampered. Some species of octocorals, when bleached by increased water temperatures, are able to survive for several months, while colonies shrink to small sizes and undergo fragmentation to produce a large number of new recruits⁸⁰.

Several sponge species that occur on the GBR range further south to the subtropics (eg calcarean *Leucetta chagosensis*²⁹⁷). Recent analyses¹²⁸ have found several major species turnover points along the eastern coast, with one around the Tweed River (border of New South Wales and Queensland) separating the northeast and southeast Australian bioregions. Indeed, it was reported that in the Moreton Bay/Stradbroke Islands region, tongues of warmer tropical and cooler temperate waters overlap with the consequence that the fauna contains a spatially discrete (vertically stratified) mix of temperate (greater than 30 metres depth) and tropical (shallower water) species⁶⁴. However, there is no direct evidence that those tropical sponges can successfully reproduce there, although they may be capable of doing so as water temperatures increase in the future. Similarly, many molluscs occur across both tropical and subtropical regions. Indeed, egg masses of a few species with typically tropical distributions, such as the cowrie, *Cypraea erosa* and the sea slug, *Berthellina citrina*, have been found in temperate waters as far south as Wollongong (Przeslawski pers obs). Numerous tropical crustaceans also regularly range into New South Wales and many are reproductive south of the GBR. Several tropical echinoderms also have a wide distribution, from the northern GBR to as far south as the Solitary Islands in New South Wales²³⁷ (Byrne unpublished data) suggesting that some species will migrate further south.

Colonisation of the southern GBR by ophiuroids will depend on the presence of suitable habitat, and the rubble banks at One Tree Reef and other locations in the southern GBR are likely to provide the habitat required by these species. One species that is likely to expand its range on the GBR in conjunction with warming is the tropical brittle star, *Ophiocoma scolopendrina*. This is probably the most abundant ophiuroid throughout the Indo-Pacific, where it forms dense aggregations in intertidal reef flat, rubble and sand/rubble habitats^{40,193}. It is highly fecund and has a planktotrophic larva with a probable two to three week dispersive phase⁵⁴. *Ophiocoma scolopendrina* seems to be an opportunistic species but, as a specialist of the intertidal, is a heat-tolerant (eurythermal) species¹⁹³.

At present, this brittle star is locally superabundant in shallow water on Lizard Island and elsewhere in the northern GBR, but is only occasionally encountered on the southern GBR (Byrne unpublished data). Although a southward expansion is likely, it is not clear how it may respond to warming of the northern regions of the GBR. *Ophiocoma scolopendrina* is a robust species and may be one of the first indicators of faunal change in the intertidal on the southern GBR.

The broad latitudinal distribution of many invertebrates along the GBR indicates that they can reproduce across a range of temperatures, including those at the northern and southern margins of the GBR. Range extensions of species southward along the GBR and changes in reproductive timing as a phenotypic response are likely to occur in response to climate change^{203,28}. The southern GBR may therefore function as a refuge of biodiversity if reproductive and recruitment failure occurs in a warmer northern GBR.

Species that now inhabit the GBR and breed successfully at their southern limits in subtropical or temperate waters are probably able to extend their range further south with increasing water temperature, subject to appropriate habitat. Such frontier species may be best adapted to temperature changes associated with global climate change. As they already occur in limited numbers in cooler waters, range shifts would probably be relatively rapid, with southern populations increasing and northern populations decreasing. Some invasive species seem to have the adaptive capacity to cope with increasing temperatures. Fields et al.⁸⁶ found that invasive species of *Mytilus* were better adapted than native species to increases in changes in temperature with regards to their physiology.

Southern extension of species will depend on available substrate. Those species associated with coral substrates may be limited in their ability to move southwards, whereas benthic invertebrates occurring on inter-reef areas are less likely to be limited by substrate availability. For many groups such as polychaetes (Hutchings unpublished data), molluscs (W Ponder pers comm) and probably Crustacea (Ahyong unpublished data), a greater diversity occurs in coral rubble and soft sediments than associated with live coral substrates. Therefore, while loss of coral through regular bleaching events would change the community, it might not appreciably impact the overall diversity of these groups. In contrast, many species of soft corals have very specific habitat requirements such as light availability, wave and flow exposure, steepness of the reef slope and sedimentation rates⁸⁰. Suitable substrate for new recruits are generally more limited for soft corals, so their ability to move south will be determined by the availability of hard substrates, which are somewhat lacking south of the current boundaries of the GBR.

11.2.4.2 Sea level rise

Mobile species can migrate landwards if suitable habitats are available, but sedentary species can only migrate through successful larval recruitment to newly established marine habitats (for further comments see chapters 8, 9 and 20).

11.2.4.3 Light spectra

Some tropical marine ecosystems seem to have marginal capacity to cope with turbid conditions, periodic storms and sedimentation that increase light attenuation as confirmed by recent observations^{165,207} and examination of the fossil record²⁴¹. On the GBR, benthic invertebrates with photosymbionts already at their range limits may become locally extinct with increased turbidity

and sedimentation. The severity of the response may depend on the animal's reliance on its photosymbionts. For example, if the animal can obtain sufficient nutrients directly from feeding during periods of turbidity and sedimentation, the lack of light may cause few problems, and increased suspended organic particles may even contribute significantly to nutrition⁸. However, if the animal depends heavily on its photosymbionts for nutrients, periods of turbidity may be fatal.

11.2.4.4 Ocean circulation, ocean acidification, physical disturbance, rainfall and river flood plumes

Some species may benefit from ocean circulation changes through recruitment, providing such changes increase favourable conditions for larvae. For example, populations of the seashell *Strombus luhuanus* on the GBR showed consistently high recruitment for two years following ENSO events, likely due to ocean circulation changes and upwelling of nutrient-rich waters⁴⁶.

In the fossil record there are many examples of dramatic changes in faunal composition following major shifts in circulation, the formation of the circumpolar current²⁴² and the Gulf Stream being two key examples. With these major changes in circulation and associated temperature changes, faunal composition changed completely, suggesting little or no adaptive capacity when changes are massive. However, smaller changes at temperate latitudes during the Pleistocene suggest that some adaptation is possible^{121,153}. Clearly, the rate and magnitude of change will determine whether the fauna can adapt.

If changes are short-term and intermittent, adults may be able to survive periods of limited food supply by absorbing body tissue and stopping or reducing reproduction (eg sea urchins^{38,30}). Some larvae have the ability to delay settlement until a suitable substrate is found (eg crustaceans²⁰⁵ and molluscs^{97,231}, but this comes at the cost of reduced growth or prolonged time in vulnerable larval stages^{42,97,231}.

The capacity of most benthic invertebrates to adapt to increased storm activity is probably limited. One area worthy of further investigation is morphological plasticity - perhaps growth forms of sedentary or colonial species may be able to change. Various coral species exhibit different degrees of arborescence according to habitat and many nephtheid species (octocorals) prevent tear damage during storms by temporarily contracting their colonies⁸⁰.

There is likely to be no short-term capacity for marine invertebrates to adapt to changing rainfall and river flood plumes, given their limited ability to osmoregulate.

The impact of ocean acidification on calcifying marine invertebrates will depend on species' adaptability and there are few experimental data on this. The genetic control of skeleton formation in marine invertebrates is precise and the physiological processes involved are complex. Skeleton formation is similar among the echinoderm classes that diverged over 500 million years ago. This indicates that these and other calcifying benthic invertebrates will have limited capacity to adapt their skeleton forming mechanisms in response to the comparatively rapid changes expected in ocean pH. The decrease in pH of sea water will be greatest in shallow water and so populations of some species living at greater depth may be less affected by ocean acidification.

A multitude of factors contribute to the effect of changes in ocean circulation on marine invertebrate distributions (eg organismal biology and life history, flow fields, coastline topography, habitat and settlement preferences, and the physics of transport) so predictions about outcomes of such circulation changes are difficult. However, some results suggest that simple, common flow fields, which are often observed in association with biogeographic boundaries worldwide, might potentially constrain the geographic range of a species, even when suitable habitat outside that range is abundant. Such boundaries can function as barriers to dispersal and range expansion, with their permeability critically depending on the species' life history and temporal variability in the nearshore flow field⁹⁶.

11.2.5 Vulnerability and thresholds

11.2.5.1 Ocean circulation

Larvae dispersed to unsuitable habitats will die, as will adults unable to feed effectively. Obviously, larvae of species dependent on coral substrate for settlement may be highly vulnerable, especially southern populations due to limited areas of reef south of the GBR^{115,116}. Species colonising inter-reef habitats may have more opportunities to settle outside of the GBR, because of the more 'generalised' habitat. Extensive studies have shown the importance of substrate for marine invertebrate settlement^{51,174,98,104}.

11.2.5.2 Water temperature

Distribution changes in direction and magnitude are largely unknown and difficult to predict for benthic invertebrates. However, inshore communities may be more at risk than those offshore, and species already at their temperature limits are most at risk. These species may be able to move south as frontier species, but this depends on the availability of suitable habitat. The fossil record indicates that migratory response to changing temperature is species-specific^{1,17,264}. For example, as a result of climate change during the late Quaternary, the bivalve *Venericardia procera* migrated northwards in the Atlantic while the gastropod *Tegula atra* became locally extinct¹.

Life-history strategies will likely play an important role in the ability of a species to migrate in response to changes in water temperature. In sponges, life-history strategies vary considerably across different taxa, with exact details frequently unknown¹⁷⁹. External gamete production is often highly synchronous and putatively controlled by diverse exogenous and endogenous events, often shortly before the peak summer temperature is reached⁸⁹. Sponges with brooded larvae, especially in sub-littoral and intertidal species, may release gametes continuously throughout the year, while others release in one or two peaks, usually during the warm season. The duration of the reproductive period may also be controlled by environmental factors such as water temperature, and significant inter-population differences in timing have been observed¹⁷⁹. Another factor that may be important is whether species with short life cycles can adapt better than longer-lived species, especially if temperature increases are rapid. Perhaps some insight could be obtained by examining invasive or 'weed' species that can build up large populations rapidly¹⁷⁸.

Temperature and developmental rates positively correlate in many marine invertebrates¹⁹⁵. Any increase in temperature will likely cause higher growth rates in embryos, larvae and juveniles, although such change would vary according to temperature change, spawning behaviour and species. However,

other abiotic factors may interact with temperature to stunt development^{125,218}, highlighting the need to consider other potential variables associated with global or local change.

In adults, temperature may not always significantly affect growth. In a survey of molluscs at Heron Island, Frank⁸⁸ found that shell growth and temperature were not related within a single population. However, shell growth preceded reproduction in some species⁸⁸, so temperature may indirectly affect adult growth by affecting the timing of reproduction.

Many invertebrates, including echinoderms and polychaetes, are known to participate in mass spawning of corals¹². This annual event is controlled by lunar cues and is potentially fine-tuned by water temperature. Lunar cues are likely to initiate this reproductive event, regardless of sea temperature change. However, too little is known about the influence of temperature to make useful predictions. On the southern GBR, echinoderms also spawn around the time that corals release. Hypotheses explain the evolution of mass spawning among different species. Firstly, there is a relationship between mass spawning and temperature differential. Mass spawning occurs in regions where there is a greater difference in seasonal temperatures. On the GBR, where thermal conditions fluctuate seasonally, this results in species taking advantage of optimal conditions. Mass spawning swamps predators and increases the survivorship potential of each species¹². Ultimately, it is unknown why species on the GBR spawn synchronously, but climate change may nevertheless interfere directly or indirectly with current spawning patterns. Climate change may also affect fecundity and body size, but there are currently limited data available for non-coral benthic marine invertebrates.

Marine intertidal molluscs, such as oysters, are exposed to multiple stressors in estuaries, including varying environmental temperature and levels of trace metals that may interactively affect their physiology. Exacerbation of cadmium effects by elevated temperature suggests that oyster populations subjected to elevated temperature may become more susceptible to trace metal pollution²⁵⁸. This is an important issue given the increasing human population along the Queensland coast and potential consequences for the aquaculture industry.

11.2.5.3 Ocean acidification

Any reductions in densities of coral skeletons will impact on the boring and cryptofaunal communities present within live and dead coral¹³⁸. Similarly, changes to encrusting communities have the potential to modify the suite of benthic invertebrates that are associated with such communities. For many benthic invertebrates the most vulnerable life stage is their pelagic larva. The threshold tolerance for survival in reduced pH conditions are known for few taxa^{162,250} and is an area identified for focused research¹⁵⁹.

11.2.5.4 Other light spectra, sea level rise, physical disturbance, rainfall and river flood plumes

Species with resident zooxanthellae are likely to be most vulnerable, as sea level rise, rainfall and physical disturbance associated with turbidity and sedimentation increase light attenuation and affect rates of photosynthesis in symbionts⁷⁵ (see section 11.2.3.4). Changes in algal distribution and loss of live coral colonies will impact on herbivores and those associated with living coral colonies, such as obligate symbionts (eg hapalogastrid and trapeziid crabs⁴⁵).

The vulnerability of invertebrates to sea level rise will largely be determined by the speed and magnitude of sea level rise. Vertical accretion rates of coral reefs are not predicted to be sufficient to keep up with an estimated sea level rise of 15 mm per year (eg Buddemeier and Smith³²). However, the fossil record shows that some Pacific coral reefs (eg the Huon Peninsula, Papua New Guinea, kept pace with sea level changes during the Younger Dryas Event at the end of the last glacial maximum (approximately 11,000 years before present), when sea level rose by 50 metres over about 5,000 years (a rate of 10 mm per year)⁴⁸. During the same period the growth on the GBR often lagged behind⁶⁷. Evidence from a Triassic reef in the Austrian Alps, however, suggests that the observed three well-defined reef growth stages were not only affected by small-scale sea level fluctuations, but also by storm damage and increased sedimentation input²⁰.

Intertidal and shallow water species are most vulnerable to increased storm activity. Increased river flow and sedimentation will most severely impact sessile or infaunal species that cannot avoid the disturbance. They will be buried, torn from the substrate or washed away. In any case, they are unlikely to be able to reburrow or reattach themselves to the substrate and will most likely perish. The success of settlement or resettlement is inversely correlated with sediment depth, and there is a general trend of shifting community structure observed for sponges based on increasing sedimentation and resuspension^{16,298,44} (see section 11.2.1.4).

Fringing reefs can effectively buffer wave action, but loss of reef framework already weakened by bioerosion, is far more susceptible to breakage during storms, which leads to increased erosion of beaches and coastal structures¹⁴³. Significant differences in bioeroding communities, strongly influenced by water quality, are present both within and between reefs and across the shelf, at least in the northern GBR¹⁹⁹. Coral substrate with boring communities dominated by boring sponges may be more flexible and better able to withstand the shearing forces of storms than communities dominated by other borers.

The timing of fresh water inputs is critical. Larvae may be far more susceptible to surface plumes than adults, so fresh water influxes during reproductive periods may have a greater impact than at other times (Przeslawski²¹⁶ and literature cited therein). This is particularly important for species that die after spawning because it may lead to loss of an entire season's recruitment.

All the above factors will act synergistically, and the impact on benthic invertebrates will vary according to existing natural and anthropogenic stressors (eg ultraviolet radiation, overfishing and terrestrial runoff) and the rates of environmental change.

11.3 Linkages with other ecosystem components

The vertical linkages that exist in lagoon systems on the GBR are detritus driven with tight nutrient cycling. One of the most important sources of detritus is coral mucous. If the linkage between coral and soft-sediment communities is lost with a reduction in productivity, the abundance of benthic species will decrease. In addition, changes in benthic-pelagic coupling may have detrimental effects on both benthic and planktonic invertebrates (eg diurnal migration of crustaceans; McKinnon et al. chapter 6, Kingsford and Welch chapter 18).

Horizontal linkages exist between reefs and soft-sediments, including seagrass beds and mangroves (Waycott et al. chapter 8 and Lovelock and Ellison chapter 9). For example, penaeid prawns support a multi-million dollar fishery off the coast of eastern Queensland. Penaeids are typically trawled from nearshore and inter-reef areas. Larvae of most commercial penaeids in GBR waters require nearshore or estuarine seagrass habitats for settlement and growth to maturity, and consequently are highly susceptible to loss of seagrass. Some species, such as the banana prawn (*Fenneropenaeus merguensis*) and giant tiger prawn (*Penaeus monodon*), favour turbid inshore habitats^{105,106}. In other species, such as the red-spot king prawn (*Melicertus longistylus*), juveniles use the reef flat as a nursery area, and adults occupy the adjacent lagoon and inter-reef carbonate sediments^{72,107}. Juveniles of most species of commercial penaeid, however, 'grow out' in estuaries and nearshore seagrass beds, and migrate to offshore lagoon and inter-reef waters. Similarly, commercial crab species, such as the blue swimming crab (*Portunus pelagicus*) and mud crab (*Scylla serrata*), are tied to seagrass beds as juveniles and move into deeper water as adults, with the latter species migrating offshore. Any factors that reduce the extent or quality of seagrass habitats could negatively impact prawn and crab populations, and the productivity of the fishery. For example, seasonal reductions in salinity and increased turbidity associated with high summer rainfall appear to be a primary determinant of seagrass species distribution^{29,60}. Moreover, increased nutrient loads from terrestrial runoff are known to be detrimental to penaeid larvae^{187,271}. High summer river flows are linked to higher productivity of several fisheries, partly through the stimulating downstream movement of individuals and partly through stimulating growth rates and survivorship through increased primary productivity. High summer flows are important for emigration of juvenile prawns and sub-adults to near- and offshore habitats, and may further stimulate production through increased food availability¹⁷⁰. Despite the complex interactions of changing environmental parameters, changes in rainfall patterns and freshwater input will directly impact seagrass communities (Waycott et al. chapter 8). Obviously, the net impact will depend on the magnitude and direction of changes in environmental parameters.

Benthic invertebrates are an important food source for many animals higher in the food chain such as fish, marine turtles and permanent and migratory birds. Therefore, reduction or loss of these invertebrate communities can have severe effects at higher trophic levels.

11.3.1 Constraints to adaptation

Lagoon and subtidal species may be more vulnerable to changing conditions than intertidal species because they presumably have not evolved the same level of protective functions to dynamic and stressful conditions. For example, interspecific comparisons of turban snails revealed that an intertidal species had more effective heat-shock responses than a subtidal species^{270,269}. However, the degree of generality of this observation is unknown. At least among polychaetes and crustaceans, many intertidal species also occur in shallow subtidal habitats, suggesting no difference in ability to respond to stressful conditions.

11.3.2 Interactions between stressors

The most tangible and visible impact of climate change on the GBR to date has been mass coral bleaching. This undoubtedly has had a major impact on obligate associates of corals and the non-coral benthos (eg lower food availability and habitat loss). Surprisingly, the impact of coral bleaching on these organisms has not yet been monitored on the GBR.

Among benthic invertebrates, interactions between environmental factors may play a particularly important role in assessing climate change impacts. Benthic invertebrates are often sessile (eg sponges and bryozoans), slow moving (eg many echinoderms and gastropods) or infaunal, and are therefore restricted in their ability to escape unfavourable conditions that may amplify the negative effects of stressors associated with climate change.

Many studies examining the impacts of climate change focus on single factors, and these may falsely suggest that increased temperature, current changes, varying precipitation or other stressors associated with climate change will not significantly affect an organism. Whereas a single factor considered in isolation may have a negligible overall effect, the combined impact of multiple factors may be significant. For example, a single-factor study examining the effects of UVR on marine invertebrate development suggested that molluscan embryos of *Siphonaria denticulata* and *Bembicium nanum* were invulnerable to natural intensities of UVR²¹⁸. Subsequent multifactor experiments revealed that these 'invulnerable' embryos are in fact susceptible to the negative effects of UVR when exposed to synchronous stressors, including those associated with climate change such as temperature, salinity and desiccation²¹⁷. Interactions between abiotic and biotic factors may also affect larval settlement and behaviour, directly affecting community composition and structure. Settlement cues for marine invertebrate larvae probably involve multiple factors^{156,282}, including temperature and salinity²⁶⁶, each of which will be modified by global climate change.

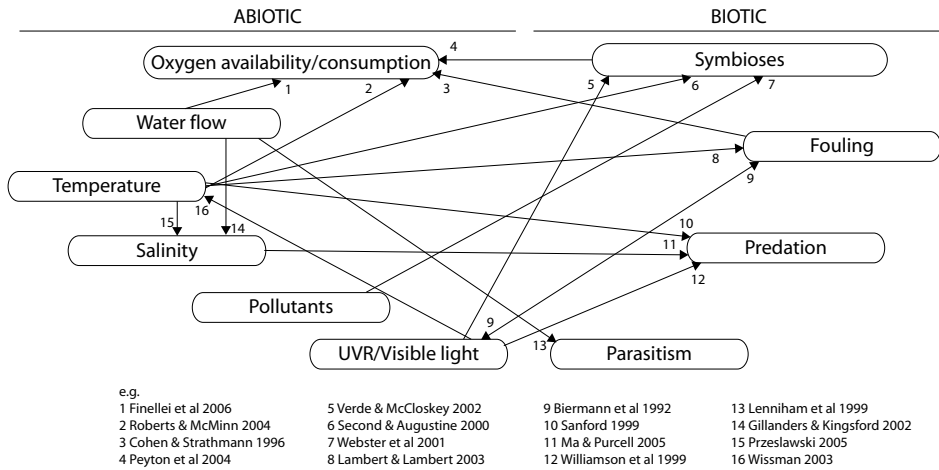
The invasive ability of marine invertebrates should also be considered in a multifactor context²³⁴. Single-factor studies are relatively simple with easily interpreted results, but they may underestimate 'real-world' effects. Such studies are most appropriate as a baseline or platform for further multifactor research. Some data suggest that impacted communities are more susceptible to invasion by introduced species⁵⁹. However, as most introduced species arrive in estuaries and tend to remain there, it is difficult to know if impacted reef environments are susceptible to these invaders.

Multifactor experiments are even more important when the relationships between potential stressors are considered. Climate change will involve multiple abiotic factors such as fresh water input (salinity) and temperature, and these factors will in turn affect other abiotic and biotic stressors such as oxygen availability and parasitism. This forms a complex web of potential interactions (Figure 11.2). To further complicate matters, the interactive effects of many stressors, including those associated with climate change, are complex¹²⁵ and have both acute and chronic effects²⁵⁶. Some stressors may even have different effects on the same species, depending on the history of the assemblage or environment¹³⁵. Thus, to avoid oversimplification, generalisations concerning interactive effects of abiotic and biotic factors should be made cautiously and only when numerous species have been examined. The use of multifactor experiments to study impacts of climate change at appropriate temporal, taxonomic, and spatial scales represents a significant challenge to ecologists but is crucial to provide an ecologically realistic assessment.

11.3.3 Threats to resilience

As stated previously, the response of marine benthic communities to climate change is difficult to assess because of the lack of knowledge about basic distribution and ecology for most species.

Figure 11.2 Interactions of abiotic and biotic variables that can affect benthic invertebrates (adapted from Przeslawski¹⁶). Variables listed do not include events associated with them (eg flooding, runoff and storms), rather only the specific stressors are included^e



Similarly, resilience to these impacts is largely unknown. While the ecosystem may be able to recover from single events, we believe the potential for recovery from multiple stressors or recurrent events expected from climate change would be significantly reduced. Such a situation is being observed with coral communities that have been bleached several times. These reefs do not recover to pre-bleached conditions¹²⁴ before being subjected to another bleaching event, supporting the contention that it is the speed, frequency and magnitude of change that are the major threats.

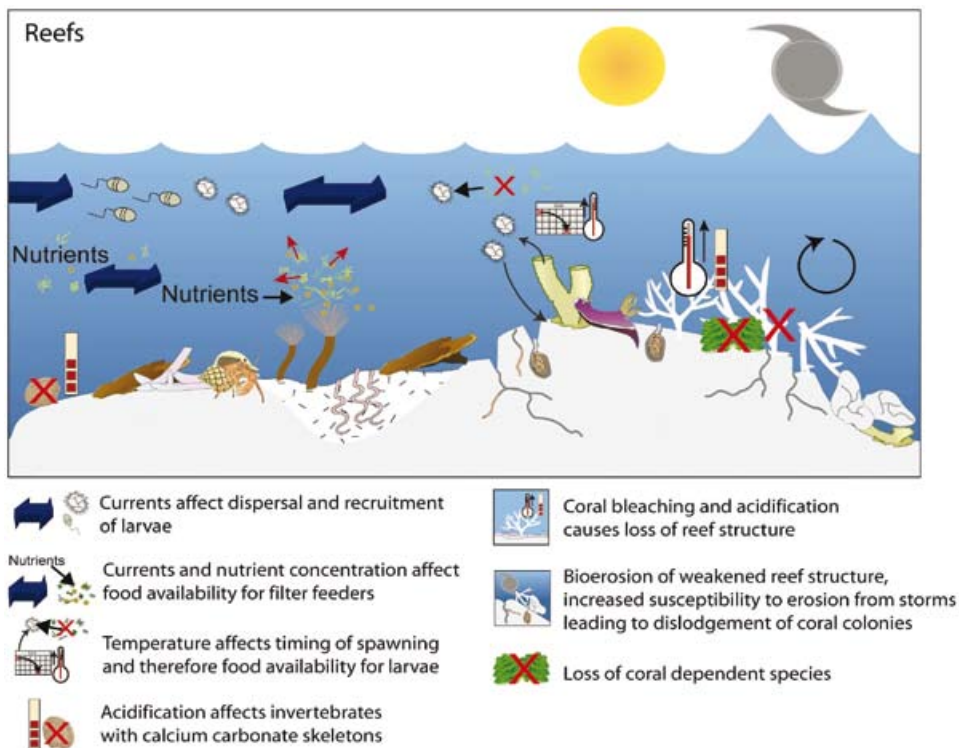
11.4 Summary and recommendations

11.4.1 Major vulnerabilities to climate change

Species that depend on coral reef substrate will have reduced success with loss of coral communities and increased rates of bioerosion, leading to reduction of available reef substrates (Hoegh-Guldberg et al. chapter 10, Fabricius et al. chapter 17) (Figure 11.3). In contrast, faunas associated with soft bottoms, including those in inter-reef/shelf habitats or small coral isolates, will primarily be affected by changes in temperature (Figure 11.4) and may be able to survive either by moving into deeper, cooler water or into higher latitudes. Intertidal communities, including coastal/estuarine communities, will be impacted by physical loss of habitat in some areas as a result of sea level rise and more frequent storm events, but perhaps also with expansion of habitat in other areas (Sheaves et al. chapter 19) (Figure 11.5). Communities will be impacted by increased air and ocean temperatures, as well as changes in rainfall patterns.

e This list is by no means comprehensive, but instead illustrates the relationships between potential stressors. The relationships illustrated are not ubiquitous or exhaustive, rather, each arrow represents a potential relationship that has been identified in at least one study. A single arrow indicates a relationship in which one variable affects the other. A double arrow indicates a relationship in which both variables affect each other.

Figure 11.3 Main climate change drivers that may affect benthic invertebrates living on reefs

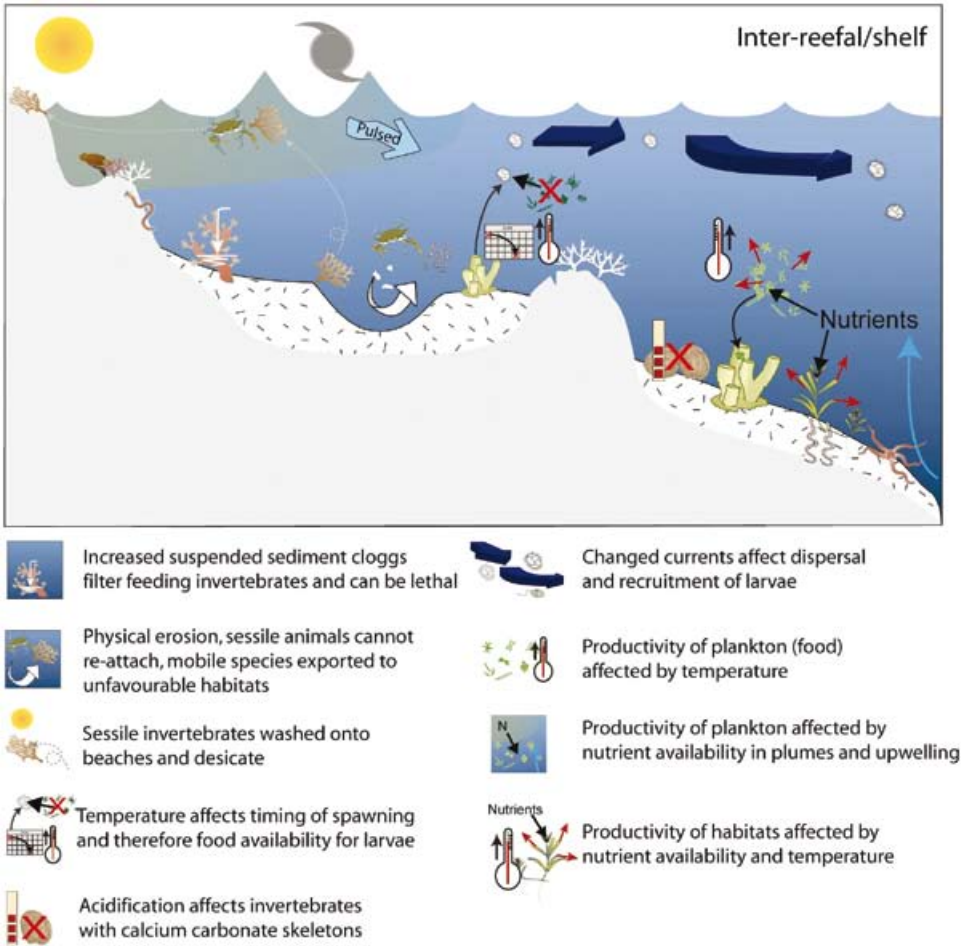


11.4.1.1 Extinctions and change of reef framework

Some populations of invertebrates, particularly those in the northern GBR, may be vulnerable to extinction due to their inability to respond phenotypically to the pace of environmental change. This may be a widespread phenomenon given that the entire Indo–Pacific will be subjected to similar warming as the northern GBR, although populations currently in the cooler part of their ranges may survive. Local extinction risk has been highlighted in terrestrial models with extinction rates between 15 and 37 percent predicted for mid-range climate change scenarios²⁶⁷. A decline in invertebrate community diversity in response to ocean warming has already been documented for intertidal habitats in North America^{240,254}, but similar studies have yet to be conducted on the GBR. Similarly, the studies of Tomanek²⁶⁹ and Sorte and Hofmann²⁶¹ have found that the gastropod *Nucella caniculata* is more stressed at its range edges, supporting the suggestion that many intertidal invertebrates may be at the limit of their ability to adapt, even to a small increase in temperature²⁶⁹. Much remains to be investigated as to the ability of invertebrates to adapt to higher temperatures.

During the Pleistocene era, sea level rise combined with increased water temperature may have contributed to periods of extinction¹⁷. However, Indo–West Pacific coral and mollusc species had a lower rate of extinction than their Caribbean counterparts²⁵⁶, suggesting that this region may be less vulnerable to species extinction than other tropical regions. Furthermore, although coral reef

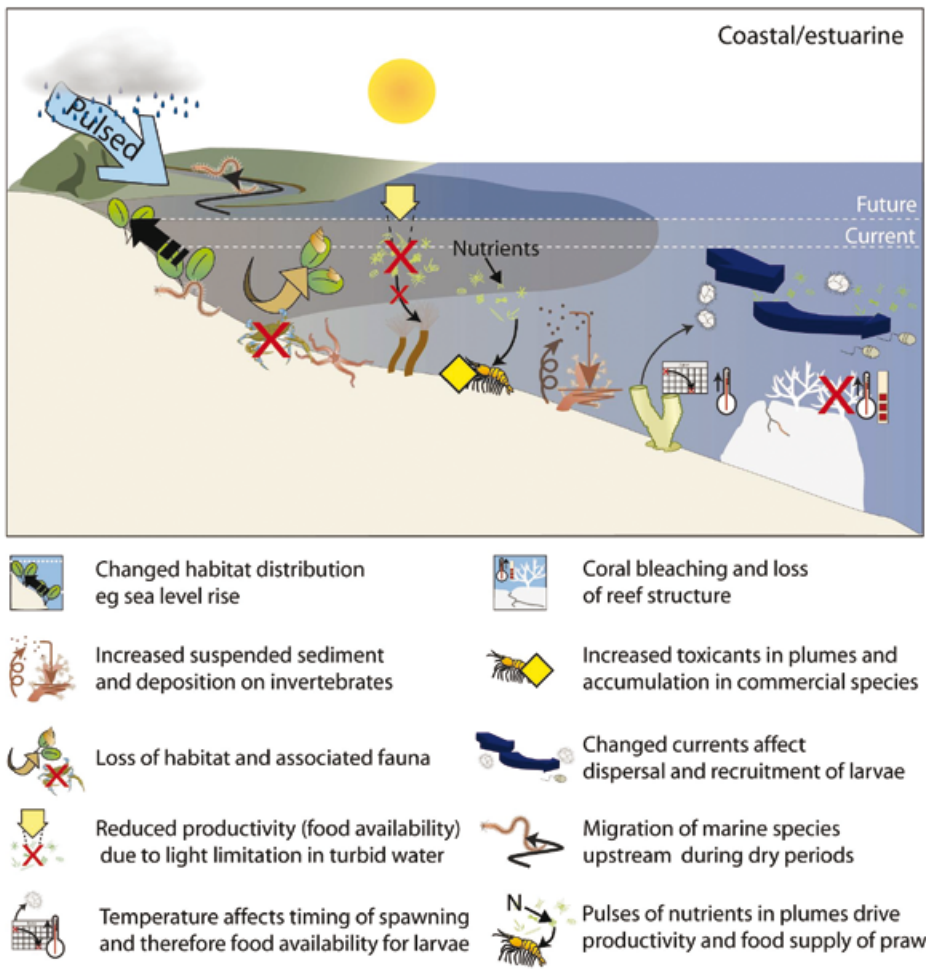
Figure 11.4 Main climate change drivers that may affect benthic invertebrates of inter-reef/shelf habitats



communities in the Pacific changed during these periods of sea level rise, there was little evidence of large-scale or permanent loss of overall diversity²⁵⁶.

Compared to other tropical marine ecosystems in the Indo–West Pacific, there are relatively few narrow-range endemics on the GBR, and the risk of complete extinction may be comparatively low overall. There are exceptions, however, including narrow-range endemic sea stars on the Queensland coast and GBR islands^{62,37}. Partial and local extinctions are a risk, perhaps particularly in the case of coastal species. Hooper and Kennedy¹²⁹ and Hooper and Ekins¹²⁸ report between 50 and 70 percent of sponge species from subtropical and tropical waters, respectively, are known only from single specimens. Thus, significant proportions of genetic diversity are at risk through small-scale regional extinctions driven by climate change.

Figure 11.5 Main climate change drivers that may affect benthic invertebrates living in coastal and estuarine habitats of the GBR



Increased rates of coral death following bleaching and other physiological stresses result in increased rates of bioerosion leading to loss of reef framework²⁰². If scleractinian corals do not readily adapt to rising sea surface temperatures and if frequency of bleaching events increases, increasing proportions of structural elements of the reef that would normally be quickly recolonised (eg coral skeletons) remain barren for longer periods. As a result, it is expected that abundance and density of bioeroding sponges (primarily the families Clionaidae, Spirastrellidae and Alecetonidae) will increase and further weaken the structural framework of the reef²³⁹. With an additional expected increase in tropical cyclone intensity and frequency, complete destruction of large reef areas, especially the more exposed parts, is likely.

Marine benthic invertebrates are not only vulnerable to extinction from overwhelming environmental stressors, but from loss of habitat. Those particularly vulnerable are obligate associates of live corals, including molluscs (both gastropods and some bivalves)²³², hapalocarinid and trapeziid crabs⁴⁵, polychaete worms²⁵⁵ and coral-associated barnacles⁶. Similarly, many sponges are niche specialists on reefs, found only in particular habitats such as in caves, overhangs and coral interstices¹²⁷, such that degradation or destruction of niches will impact on the constituent species. Crinoids are a diverse assemblage of coral reef specialists^{78,39} that depend on live coral reef habitat and are depleted when corals are impacted by crown-of-thorns starfish⁷⁸.

11.4.1.2 Range extensions of keystone species

Range extensions of keystone species can have a disproportionate effect on community structure. A recent example is the range extension of the sea urchin *Centrostephanus rodgersii* into Tasmania, likely due to changes in current flow associated with climate change⁷. In Tasmania this urchin has contributed to a phase shift from a kelp-dominated community to a barren seascape⁷. Another example is the recent invasion of the clam *Potamocorbula amurensis* in San Francisco Bay. This species has greatly contributed to the regional CO₂ source through its respiration and calcification, with associated implications for ocean acidification⁵⁰. With range shifts of keystone species, the GBR may be similarly vulnerable to invasive species, particularly if invasive species are able to recruit earlier than native species²⁶².

The corallivorous crown-of-thorns starfish, *Acanthaster planci*, has caused well-documented and widespread damage to many coral reefs in the Indo-Pacific over the past four decades²³. Crown-of-thorns starfish generally occur in low densities on the GBR, but periodically appear in large numbers. These cycles on the GBR have occurred from 1962 to 1976, 1979 to 1991 and 1993 to the present³¹. The outbreak ends when coral prey is exhausted. Reef recovery following intense predation by the starfish is variable, with some reefs not recovering for 10 to 15 years⁶¹. The starfish, while reasonably common in the southern GBR, does not appear to exhibit the characteristic outbreak cycle in the south that it does in the north, although there was a major outbreak at Elizabeth and Middleton reefs in the mid-1980s¹³⁹. It is likely that sea temperature has a major influence on the timing of spawning and on the larval performance in this species. There is potential that populations of the starfish may become larger in the south, facilitated by increased temperatures associated with climate change. If this temperature rise is accompanied by increased intensity flood plumes and associated nutrients, as is predicted, then plagues are likely to become more common in the southern GBR. There is good evidence that plagues are facilitated by eutrophic terrestrial runoff^{21,31}.

Many invertebrates on the GBR have a wide latitudinal distribution, and it is likely that reproduction varies markedly between the northern and the southern regions, as shown for corals. For example, the echinoderm *Ophiocoma dentata* spawns at the same time as the corals (November to December) on the northern GBR, but in summer and winter on the southern GBR (Byrne unpublished data). The generality of this phenomenon on the GBR is unknown.

11.4.1.3 Community structure

As already mentioned, range extensions of keystone species can affect community structure⁷. Community structure can also be dramatically altered by changes in substrate. Modeling of bleaching events on coral reefs and rates of recovery clearly show that the persistence of hard corals will depend

in part on the factors that constrain excessive algal biomass²⁹⁵. If the proportion of algae cover on the reef increases – as is already occurring on inshore reefs – this will modify the ability of non-corals to recruit to the reef. Relatively few species of molluscs²³² and polychaetes¹³⁸ are associated with live corals as opposed to soft sediments or coral rubble. However, changes from living coral substrate to dead coral or algae would change these communities dramatically³⁰², not only for the molluscs and polychaetes, but also for all other groups that are found predominantly on or in living corals. Following from this scenario, increasing algal proliferation would lead to a higher abundance of grazers (eg echinoids, gastropods and chitons), followed by excessive bioerosion and loss of reef framework and biodiversity²⁰².

11.4.2 Potential management responses

Multi-scale approaches may provide suitable management strategies for benthic invertebrates of the GBR. This approach is advocated by Chabanet et al.⁴⁷ to quantify anthropogenic disturbance at various scales on tropical reefs, but could be modified to quantify effects of various stressors associated with both climate change and direct anthropogenic disturbance. Climate change can be viewed as a series of disturbances, some continuous (eg ocean temperature and acidification) and some stochastic (eg storms and flooding). A multi-scale approach to climate change on the GBR may allow comparison and impact assessment over a range of scales, which is particularly suited to the spatial heterogeneity, diversity of life histories and substrate-specificity of benthic invertebrates.

Building resilience to climate change impacts could be achieved by reducing the impact of other anthropogenic stressors such as eutrophication from land runoff, trawling, recreational fishing and tourism.

Education of the public to engender stewardship and community awareness of benthic invertebrates and their critical role in GBR ecosystem health will be important to the success of protective management strategies.

Marine invertebrate conservation strategies on the GBR should recognise the possibility of locally unique bioactives and intraspecific genetic variation that may be important to the success of species, including widespread species.

11.4.3 Recommendation for future studies

Given the short time available it is imperative that future studies to assess the impacts of climate change are clearly targeted. We suggest that the primary purposes of these studies as related to benthic invertebrates should be to:

- detect change
- implement management strategies
- attempt to stop or reduce predicted impacts.

Targeted surveys should be undertaken for a limited number of invertebrate species, which should be selected to encompass the range of reproductive strategies found in invertebrates, including both sexual and asexual reproduction, brooders and free-spawners, and species with long- and short-lived

larvae. These species should also exhibit a range of distributions along the GBR, from widely distributed Indo–Pacific species, to ones restricted to particular regions of the GBR and narrow range endemics. In addition, targeted species should exhibit a range of life styles and occupy varying habitats both on reefs and in inter-reef areas. Species selected should be taxonomically well known and easy to identify by non-specialists with limited training (a small workshop of invertebrate biologists could develop such a list of target species). The selected taxa should be sampled seasonally to document changes in density, timing of spawning, reproductive success, size and community interactions. In addition, both commercially and non-commercially important species should be targeted. By sampling along the GBR, regional differences should be detected. The surveys must use statistically valid sampling techniques to ensure that the results are robust.

The data from these targeted surveys will highlight the types of species that are most impacted, as well as the regions of the reef where maximum impact is occurring. Combining this data with concurrently measured physical data, it may be possible to identify other factors that are contributing to these highly impacted sites, such as excessive trawling causing increased suspended matter in the water column, high nutrient levels from land runoff, high tourist activity, etc. The impact of these factors can then be modified by management strategies.

To accurately assess the impacts of climate change and implement appropriate conservation management strategies, a measure of stress on GBR organisms is required before they will show visible sub-lethal effects. Biochemical measurements of stress seem the most promising method, including quantification of heat-shock proteins and thermal acclimation, DNA repair rates and antioxidant measurements. Benthic invertebrates are ideal for these studies²⁶⁹. They are relatively easy to collect, monitor and culture in the laboratory; represent a huge range of phyla, habitats and life histories for comparative analyses; and include genera in which similar work has already been conducted in other regions (eg *Nucella*²⁶¹ and *Tegula*²⁶⁹).

The results of these studies will need to be published in recognised scientific journals, but precise summaries in plain English also need to be made available to the general public through the media. Only then is it likely that there will be enough political will to implement actions to either stop or reduce the impacts.

Finally, given the high profile of the GBRMPA, these results and strategies should then be made available worldwide for other managers of tropical marine ecosystems to implement.

References

- 1 Aguirre ML, Sirch Y and Richiano S (2005) Late Quaternary molluscan assemblages from the coastal area of Bahia Bustamante (Patagonia, Argentina): paleoecology and paleoenvironments. *Journal of South American Earth Sciences* 20, 13–32.
- 2 Ahyong ST (2001) Revision of the Australian Stomatopod Crustacea. *Records of the Australian Museum*, Supplement 26, 1–326.
- 3 Ahyong ST (2006) Shallow water Stomatopoda of New Caledonia (0–100 m). In: CE Payri and B Richer de Forges (eds) *Compendium of Marine Species from New Caledonia*. Documents Scientifiques et Techniques 117. pp. 291–293.
- 4 Allen GR and Steene R (1994) *Indo-Pacific Coral Reef Field Guide*. Tropical Reef Research, Singapore.
- 5 Alongi DM (1990) The ecology of tropical soft-bottom benthic ecosystems. *Oceanography Marine Biology Annual Review* 28, 381–496.
- 6 Anderson DT (2003) *Barnacles: Structure, Function, Development and Evolution*. Chapman and Hall, London.
- 7 Andrew NL and Byrne M (2007) *Centrostephanus*. In: J Lawrence (ed) *The Biology and Ecology of Edible Urchins*. Elsevier Science, Amsterdam, pp. 191–204.
- 8 Anthony KRN and Fabricius K (2000) Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. *Journal of Experimental Marine Biology and Ecology* 252, 221–253.
- 9 Anthony KRN, Ridd PV, Orpin AR, Larcombe P and Lough J (2004) Temporal variation of light availability in coastal benthic habitats: effects of clouds, turbidity, and tides. *Limnology and Oceanography* 49, 2201–2211.
- 10 Arinardi OH (1978) Seasonal variations of certain major zooplankton groups around Panggang Island, northwest of Jakarta. *Marine Research in Indonesia* 21, 61–80.
- 11 Augustin D, Richard G and Salvat B (1999) Long-term variation in mollusc assemblages on a coral reef, Moorea, French Polynesia. *Earth and Environmental Science* 18, 293–296.
- 12 Babcock R, Mundy C, Keesing J and Oliver J (1992) Predictable and unpredictable spawning events: *in situ* behavioural data from free-spawning coral reef invertebrates. *Invertebrate Reproduction and Development* 22, 213–228.
- 13 Bak RPM (1990) Patterns of echinoid bioerosion in two Pacific coral reef lagoons. *Marine Ecology Progress Series* 66, 267–272.
- 14 Barry JP, Baxter CH, Sagarin R and Gilman SE (1995) Climate-related long term faunal changes in a California rocky intertidal community. *Science* 267, 672–675.
- 15 Bates WR (2005) Environmental factors affecting reproduction and development in ascidians and other protochordates. *Canadian Journal of Zoology* 83, 51–61.
- 16 Battershill CN and Bergquist PR (1990) The influence of storms on asexual reproduction, recruitment, and survivorship of sponges. In: K Rützler (ed) *New Perspectives in Sponge Biology*. Smithsonian Institution Press, Washington, DC, pp. 397–403.
- 17 Ben AG (2004) Marine Mollusca of oxygen isotope stages of the last 2 million years in New Zealand. Part 1: Revised generic positions and recognition of warm-water and cool-water migrants. *Journal of the Royal Society of New Zealand* 34, 111–265.
- 18 Benzie JAH (1999) Major genetic differences between crown-of-thorns starfish (*Acanthaster planci*) populations from the Indian and Pacific Oceans. *Evolution* 53, 132–145.
- 19 Benzie JAH and Williams ST (1997) Genetic structure of giant clam (*Tridacna maxima*) populations in the West Pacific is not consistent with dispersal by present-day ocean currents. *Evolution* 51, 768–783.
- 20 Bernecker M, Weidlich O and Flügel E (1999) Response of triassic reef coral communities to sea-level fluctuations, storms and sedimentation: evidence from a spectacular outcrop (Adnet, Austria). *Facies* 40, 229–279.
- 21 Birkeland C (1982) Terrestrial run-off as a cause of outbreaks of *Acanthaster planci* (Echinodermata: Asteroidea). *Marine Biology* 69, 175–185.
- 22 Birkeland C (1988) The influence of echinoderms on coral-reef communities. In: M Jangoux and JM Lawrence (eds) *Echinoderm Studies*. Vol 3 AA, Balkema, Rotterdam, pp. 1–79.
- 23 Birkeland C and Lucas JS (1990) *Acanthaster planci* a major management problem of coral reefs. CRC Press, Boca Raton.
- 24 Birtles A and Arnold P (1983) Between the reefs: some patterns of soft substrate epibenthos on the central Great Barrier Reef. In: JT Baker, RM Carter, PW Sammarco and KP Stark (eds) *Inaugural Great Barrier Reef Conference*, James Cook University Press, Townsville, pp. 159–163.
- 25 Birtles A and Arnold P (1988) Distribution of trophic groups of epifaunal echinoderms and molluscs in the soft sediment areas of the central Great Barrier Reef. *Proceedings of the 6th International Coral Reef Symposium* 3, 325–332.

- 26 Borsa P and Benzie JAH (1996) Population genetics of *Trochus niloticus* and *Tectus coeruleus*, topshells with short-lived larvae. *Marine Biology* 125, 531–541.
- 27 Bouchet P, Lozouet P, Maestrati P and Heros V (2002) Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site. *Biological Journal of the Linnean Society* 75, 421–436.
- 28 Bradshaw WE and Holzapfel CM (2006) Evolutionary response to rapid climate change. *Science* 312, 1477–1478.
- 29 Bridges KW, Phillips RC and Young PC (1982) Patterns of some seagrass distributions in the Torres Strait, Queensland. *Australian Journal of Marine and Freshwater Research* 33, 273–283.
- 30 Brockington S and Clarke A (2001) The relative influence of temperature and food on the metabolism of a marine invertebrate. *Journal of Experimental Marine Biology and Ecology* 258, 87–99.
- 31 Brodie J, Fabricius K, De'ath G and Okaji K (2005) Are increased nutrient inputs responsible for more outbreaks of crown-of-thorns starfish? An appraisal of the evidence. In: PA Hutchings and D Haynes (eds) Proceedings of Catchment to Reef: Water Quality Issues in the Great Barrier Reef Region Conference. *Marine Pollution Bulletin* 51, 266–278.
- 32 Buddemeier RW and Smith SV (1988) Coral reef growth in an era of rapidly rising sea level: predictions and suggestions for long-term research. *Coral Reefs* 7, 51–56.
- 33 Buitrago J, Capelo J, Gutierrez J, Rada M, Hernandez R and Grune S (2006) Living macromolluscs from a paleo-reef region on the northeastern Venezuelan continental shelf. *Estuarine Coastal and Shelf Science* 66, 634–642.
- 34 Byrne M (1995) Changes in larval morphology in the evolution of benthic development by *Patiriella exigua* (Asteroidea), a comparison with the larvae of *Patiriella* species with planktonic development. *Biological Bulletin* 188, 293–305.
- 35 Byrne M (2006) Life history evolution in the Asterinidae. *Integrative and Comparative Biology* 46, 243–254.
- 36 Byrne M (In press) Species composition of Australia's tropical bêche-de-mer sea cucumbers (Echinodermata: Holothuroidea) in the *Stichopus* complex. *Biologist* 32.
- 37 Byrne M and Walker SJ (In press) Distribution and reproduction of intertidal *Aquilonastra* and *Cryptasterina* species (Asterinidae) from One Tree Island, Southern Great Barrier Reef. *Bulletin of Marine Science*.
- 38 Byrne M, Andrew NL, Worthington DG and Brett PA (1998) The influence of latitude and habitat on reproduction in the sea urchin *Centrostephanus rodgersii* in New South Wales, Australia. *Marine Biology* 132, 305–318.
- 39 Byrne M, Cisternas P, Hoggett A, O'Hara T and Uthicke S (2004a) Diversity of echinoderms at Raine Island, Great Barrier Reef. In: T Heinzeller and JH Nebelsick (eds) *Echinoderms: München*. Taylor and Francis Group, London, pp. 159–164.
- 40 Byrne M, Smoothery A, Hoggett A and Uthicke S (2004b) Population biology of shallow water ophiuroids from Raine Island and Moulter Cay, Northern Great Barrier Reef. In: T Heinzeller and JH Nebelsick (eds) *Echinoderms: München*. Taylor and Francis Group, London, pp. 165–170.
- 41 Caldeira K and Wickett ME (2003) Anthropogenic carbon and ocean pH. *Nature* 425, 365.
- 42 Cancino JM and Gallardo JS (2004) Effects of delaying settlement on the life expectancy of the bryozoan *Bugula flabellata* (Bryozoa: Gymnolaemata). *Revista Chilena de Historia Natural* 77, 227–234.
- 43 Cappel M and Kelley R (2001) Connectivity in the Great Barrier Reef World Heritage Area – an overview of pathways and processes. In: E Wolanski (ed) *Oceanographic Processes of Coral Reefs: Physical and Biological Links in the Great Barrier Reef*. CRC Press, Boca Raton, pp 161–188.
- 44 Carballo JL (2006) Effect of natural sedimentation on the structure of tropical rocky sponge assemblages. *Écoscience* 13, 119–130.
- 45 Castro P, Ng PKL and Ahyong ST (2004) Phylogeny and systematics of the Trapeziidae Miers, 1886 (Crustacea: Brachyura), with the description of a new family. *Zootaxa* 643, 1–70.
- 46 Catterall CP, Poiner IR and O'Brien CJ (2001) Long-term population dynamics of a coral reef gastropod and responses to disturbance. *Austral Ecology* 26, 604–617.
- 47 Chabanet P, Adjeroud M, Andrefouet S, Bozec YM, Ferraris J, Garcia-Charton JA and Schrimm M (2005) Human-induced physical disturbances and their indicators on coral reef habitats: a multi-scale approach. *Aquatic Living Resources* 18, 215–230.
- 48 Chappell J and Polach H (1991) Post-glacial sea-level rise from a coral record at Huon Peninsula, Papua New Guinea. *Nature* 349, 147–149.
- 49 Chapple JP, Smerdon GR, Berry RJ and Hawkins AJS (1998) Seasonal changes in stress-70 protein levels reflect thermal tolerance in the marine bivalve *Mytilus edulis* L. *Journal of Experimental Marine Biology and Ecology* 229, 53–68.

- 50 Chauvaud L, Thompson JK, Cloern JE and Thouzeau G. (2003) Clams as CO₂ generators: The *Potamocorbula amurensis* example in San Francisco Bay. *Limnology and Oceanography* 56, 391–407.
- 51 Chia FS and Rice ME (eds) (1978) *Settlement and Metamorphosis of Marine Invertebrate Larvae*. Elsevier, New York.
- 52 Church JA and White NJ (2006) A 20th century acceleration in global sealevel rise. *Geophysical Research Letters* 33, LO1602, doi: 10.1029/2005GL024862
- 53 Cimino G, Fontana A and Gavagnin M (1999) Marine opisthobranch molluscs: Chemistry and ecology in sacoglossans and dorids. *Current Organic Chemistry* 3, 327–372.
- 54 Cisternas P, Selvakumaraswamy P and Byrne M (2004) Evolution of development and the Ophiuroidea – revisited. In: T Heinzeller and JH Nebelsick (eds) *Echinoderms: München*. Taylor and Francis Group, London, pp. 521–526.
- 55 Clark AM (1976) Echinoderms of coral reefs. In: OA Jones and R Endean (eds) *Biology and Geology of Coral Reefs VIII. Biology 2*. Academic, New York 10, pp. 105–204.
- 56 Clark AM and Rowe FWE (1971) *Monograph of Shallow-water Indo-West Pacific Echinoderms*. Trustees of the British Museum (Natural History), London.
- 57 Clark HL (1946) The echinoderm fauna of Australia: its composition and its origin. *Papers Department of Marine Biology Carnegie Institution Washington* 566, 1–567.
- 58 Clark TH and Morton B (1999) Relative roles of bioerosion and typhoon-induced disturbance on the dynamics of a high latitude scleractinian coral community. *Journal of the Marine Biological Association of U.K.* 79, 803–820.
- 59 Cohen AN and Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. *Science* 379, 555–559.
- 60 Coles RG, Lee Long WJ, Squire BA, Squire LC and Bibby JM (1987) Distribution of seagrasses and associated juvenile commercial penaeid prawns in north-eastern Queensland waters. *Australian Journal of Marine and Freshwater Research* 38, 103–119.
- 61 Colgan MW (1987) Coral reef recovery on Guam (Micronesia) after catastrophic predation by *Acanthaster planci*. *Ecology* 68, 1592–1605.
- 62 Dartnall AJ, Byrne M, Collins J and Hart MW (2003) A new viviparous species of asterinid (Echinodermata, Asteroidea, Asterinidae) and a new genus to accommodate the species of pan-tropical exiguoid sea stars. *Zootaxa* 359, 1–14.
- 63 Davie PJF (2002) Crustacea: Malacostraca: Phyllocarida, Hoplocarida, Eucarida (Part 1). In: A Wells and WWK Houston (eds) *Zoological catalogue of Australia*. Vol. 19.3A. CSIRO Publishing, Collingwood.
- 64 Davie PJ and Hooper JNA (1994) The Queensland Museum and marine studies in Moreton Bay. In: JG Greenwood and NJ Hall (eds) *The Future of Marine Science in Moreton Bay*. University of Queensland Press, St. Lucia, pp. 105–112.
- 65 Davies PJ (1992) Origins of the Great Barrier Reef. *Search* 23, 193–196.
- 66 Davies PJ (1994) Evolution of the Great Barrier Reef. *Australian Geologist* 92, 21–24.
- 67 Davies PJ and Hopley D (1983) Growth fabrics and growth rates of Holocene reefs in the Great Barrier Reef. *Journal of Australian Geologists and Geophysicists* 8, 237–251.
- 68 Day J, Fernandes L, Lewis A, De'ath G, Slegers S, Barnett B, Kerrigan B, Breen D, Innes J, Oliver J, Ward T and Lowe D (2002) The Representative Areas Program for protecting biodiversity in the Great Barrier Reef World Heritage Area. In: K Moosa, S Soemodihardjo, A Nontji, A Soegiarto, K Romimohtarto, Sukarno, and Suharsono (eds) *Proceedings of the Ninth International Coral Reef Symposium*. pp. 687–696.
- 69 DeFelice RC and Parrish JD (2001) Physical processes dominate in shaping invertebrate assemblages in reef-associated sediments of an exposed Hawaiian coast. *Marine Ecology Progress Series* 215, 121–131.
- 70 DEH (Department of Environment and Heritage) (2004) *Assessment of the Queensland East Coast Tropical Rock Lobster Fishery*. Australian Government, Department of the Environment and Heritage, pp. 1–20.
- 71 Devaney DM (1974) Shallow-water asterozoans of Southeastern Polynesia. *Micronesica* 10, 105–204.
- 72 Dredge MCL (1990) Movement, growth and natural mortality rate of the red spot king prawn, *Penaeus longistylus* Kubo, from the Great Barrier Reef Lagoon. *Australian Journal of Marine and Freshwater Research* 41, 399–410.
- 73 Drew EA and Abel KM (1988) Studies on *Halimeda*. I. The distribution and species composition of the *Halimeda* meadows through the Great Barrier Reef Province. *Coral Reefs* 6, 195–205.
- 74 Duran S and Rützler K (2006) Ecological speciation in a Caribbean marine sponge. *Molecular Phylogenetics and Evolution* 40, 292–297.
- 75 Elfving T, Blidberg E, Sison M and Tedengren M (2003) A comparison between sites of growth, physiological performance and stress responses in transplanted *Tridacna gigas*. *Aquaculture* 219, 815–828.
- 76 Endean R (1957) The biogeography of Queensland's shallow water echinoderm fauna (excluding Crinoidea) with a re-arrangement of the faunistic provinces of tropical Australia. *Australian Journal of Marine and Freshwater Research* 8, 233–273.

- 77 Erdmann MV (1997) *The ecology, distribution and bioindicator potential of Indonesian coral reef stomatopod communities*. PhD Thesis, University of California, Berkeley.
- 78 Fabricius K (1994) Spatial patterns in shallow-water crinoid communities in the central Great Great Barrier Reef. *Australian Journal of Marine and Freshwater Research* 45, 1225–1236.
- 79 Fabricius K (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin* 50, 125–146.
- 80 Fabricius K and Alderslade P (2001) *Soft corals and sea fans. A comprehensive guide to the tropical shallow-water genera of the Central–West pacific, the Indian Ocean and the Red Sea*. Australian Institute of Marine Science Townsville.
- 81 Fabricius K and De'ath G (2000) *Soft Coral Atlas of the Great Barrier Reef*. Australian Institute of Marine Science, <http://www.aims.gov.au/pages/research/soft-corals/soft-corals00.html>.
- 82 Fabricius K, De'ath G, McCook L, Turak E and Williams DM (2005) Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. *Bulletin of Marine Science* 51, 384–398.
- 83 Fahey SJ and Garson MJ (2002) Geographic variation of natural products of tropical nudibranch *Asteronotus cespitosus*. *Journal of Chemical Ecology* 28, 1773–1785.
- 84 Faulkner J (2002) Marine natural products. *Natural Products Reports* 19, 1–48.
- 85 Feely R, Sabine CL, Lee K, Berelson W, Kleyvas J, Fabry VJ and Millero FJ (2004) Impact of anthropogenic CO₂ on the CaCO₃ systems in the oceans. *Science* 305: 362.
- 86 Fields PA, Rudomin EL and Somero GN (2006) Temperature sensitivities of cytosolic malate dehydrogenases from native and invasive species of marine mussels (genus *Mytilis*): sequences-function linkages and correlations with biogeographic distribution. *Journal of Experimental Biology* 209, 656–667.
- 87 Fitzhenry TM and Podolsky BE (2003) Consequences of site selection, temperature stress and its effects on reproductive success in *Chthamalus fragilis*. Annual Meeting of the Society for Integrative and Comparative Biology 2004, New Orleans LA, USA. *Integrative and Comparative Biology* 43, 963.
- 88 Frank PW (1969) Growth rates and longevity of some gastropod mollusks on the coral reef at Heron Island. *Oecologia* 2, 232–250.
- 89 Fromont J (1994) Reproductive development and timing of tropical sponges (Order Haplosclerida) from the Great Barrier Reef, Australia. *Coral Reefs* 13, 127–133.
- 90 Fromont J and Bergquist PR (1994) Reproductive biology of three sponge species of the genus *Xestospongia* (Porifera: Demospongiae: Petrosida) from the Great Barrier Reef. *Coral Reefs* 13, 119–126.
- 91 Fromont J and Garson M (1999) Sponge bleaching on the West and East coasts of Australia. *Coral Reefs* 18, 340.
- 92 Frouin P and Hutchings PA (2001) Macrobenthic communities in a tropical lagoon (Tahiti, French Polynesia, Central Pacific). *Coral Reefs* 19, 277–285.
- 93 Fujisawa H (1989) Differences in temperature dependence of early development of sea urchins with different growing seasons. *Biological Bulletin* 176, 96–102.
- 94 Garcia A, Jones BG, Chenhall BE and Murray-Wallace CV (2002) The charophyte *Lamprothamnium succinctum* as an environmental indicator: a Holocene example from Tom Thumbs Lagoon, eastern Australia. *Alcheringa* 26, 507–518.
- 95 Garzón-Ferreira J and Zea S (1992) A mass mortality of *Gorgonia ventalina* (Cnidaria: Gorgoniidae) in the Santa Marta area, Caribbean coast of Columbia. *Bulletin of Marine Science* 50, 522–526.
- 96 Gaylord B and Gaines SD (2000) Temperature or Transport? Range Limits in Marine Species Mediated Solely by Flow. *The American Naturalist* 155, 769–789.
- 97 Gebauer P, Paschke K, and Anger K (2003) Delayed metamorphosis in Decapod crustaceans: evidence and consequences. *Revista Chilena de Historia Natural* 76, 169–175.
- 98 Giangrande A (1997) Polychaete reproductive patterns, life cycles and life histories: an overview. *Oceanography and Marine Biology: An Annual review* 35, 323–386.
- 99 Gibbs PE, Clark AM and Clark CM (1979) Echinoderms from the northern region of the Great Barrier Reef, Australia. *Bulletin British Museum Natural History (Zoology)* 30, 103–144.
- 100 Gordon D and Bock P (In press) Bryozoans. In: PA Hutchings, MJ Kingsford and O Hoegh-Guldberg (eds) *The Great Barrier Reef; Biology, environment, and management*. CSIRO Publishing, Collingwood.
- 101 Gosliner TM and Draheim R (1996) Indo-Pacific opisthobranch gastropod biogeography: how do we know what we don't know? *American Malacological Bulletin* 12, 37–43.
- 102 Gosliner TM, Behrens DW and Williams GC (1996) *Coral reef animals of the Indo-Pacific*. Sea Challengers: Monterey.
- 103 Grassle JF (1973) Variety in Coral Reef Communities. In: OA Jones and R Endean (eds) *The Biology and Geology of Coral Reefs*. Volume 11, Biology 1. Academic Press. New York and London, pp. 247–270.

- 104 Green KM, Russell BD, Clark RJ, Jones MK, Garson MJ and Skilleter GA (2002) A sponge allelochemical induces ascidian settlement but inhibits metamorphosis. *Marine Biology* 140, 355–363.
- 105 Grey DL, Dall W and Baker A (1983) *A Guide to the Australian Penaeid Prawns*. Department of Primary Production of the Northern Territory, Darwin, pp. 1–140.
- 106 Gribble NA (2002) Tiger Prawns In: LE Williams (ed) *Queensland's fisheries resources: current condition and recent trends 1988-2000*. Department of Primary Industries Queensland, Brisbane, pp. 47–50.
- 107 Gribble NA and Dredge MCL (2002) Northern King Prawns In: LE Williams (ed) *Queensland's fisheries resources: current condition and recent trends 1988-2000*. Department of Primary Industries Queensland, Brisbane, pp. 39–41.
- 108 Grosberg RK (1988) Life history variation within a population of the colonial ascidian *Botryllus schlosseri*: The genetic and environmental control of seasonal variation. *Evolution* 42, 900–920.
- 109 Guille AL, Laboute P and Menou J-L (1986) Guide des étoiles de mer, oursins et autres échinodermes du lagon de Nouvelle-Calédonie. ORSTOM, Paris.
- 110 Hammond LS, Birtles RA and Reichelt RE (1985) Holothuroid assemblages on coral reefs across the central section of the Great Barrier Reef. *Proceedings of the Fifth International Coral Reef Congress 2*, 285–290.
- 111 Hamner WM, Jones MS, Carleton JH, Hauri IR and Williams DMcB (1988) Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. *Bulletin of Marine Science* 42, 459–479.
- 112 Harriott VJ (1980) The ecology of the holothurian fauna of Heron Reef and Moreton Bay. MSc Thesis, University of Queensland, St. Lucia.
- 113 Harriott VJ (1982) Sexual and asexual reproduction of *Holothuria atra* Jaeger at Heron Island reef Great Barrier Reef. *Australian Museum Memoir* 16, 53–66.
- 114 Harriott VJ (1996) Heron Island reef flat: 15 years of change. *The Great Barrier Reef. Science, Use and Management. Volume 2*, 145–149.
- 115 Harriott VJ and Banks SA (2002) Latitudinal variation in coral communities in eastern Australia: a qualitative biophysical model of factors regulating coral reefs. *Coral Reefs* 21, 83–94.
- 116 Harriott VJ, Banks SA, Mau RL, Richardson D and Roberts LG (1999) Ecological and conservation significance of the subtidal coral reef communities of northern New South Wales, Australia. *Marine and Freshwater Research* 50, 299–306.
- 117 Hartmann DL, Wallace JM, Limpasuvan V, Thompson DJW and Wolton JR (2000) Can ozone depletion and climate change interact to produce rapid climate change? *Proceedings of the National Academy of Science* 9, 1412–1417.
- 118 Hay GC, Richardson AJ, and Robinson C (2005) Climate change and marine plankton. *Trends in Ecology and Evolution* 20, 338–344.
- 119 Hayward BW, Grenfell HR, Nicholson K, Parker R, Wilmhurst J, Horrocks M, Swales A and Sabaa AT (2004) Foraminiferal record of human impact on intertidal estuarine environments in New Zealand's largest city. *Marine micropaleontology* 53, 37–66.
- 120 Henkel TP and Pawlik JR (2005) Habitat use by sponge-dwelling brittlestars. *Marine Biology* 146, 301–313.
- 121 Hetherington R and Reid RGB (2003) Malacological insights into the marine ecology and changing climate of the late Pleistocene-early Holocene Queen Charlotte Islands archipelago, western Canada, and implications for early peoples. *Canadian Journal of Zoology* 81, 626–661.
- 122 Hill M and Wilcox T (1998) Unusual mode of symbiont repopulation after bleaching in *Anthosigmella varians*: acquisition of different Zooxanthellae strains. *Symbiosis* 25, 279–289.
- 123 Hiscock K, Southward A, Tittley I and Hawkins S (2004) Effects of changing temperature on benthic marine life in Britain and Ireland. *Aquatic Conservation: Marine and Freshwater Ecosystems* 14, 333–362.
- 124 Hoegh-Guldberg O (2005) Low coral cover in a high-CO₂ world. *Journal of Geophysical Research* 110, C09S06, doi:10.1029/2004JC002528.
- 125 Hoffman JR, Hansen LJ and Klinger T (2003) Interactions between UV radiation and temperature limit inferences from single-factor experiments. *Journal of Phycology* 39, 268–272.
- 126 Hooper J (1998) Sponge biodiversity, distribution and biogeography. In: C. Levi (ed) *Sponges of the New Caledonian lagoon*. Editions de l'Orstom, Collection Faune et Flore Tropicales, Paris, pp. 65-73.
- 127 Hooper JNA (1994) Coral reef sponges of the Sahul Shelf - a case for habitat preservation. *Memoirs of the Queensland Museum* 36, 93–106.
- 128 Hooper JNA and Ekins M (2005) *Collation and validation of museum collection databases related to the distribution of marine sponges in northern Australia*. Report to the National Oceans Office, Australia. <http://www.oceans.gov.au/NMB.jsp>
- 129 Hooper JNA and Kennedy JA (2002) Small-scale patterns of sponge biodiversity (Porifera) on Sunshine Coast reefs, eastern Australia. *Invertebrate Systematics* 16, 637–653.

- 130 Hooper JNA and Lévi C (1994) Biogeography of Indo-West Pacific sponges: Microcionidae, Raspailiidae, Axinellidae. In: RWM Soest, TMG Kempen and J-C Braekman (eds) *Sponges in Time and Space*. Balkema, Rotterdam, pp. 191–212.
- 131 Hooper JNA, Kennedy JA, List-Armitage SE, Cook SD and Quinn R (1999) Biodiversity, species composition and distribution of marine sponges in northeast Australia. *Memoirs of the Queensland Museum* 44, 263–274.
- 132 Hooper JNA, Kennedy JA and Quinn RJ (2002) Biodiversity 'hotspots', patterns of richness and endemism, and taxonomic affinities of tropical Australian sponges (Porifera). *Biodiversity and Conservation* 11, 851–885.
- 133 Hopley D, Parnell KE and Isdale PJ (1989) The Great Barrier Reef Marine Park: dimensions and regional patterns. *Australian Geographical Studies* 27, 47–66.
- 134 Hopley D, Smithers SG and Parnell KE (2007). *The Geomorphology of the Great Barrier Reef : Development, Diversity and Change*. Cambridge University Press.
- 135 Hughes TP and Connell JH (1999) Multiple stressors on coral reefs: A long-term perspective. *Limnology and Oceanography* 44, 932–940.
- 136 Hughes TP, Baird AH, Dinsdale EA, Moltischniowskyj NA, Pratchett MS, Tanner JE, Willis BL (1990) Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* 397, 59–63.
- 137 Hutchings PA (1974) A preliminary report on the density and distribution of invertebrates living in coral reefs. *Proceedings of the Second International Coral Reef Symposium* 2, 285–296.
- 138 Hutchings PA (1986) Biological Destruction of Coral Reefs—A review. *Coral Reefs* 4, 239–252.
- 139 Hutchings PA (ed) (1988) A biological survey of Middleton and Elizabeth Reefs. Report prepared for Australian National Parks and Wildlife. Canberra.
- 140 Hutchings PA (1990) A review of the effects of trawling on macro benthic epifaunal communities. *Australian Journal of Marine and Freshwater Research* 41, 111–120.
- 141 Hutchings PA (1998) Biodiversity and functioning of polychaetes in benthic sediments. *Biodiversity and Conservation* 7, 1133–1145 .
- 142 Hutchings PA and Glasby CJ (1991) Phylogenetic Implications of the Biogeography of Australian Terebellidae. *Ophelia Supplement* 5, 565–572.
- 143 Hutchings PA and Salvat B (2000) French Polynesia In: C Sheppard (ed) *Seas at the Millennium: An Environmental Evaluation Volume II*, Elsevier, pp.813–826.
- 144 Hutchings PA, Kingsford MJ and Hoegh-Guldberg O (eds) (In press) *The Great Barrier Reef Biology, environment, and management* CSIRO Publishing, Collingwood.
- 145 Irie T and Iwasa Y (2005) Optimal growth pattern of defensive organs: The diversity of shell growth among mollusks. *American Naturalist* 165, 238–249.
- 146 Jackson JBC and Johnson KG (2000) Life in the last few million years. *Paleobiology* 26, 221–235.
- 147 Jackson JBC and Sheldon PR (1994) Constancy and change of life in the sea. *Philosophical Society of London B Biological Sciences* 344, 55–60.
- 148 Johannesson K (1988) The paradox of Rockall: why is a brooding gastropod (*Littorina saxatilis*) more widespread than one having a planktonic larval dispersal stage. *Marine Biology* 99, 507–513.
- 149 Johnson C (ed) (1992) Crown-of-thorns starfish on the Great Barrier Reef: reproduction, recruitment and hydrodynamics. *Australian Journal of Marine and Freshwater Research* 43,1–146.
- 150 Johnson LG and Babcock RC (1994) Temperature and the larval ecology of the crown-of-thorns starfish, *Acanthaster planci*. *Biological Bulletin* 187, 304–308.
- 151 Johnstone RW, Koop K and Larkum AWD (1990) Physical aspects of coral reef lagoon sediments in relation to detritus processing and primary production. *Marine Ecology Progress Series* 66, 273–283.
- 152 Kamimura S and Tsuchiya M (2004) The effect of feeding behavior of the gastropods *Batillaria zonalis* and *Cerithiopsisilla cingulata* on their ambient environment. *Marine Ecology Progress Series* 144, 705–712.
- 153 Kawahata H and Awaya Y (eds) (2006) *Global Climate Change and Response of Carbon cycle in the Equatorial Pacific and Indian Oceans and Adjacent Landmasses*, Elsevier Oceanography Series Vol. 73, Elsevier, Amsterdam.
- 154 Keable SJ (1995) Structure of marine invertebrate scavenging guild of a tropical reef ecosystem: field studies at Lizard Island, Queensland, Australia. *Journal of Natural History* 29, 27–45.
- 155 Kensley BF (1983) The role of isopod crustaceans in the reef crest community at Carrie Bow Cay, Belize. *Marine Ecology* 5, 29–44.
- 156 Kingsford MJ, Leis JM, Shanks A, Lindeman KC, Morgan SG and Pineda J (2002) Sensory environments, larval abilities and local self-recruitment. *Bulletin of Marine Science* 70, 309–340.

- 157 Kleypas JA, McManus JW and Menez LAB (1999) Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* 284, 118–120.
- 158 Kleypas JA, Buddemeier RW, Eakin CM, Gattuso J-P, Guinotte J, Hoegh-Guldberg O, Iglesias-Prieto T, Jokiel PL, Langdon C, Skirving W and Strong AE (2005) Comment on “Coral reef calcification and climate change: The effect of ocean warming” *Geophysical Research Letters* 32: L08601, doi:10.1029/2004GL022329.
- 159 Kleypas JA, Feely RA, Fabry VJ, Langdon C, Sabine CL and Robbins LL (2006) *Impacts of ocean acidification on coral reefs and other marine calcifiers: A guide for future research*, report of a workshop held 18–20 April 2005, sponsored by the National Science Foundation, National Oceanographic and Atmospheric Administration and the US Geological Survey, St. Petersburg, Florida.
- 160 Klumpp DW and Lucas JS (1994) Nutritional ecology of the giant clams *Tridacna tevoroa* and *T. derasa* from Tonga: influence of light on filter-feeding and photosynthesis. *Marine Ecology Progress Series* 107, 147–156.
- 161 Kohn AJ and Levettin PJ (1976) Effect of habitat complexity on population density and species richness in tropical intertidal predatory gastropod assemblages. *Oecologia* 25, 199–210.
- 162 Kurihara H and Shirayama Y (2004) Effects of increased atmospheric CO₂ on sea urchin early development. *Marine Ecology Progress Series* 274, 161–169.
- 163 Lambert G (2005) Ecology and natural history of the protochordates. *Canadian Journal of Zoology* 83, 34–50.
- 164 Larcombe P, Carter RM, Dye J, Gagan MK and Johnson DP (1995) New evidence for episodic post-glacial sea-level rise, central Great Barrier Reef, Australia. *Marine Geology* 127, 1–44.
- 165 Larcombe P, Costen A and Woolfe KJ (2001) The hydrodynamic and sedimentary setting of nearshore coral reefs, central Great Barrier Reef shelf, Australia: Paluma Shoals, a case study. *Sedimentology* 48, 811–835.
- 166 Laurent V, Planes S and Salvat B (2002) High variability of genetic pattern in giant clam (*Tridacna maxima*) populations within French Polynesia. *Biological Journal of the Linnean Society* 77, 221–231.
- 167 Lee J, Byrne M and Uthicke (In press) Asexual and sexual reproduction in the aspidochirotid sea cucumber *Holothuria difficilis* at One Tree Island, Great Barrier Reef. In: L Harris (ed) *International Echinoderms Conference, New Hampshire, AA Balkema, Rotterdam*.
- 168 Leys SP and Degnan BM (2001) Cytological Basis of Photoresponsive Behavior in a Sponge Larva. *Biological Bulletin* 201, 323–338.
- 169 Loch I and Rudman WB (1992) Molluscs. In: R Longmore (ed) *Reef Biology: a survey of Elizabeth and Middleton Reefs, South Pacific*. Australian National Parks and Wildlife Service, Canberra, 3, 69–88.
- 170 Loneragan NR and Bunn SE (1999) River flows and estuarine ecosystems: implications for coastal fisheries from a review and a case study of the Logan River, southeast Queensland. *Australian Journal of Ecology* 24, 431–440.
- 171 Lucas PH, Webb T, Valentine PS and Marsh H (1997) *The Outstanding Universal Value of the Great Barrier Reef World Heritage Area*. Great Barrier Reef Marine Park Authority, Townsville, Qld.
- 172 Lüter C, Wörheide G and Reitner J (2003) A new thecideid genus and species (Brachiopoda, Recent) from submarine caves of Osprey Reef (Queensland Plateau, Coral Sea, Australia). *Journal of Natural History* 37, 1423–1432.
- 173 McClanahan TR (1992) Epibenthic gastropods of the Middle Florida Keys: the role of habitat and environmental stress on assemblage composition. *Journal of Experimental Marine Biology and Ecology* 160, 169–190.
- 174 McEdward LR (ed) (1995) *Ecology of Marine Invertebrate Larvae*. CRC Press, Boca Raton.
- 175 McManus JW and Menez LAB (1999) Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* 284, 118–120.
- 176 McNeil BI, Matear RJ and Barnes D (2004) Coral reef calcification and climate change: The effect of ocean warming. *Geophysical Research Letters* 31: L22309, doi:10.1029/2004GL021541.
- 177 MacDonald IA and Perry CT (2003) Biological degradation of coral framework in a turbid lagoon environment, Discovery Bay, north Jamaica. *Coral Reefs* 22, 523–535.
- 178 MacDougall AS and Turkington R (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86, 42–55.
- 179 Maldonado M (2006) The ecology of sponge larvae. *Canadian Journal of Zoology* 84, 175–194.
- 180 Matear RJ and McNeil BI (2006) Comment on “Preindustrial to modern interdecadal variability in coral reef pH”. *Science* 314, 595b.
- 181 Mather P (In press) Ascidiaceans. In: PA Hutchings, MJ Kingsford and O Hoegh-Guldberg (eds) *The Great Barrier Reef: Biology, environment, and management*. CSIRO Publishing, Collingwood.
- 182 Metaxas A and Young CM (1998) Behaviour of echinoid larvae around sharp haloclines: effects of salinity gradient and dietary conditioning. *Marine Biology* 131, 443–459.

- 183 Meyer CP, Geller JB and Paulay G (2005) Fine scale endemism on coral reefs: archipelagic differentiation in turbinid gastropods. *Evolution* 59, 113–125.
- 184 Michaelidis B, Ouzounis C, Palaras A and Portner HO (2005) Effects of long-term moderate hypercapnia on acid-base balance and growth rate in marine mussels *Mytilus galloprovincialis*. *Marine Ecology Progress Series* 293, 109–118.
- 185 Moran PJ (1986) The *Acanthaster* phenomenon. *Oceanography and Marine Biology: Annual Review* 24, 379–480.
- 186 Morton B (1983) Coral associated bivalves of the Indo-Pacific. In: KM Wilbur and WD Russell-Hunter (eds) *The Mollusca* Vol. 6 Ecology. Academic Press, New York, pp. 139–224.
- 187 Muir P, Sutton D and Owens L (1991) Nitrate toxicity in *Penaeus monodon* protozoa. *Marine Ecology* 108, 67–71.
- 188 Munro MHG, Blunt JW, Dumdei EJ, Hickford SJH, Lill RE and Li S (1999) The discovery and development of marine compounds with pharmaceutical potential. *Journal of Biotechnology* 70, 15–25.
- 189 Murphy RC and Kremer JN (1992) Benthic community metabolism and the role of deposit-feeding callianassid shrimp. *Journal of Marine Research* 50, 321–340.
- 190 Nagelkerken I, Buchan K, Smith GW, Bonair K, Bush P, Garzón-Ferreira J, Botero L, Gayle P, Heberer C, Petrovic C, Pors L and Yoshioka P (1997) Widespread disease in Caribbean sea fans. 1. Spreading and general characteristics. *Proceedings of the 8th International Coral Reef Symposium* 1, 679–682.
- 191 Newman L and Cannon L (2005) *Fabulous Flatworms: a guide to marine polyclads*. CD ROM, Australian Biological Resources Study/CSIRO Publishing, Collingwood.
- 192 Nicholls N, Landsea C and Gill J (1998) Recent trends in Australian region tropical cyclone activity. *Meteorology and Atmospheric Physics* 65, 197–205.
- 193 Oak T and Scheibling RE (2006) Tidal activity pattern and feeding behaviour of the ophiuroid *Ophiocoma scolopendrina* on a Kenyan reef flat. *Coral Reefs* 25, 213–222.
- 194 Oglesby LC (1978) Salt and water balance. In: PJ Mill (ed) *Physiology of Annelids*. Academic Press, London, pp 555–658.
- 195 O'Connor ML, Brune JF, Gaines SD, Halpern BS, Lester SE, Kinlan BP and Weiss JM (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences* 104, 1266–1271.
- 196 O'Hara TD, Byrne M and Cisternas PA (2004) The *Ophiocoma erinaceus* complex: another case of cryptic speciation in echinoderms. In: T Heinzeller and JH Nebelsick (eds) *Echinoderms: München*. Taylor and Francis Group, London, pp. 537–542.
- 197 O'Loughlin PM and Rowe FWE (2006) A systematic revision of the asterinid genus *Aquilonastra* O'Loughlin, 2004 (Echinodermata: Asteroidea). *Memoirs of Museum Victoria* 63, 257–267.
- 198 Orr JC, Fabry VJ, Aumont O, Bopp L, Doney SC, Feely RE, Gnanadesikan A, Gruber N, Ishida A, Joos F, Key RM, Lindsay K, Maier-Reimer E, Matear R, Monfray P, Mouchet A, Najjar RG, Plattner GK, Rodgers KB, Sabine CL, Sarmiento JL, Schlitzer R, Slater RD, Totterdell IJ, Weirig MF, Yamanaka Y and Yool A (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437, 681–686.
- 199 Osorno A, Peyrot-Clausade M and Hutchings PA (2005) Patterns and rates of erosion in dead *Porites* across the Great Barrier Reef, Australia after 2 and 4 years of exposure. *Coral Reefs* 24, 292–303.
- 200 Palmer AR (1994) Temperature sensitivity, rate of development, and time to maturity: geographic variation in laboratory-reared *Nucella* and a cross-phyletic overview. In: WH Wilson Jr, SA Stricker and GL Shinn (eds) *Reproduction and development of marine invertebrates*. Johns Hopkins University Press, Baltimore, pp. 177–194.
- 201 Pandolfi JA (1999) Response of Pleistocene Coral Reefs to Environmental Change Over Long Temporal Scales. *American Zoologist* 39, 113–130.
- 202 Pari N, Peyrot-Clausade M and Hutchings PA (2002) Bioerosion of experimental substrates on high islands and atoll lagoons (French Polynesia) during 5 years of exposure. *Journal Experimental Marine Biology and Ecology* 276, 109–127.
- 203 Parmesan C and Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 42, 37–42.
- 204 Pawlik JR, Kernan MR, Molinski TF, Harper MK and Faulkner DJ (1988) Defensive chemicals and the Spanish dancer nudibranch *Hexabranche sanguineus* and its egg ribbons macrolides derived from a sponge diet. *Journal of Experimental Marine Biology and Ecology* 119, 99–110.
- 205 Pechenik JA and Eyster LS (1989) Influence of delayed metamorphosis on the growth and metabolism of young *Crepidula fornicata* (Gastropoda) juveniles. *Biological Bulletin* 176, 14–24.
- 206 Pelejero C, Calvo E, McCulloch MT, Marshal JF, Gagan MK, Lough JM and Opdyke BN (2005) Preindustrial to modern interdecadal variability in coral reef pH. *Science* 309, 2204–2207.
- 207 Perry CT (2004) Structure and development of detrital reef deposits in turbid nearshore environments, Inhaca Island, Mozambique. *Marine Geology* 214, 143–161.

- 208 Peyrot-Clausade M, Hutchings PA and Richard G (1992) Successional patterns of macroborers in massive *Porites* at different stages of degradation on the barrier reef, Tiahura, Moorea, French Polynesia. *Coral Reefs* 11, 161–166.
- 209 Pillay KK and Nair NB (1971) The annual reproductive cycles of *Uca annulipes*, *Portunus pelagicus* and *Metapenaeus affinis* (Decapoda: Crustacea) from the south-west coast of India. *Marine Biology* 11, 152–166.
- 210 Ponder WF and Grayson JE (1998) *The Australian Marine Molluscs considered to be potentially vulnerable to the shell trade*. <http://www.deh.gov.au/biodiversity/trade-use/wild-harvest/pubs/pondrpt1.pdf>.
- 211 Ponder WF, Hutchings PA and Chapman R (2002) Overview of the Conservation of Australia's marine invertebrates. A report for Environment Australia, Canberra http://www.amonline.net.au/invertebrates/marine_overview/index.html.
- 212 Potter IC, Chrystal PJ and Loneragan NR (1983) The biology of the blue manna crab *Portunus pelagicus* in an Australian estuary. *Marine Biology* 78, 75–85.
- 213 Praseno DP and Arinardi OH (1974) Plankton volumes and their distribution in "perairan Pulau-Pulau Seribu" during the west and east monsoons 1971. *Oseanologi di Indonesia* 2, 27–40 (in Indonesian).
- 214 Preston NP and Doherty PJ (1990) Cross-shelf patterns in the community structure of coral-dwelling Crustacea in the central region of the Great Barrier Reef. I. Agile shrimps. *Marine Ecology Progress Series* 66, 47–61.
- 215 Preston NP and Doherty PJ (1994) Cross-shelf patterns in the community structure of coral-dwelling Crustacea in the central region of the Great Barrier Reef. II. Cryptofauna. *Marine Ecology Progress Series* 104, 27–38.
- 216 Przeslawski R (2004) A review of the effects of environmental stress on embryonic development within intertidal gastropod egg masses. *Molluscan Research* 24, 43–63.
- 217 Przeslawski R (2005) Combined effects of solar radiation and desiccation on the mortality and development of encapsulated embryos of rocky shore gastropods. *Marine Ecology Progress Series* 298, 169–177.
- 218 Przeslawski R, Davis AR and Benkendorff K (2005) Synergies, climate change and the development of rocky shore invertebrates. *Global Change Biology* 11, 515–522.
- 219 Przeslawski R and Davis AR (In press) Does spawning behavior minimize exposure to environmental stressors for encapsulated gastropod embryos on rocky shores? *Marine Biology*.
- 220 Ramafofia C, Byrne M and Battaglene S (2003) Reproduction of the commercial sea cucumber *Holothuria scabra* in Solomon Islands. *Marine Biology* 142, 281–288.
- 221 Reaka-Kudla M, Feingold JS and Glynn W (1996) Experimental studies of rapid bioerosion of coral reefs in the Galapagos Islands. *Coral Reefs* 15, 101–107.
- 222 Rees SA, Opdyke BN, Wilson PA, Fifield LK and Vladimir L (2006) Holocene evolution of the granite based Lizard Island and MacGillivray Reef systems, Northern Great Barrier Reef. *Coral Reefs* 25, 555–565.
- 223 Reigel B and Branch GM (1995) Effects of sedimentation on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. *Journal of Experimental Marine Biology and Ecology* 186, 259–275.
- 224 Ribes M, Coma R, Atkinson MJ and Kinzie RA III (2005) Sponges and ascidians control removal of particulate organic nitrogen from coral reef water. *Limnology and Oceanography* 50, 1480–1489.
- 225 Richer de Forges B and Moosa MK (1992) Distribution of stomatopods (Crustacea) in the lagoons of New Caledonia and Chesterfield Atoll. *Raffles Bulletin of Zoology* 40, 149–162.
- 226 Richter C and Wunsch M (1999) Cavity-dwelling suspension feeders in coral reefs - A new link in reef trophodynamics. *Marine Ecology Progress Series* 188, 105–116.
- 227 Richter C, Wunsch M, Rasheed M, Kotter I and Badran MI (2001) Endoscopic exploration of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges. *Nature* 413, 726–730.
- 228 Risk MJ, Sammarco PW and Edinger EN (1995) Bioerosion in *Acropora* across the continental shelf of the Great Barrier Reef. *Coral Reefs* 14, 79–86.
- 229 Roberts DE and Davis AR (1996) Patterns in sponge (Porifera) assemblages on temperate coastal reefs off Sydney. *Australian Marine and Freshwater Research* 47, 897–906.
- 230 Roberts DE, Davis AR and Cummins SP (2006) Experimental manipulation of shade, silt, nutrients and salinity on the temperate reef sponge *Cymbastela concentrica*. *Marine Ecology Progress Series* 307, 143–154.
- 231 Roberts RD and Lapworth C (2001) Effect of delayed metamorphosis on larval competence, and post-larval survival and growth, in the abalone *Haliotis iris* Gmelin. *Journal of Experimental Marine Biology and Ecology* 258, 1–13
- 232 Robertson R (1970) Review of the predators and parasites of stony corals, with special reference to symbiotic prosobranch gastropods. *Pacific Science* 24, 43–54.
- 233 Roemmich D and McGowan J (1995) Climatic warming and decline of zooplankton in the Californian current. *Science* 267, 1324–1326.

- 234 Romanuk TN and Kolasa J (2005) Resource limitation, biodiversity, and competitive effects interact to determine the invasibility of rock pool microcosms. *Biological Invasions* 7, 711–722.
- 235 Rowe FWE (1985) Preliminary analysis of distribution patterns of Australia's non-endemic, tropical echinoderms. In: BF Keegan and BDS O'Connor (eds) *Proceedings of the Fifth International Echinoderms Conference*. Balkema, Rotterdam, pp. 91–98.
- 236 Rowe FWE and Doty JE (1977) The shallow-water holothurians of Guam. *Micronesica* 13, 217–250.
- 237 Rowe FEW and Gates J (1995) *Echinodermata. Zoological Catalogue of Australia* vol 33. CSIRO Publishing, Collingwood.
- 238 Royal Society (2005) Ocean acidification due to increasing atmospheric carbon dioxide 30 Jun 2005 <http://www.royalsoc.ac.uk/document.asp?latest=1&id=3249>.
- 239 Rützler K (2002) Impact of crustose clonid sponges on Caribbean reef corals. *ACTA Geologica Hispanica* 37, 61–72.
- 240 Sagarin RD, Barry JP, Gilman SE and Baxter CH (1999) Climate related change in an intertidal community over short and long time scales. *Ecological Monographs* 69, 465–490.
- 241 Sanders D and Baron-Szabo RC (2005) Scleractinian assemblages under sediment input: their characteristics and relation to the nutrient input concept. *Paleogeography, Paleoclimatology and Paleoecology* 216, 139–181.
- 242 Scher H and Martin E (2006) Timing and climatic consequences of the opening of Drake Passage. *Science* 312, 428–430.
- 243 Schiel DR, Steinbeck JR and Foster MS (2004) Ten years of induced ocean warming cause comprehensive changes in benthic communities. *Ecology* 859, 1833–1839.
- 244 Schindler DW, Curtis PJ, Bayley SE, Parker BR, Beaty KG and Stainton MP (1997) Climate-induced changes in the dissolved organic carbon budgets of boreal lakes. *Biogeochemistry* 36, 9–28.
- 245 Schnadt C, Dameris M, Ponater M, Hein R, Grewe V and Steil B (2004) Interaction of atmospheric chemistry and climate and its impact on stratospheric ozone. *Climate Dynamics* 18, 501–517.
- 246 Shanks AL, Grantham BA and Carr MH (2003a) Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications* 13, S159–S169.
- 247 Shanks AL, McCulloch A and Miller J (2003b) Topographically generated fronts, very nearshore oceanography and the distribution of larval invertebrates and holoplankters. *Journal of Plankton Research* 25, 1251–1277.
- 248 Sheppard C, Dixon DJ, Gourlay MJ, Sheppard A and Payet R (2005) Coral mortality increases wave energy reaching shores protected by reef flats: examples from the Seychelles. *Estuarine Coastal and Shelf Science* 64, 223–234.
- 249 Shick JM and Dunlap WC (2002) Mycosporine-like amino acids and related gadusols: Biosynthesis, accumulation, and UV-protective functions in aquatic organisms. *Annual Review of Physiology* 64, 223–262.
- 250 Shirayama Y and Thornton H (2005) Effect of increased atmospheric CO₂ on shallow water marine benthos. *Journal Geophysical Research* 110, C09S08, doi: 10.1029/2004JC002618.
- 251 Skilleter GA and Underwood AJ (1993) Intra- and inter-specific competition for food in infaunal coral reef gastropods. *Journal of Experimental Marine Biology and Ecology* 173, 29–55.
- 252 Sloan NA, Clark AM and Taylor JD (1979) The echinoderms of Aldabra and their habitats. *Bulletin of the British Museum of Natural History Zoology* 37, 81–128.
- 253 Smith G, Ives LD, Nagelkerken IA and Ritchie KB (1996) Caribbean sea fan mortalities. *Nature* 383, 487.
- 254 Smith JR, Fong P and Ambrose RF (2006) Dramatic declines in mussel bed community diversity: response to climate change? *Ecology* 87, 1153–1161.
- 255 Smith R (1985) *Photoreceptors of serpulid polychaetes*. PhD Thesis. James Cook University of North Queensland, Townsville.
- 256 Smith SV and Buddemeier RW (1992) Global change and coral reef ecosystems. *Annual Review of Ecology and Systematics* 23, 89–118.
- 257 Snelgrove PVR (1998) The biodiversity of macrofaunal organisms in marine sediments. *Biodiversity and Conservation* 7, 1123–1132.
- 258 Sokolova IM (2004) Cadmium effects on mitochondrial function are enhanced by elevated temperatures in a marine poikilotherm, *Crassostrea virginica* Gmelin (Bivalvia : Ostreidae). *Journal of Experimental Biology* 207, 2639–2648
- 259 Sokolova IM and Pörtner H (2001) Temperature effects on key metabolic enzymes in *Littorina saxatilis* and *L. obtusata* from different latitudes and shore levels. *Marine Biology* 139, 113–126.
- 260 Somers IF (1987) Sediment type as a factor in the distribution of the commercial penaeid prawn species of the western Gulf of Carpentaria. *Australian Journal of Marine and Freshwater Research* 38, 133–149.

- 261 Sorte CJB and Hofmann GE (2004) Changes in latitudes, changes in aptitudes: *Nucella canaliculata* (Mollusca : Gastropoda) is more stressed at its range edge. *Marine Ecology Progress Series* 274, 263–268.
- 262 Stachowicz JJ, Terwin JR, Whitlatch RB and Osman RW (2002) Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. *Proceedings of the National Academy of Science* 99, 15497–15500.
- 263 Staples DJ and Vance DJ (1986) Emigration of juvenile banana prawns, *Penaeus merguianus*, from a mangrove estuary and recruitment to offshore areas in the wet-dry tropics of the Gulf of Carpentaria, Australia. *Marine Ecology Progress Series* 27, 239–252.
- 264 Stilwell JD (2003) Patterns of biodiversity and faunal rebound following the K-T boundary extinction event in Austral Palaeocene molluscan faunas. *Paleogeography, Paleoclimatology, and Paleoecology* 195, 319–356.
- 265 Sturman A and Tapper N (1996) *The Weather and Climate of Australia and New Zealand*. Oxford University Press.
- 266 Thiyagarajan V, Harder T and Qian P-Y (2003) Combined effects of temperature and salinity on larval development and attachment of the subtidal barnacle *Balanus trigonus* Darwin. *Journal of Experimental Marine Biology and Ecology* 287, 223–236.
- 267 Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, de Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Townsend Peterson A, Phillips OL and Williams SE. (2004) Extinction risk from climate change. *Nature* 427, 145–148.
- 268 Thompson TE (1958) The influence of temperature on spawning in *Aldaria proxima* (A. and H.) (Gastropoda: Nudibranchia). *Oikos* 9, 246–252.
- 269 Tomanek L (2005) Two-dimensional gel analysis of the heat-shock response in marine snails (genus *Tegula*): interspecific variation in protein expression and acclimation ability. *Journal of Experimental Biology* 208, 3133–3143.
- 270 Tomanek L and Somero GN (2000) Time course and magnitude of synthesis of heat-shock proteins in congeneric marine snails (Genus *Tegula*) from different tidal heights. *Physiological and Biochemical Zoology* 73, 249–256.
- 271 Tsai S-J and Chen J-C (2002) Acute toxicity of nitrate on *Penaeus monodon* juveniles at different salinity levels. *Aquaculture* 213, 163–170.
- 272 Tsubokura T, Goshima S and Nakao S (1997) Seasonal horizontal and vertical distribution patterns of the supralittoral amphipod *Trinorchestia trinitatis* in relation to environmental variables. *Journal of Crustacean Biology* 17, 674–686.
- 273 Usher KM, Sutton DC, Toze S, Kuo J and Fromont J (2004) Biogeography and phylogeny of *Chondrilla* species (Demospongiae) in Australia. *Marine Ecology Progress Series* 270, 117–127.
- 274 Uthicke S (1999) Sediment bioturbation and impact of feeding activity of *Holothuria* (Halodeima) *atra* and *Stichopus chloronotus*, two sediment feeding holothurians, at Lizard Island, Great Barrier Reef. *Bulletin of Marine Science* 64, 129–141.
- 275 Uthicke S (2001a) Nutrient regeneration by abundant coral reef holothurians. *Journal Experimental Marine Biology and Ecology* 265, 153–170.
- 276 Uthicke S (2001b) Interactions between sediment-feeders and microalgae on coral reefs: Grazing losses versus production enhancement. *Marine Ecology Progress Series* 210, 125–138.
- 277 Uthicke S, O'Hara TD and Byrne M (2004) Species composition and molecular phylogeny of the Indo-Pacific teatfish (Echinodermata: Holothuroidea) *bêche-de-mer* fishery. *Marine and Freshwater Research* 55, 1–12.
- 278 Verde EA and McCloskey LR (2002) A comparative analysis of the photobiology of zooxanthellae and zoochlorellae symbiotic with the temperate clonal anemone *Anthopleura elegantissima* (Brandt) - II. Effect of light intensity. *Marine Biology* 141, 225–239.
- 279 Vermeji GJ (1987) The dispersal barrier in the tropical Pacific: Implications for molluscan speciation and extinction. *Evolution* 41, 1046–1058.
- 280 Veron JEN and Stafford-Smith M (2000) *Coral reefs of the World*. Australian Institute of Marine Science, Townsville.
- 281 Vicente VP (1990) Response of sponges with autotrophic endosymbionts during the coral-bleaching episode in Puerto Rico. *Coral Reefs* 8, 199–202.
- 282 Walters LJ, Miron G and Bourget E (1999) Endoscopic observations of invertebrate larval substratum exploration and settlement. *Marine Ecology Progress Series* 182, 95–108.
- 283 Warwick RM and Turk SM (2005) Predicting climate change, effects on marine biodiversity: comparison of recent and fossil molluscan death assemblages. *Journal of the Marine Biological Association of the United Kingdom* 303, 167–175.
- 284 Wassenberg TJ and Hill BJ (1990) Partitioning of material discarded from prawn trawlers in Moreton Bay. *Australian Journal of Marine and Freshwater Research* 41, 27–36.
- 285 Weis A, Dunning M and Gaffney P (2004) *Ecological assessment of Queensland's marine specimen shell collection fishery*. A Report Prepared for Queensland Government Department of Heritage and Environment, Canberra.

- 286 Wesseling I, Uychiaoco AJ, Alino PM, Aurin T and Vermaat JE (1999) Damage and recovery of four Philippine corals from short-term sediment burial. *Marine Ecology Progress Series* 176, 11–15.
- 287 Wieters EA, Kaplan DM, Navarrete SA, Sotomayor A, Largier J, Nielsen KJ and Veliz F (2003) Alongshore and temporal variability in chlorophyll a concentration in Chilean nearshore waters. *Marine Ecology Progress Series* 249, 93–105.
- 288 Wilkinson CR and Cheshire AC (1989) Patterns in the distribution of sponge populations across the central Great Barrier Reef. *Coral Reefs* 8, 27–134.
- 289 Williams D McB, Dixon P and English S (1988) Cross-shelf distribution of copepods and fish larvae across the central Great Barrier Reef. *Marine Biology* 99, 577–589.
- 290 Williams LE (2002) Queensland's fisheries resources: current condition and recent trends 1988–2000. Department of Primary Industries Queensland, Brisbane, pp. 1–24.
- 291 Williams LE and Dredge MCL (2002) Trawl fisheries in Queensland. In: LE Williams (ed) *Queensland's fisheries resources: current condition and recent trends 1988–2000*. Department of Primary Industries Queensland, Brisbane, pp. 16–21.
- 292 Williams ST and Benzie JAH (1996) Genetic uniformity of widely separated populations of the coral reef starfish *Linckia laevigata* from the West Pacific and East Indian Ocean, revealed by allozyme electrophoresis. *Marine Biology* 126, 99–108.
- 293 Williams ST, Jara J, Gomez E and Knowlton N (2002) The marine Indo-West Pacific break: contrasting the resolving power of mitochondrial and nuclear genes. *Integrative and Comparative Biology* 42, 941–952.
- 294 Wilson WH Jr. (1986) Detachment of egg masses of a polychaete: environmental risks of benthic protective development. *Ecology* 67, 810–813.
- 295 Wooldridge S, Done T, Berkelmans R, Jones R and Marshall P (2005) Precursors for resilience in coral communities in a warming climate: a belief network approach. *Marine Ecology Progress Series* 295, 157–169.
- 296 Wörheide GB, Degnan M, Hooper JNA and Reitner J (2002a) Phylogeography and taxonomy of the Indo-Pacific reef cave dwelling coralline demosponge *Astrosclera willeyana* – new data from nuclear internal transcribed spacer sequences. In: KM Moosa, S Soemodihardjo, A Soegiarto, K Romimohtarto, A Nontji, Soekarno and Suharsono (eds) *Proceedings of the 9th International Coral Reef Symposium*, pp. 339–346.
- 297 Wörheide G, Hooper JNA and Degnan BM (2002b) Phylogeography of western Pacific *Leucetta 'chagosensis'* (Porifera: Calcarea) from ribosomal DNA sequences: implications for population history and conservation of the Great Barrier Reef World Heritage Area (Australia). *Molecular Ecology* 11, 1753–1768.
- 298 Wulff JL (1995) Effects of a hurricane on survival and orientation of large erect coral reef sponges. *Coral Reefs* 14, 55–61.
- 299 Yamano H, Miyajima T and Koike I (2000) Importance of foraminifera for the formation and maintenance of a coral sand cay: Green Island, Australia. *Coral Reefs* 19, 51–58.
- 300 Yentsch CS, Yentsch CM, Cullen JJ, Lapointe B, Phinney DA and Yentsch SW (2002) Sunlight and water transparency: cornerstones in coral research. *Journal of Experimental Marine Biology and Ecology* 268, 171–183.
- 301 Young B and Challen S (2004) *Ecological assessment of Queensland's East Coast Trochus Fishery*. A report to the Australian Government Department of Environment and Heritage from the Queensland Government Department of Primary Industries and Fisheries, Brisbane.
- 302 Zuschin M, Hohenegger J and Steininger F (2001) Molluscan assemblages on coral reefs and associated hard substrata in the northern Red Sea. *Coral Reefs* 20, 107–116.