Part II: Species and species groups

Chapter 11

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

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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 represented[257], 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 aquaculture[211]. 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 GBR[73]. Sediments range from fine mud at the mouth of rivers to calcareous sands[151,251] (Figure 11.1) that largely determine species composition[141]. 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*
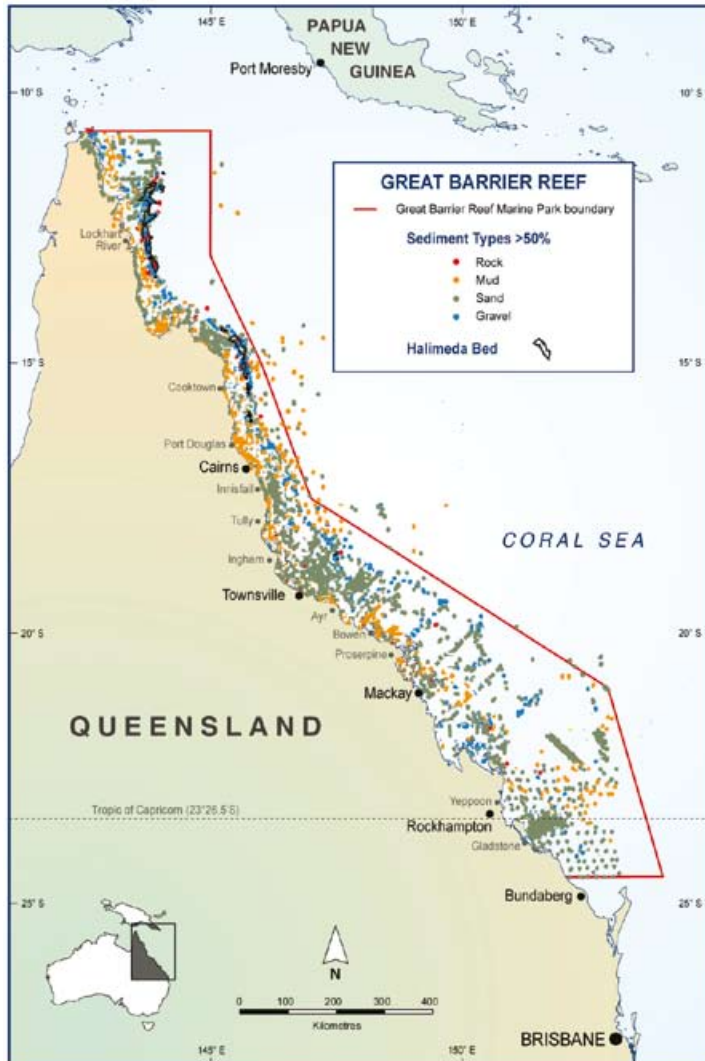
Prepared using data from the GBRMPA and Australian Institute of Marine Science.

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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 variation[280], 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]. Hutchings[137] 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 bioeroded[202].

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 distributions[129], sometimes with as little as 15 percent similarity in species composition between geographically adjacent reef sites[126]. 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 territories[130]. Those differences might be the result of glacial sea-level changes that have impacted current systems and the resulting connectivity among regions.

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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 Plateau[132]. 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 fauna[130], Sahul Shelf fauna[127]) 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 GBR[37]. 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 level[18]. 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 Pacific[277]. The taxonomy of several other commercially important sea cucumber species and species complexes on the GBR is currently being investigated[36].

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 areas[39]. 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 diversity[27]. 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 undescribed[101]. Intensive surveys in New Caledonia revealed 2738 species of molluscs, an order of magnitude larger than previously reported for this region[27] 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 diversity[27]. 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 species[27], 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 beds[173], 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 areas[33]. 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 substrates[302]. 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 surfaces[161]. 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 gradients[69].

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 endemic[169]. Despite their low richness, endemic species may be the most abundant on some reefs[169]. 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 Queensland[171].

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 *Astralium*[183]. Similarly, the giant clam *Tridacna maxima* shows significant genetic variation between archipelagos in French Polynesia, but even with its high dispersal capabilities[166], shows little differentiation on the GBR[19]. 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 populations[26]. Reasons for these patterns remain unknown but suggest that distance alone does not control marine speciation[183].

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 merguiensis*) and red-spot king prawns (*Melicertus longistylus*), and bay (*Metapenaeus* spp.) and eastern king prawns (*Melicertus plebejus*), respectively[291]. 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 waters[289].

Similar patterns have also been observed for Indonesian coral-dwelling Stomatopoda, with highest species richness on mid-shelf reefs[77]. 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 hydrodynamics[225]. On the GBR, distribution patterns of Stomatopoda remain to be thoroughly examined. Nevertheless, based on data derived from Ahyong[2], 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 valid[142]. 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 underestimate[100]. Many of the ascidians found on the GBR range widely throughout the Indo–Pacific; particularly common are large mats of diademnids with algal symbionts[181].

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 be limited to specific environments[82]. 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' influence[77] (Ahyong unpublished data). Some sponges are well adapted to live in more turbid environments (eg mangroves[74]) 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 environments[199]. 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 larvae[136]. Populations of tiger prawns (several *Penaeus* spp.) in Queensland, though exhibiting a degree of sub-structuring, are also genetically continuous[106]. 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 Pacific[183], and genetic diversity may follow latitudinal gradients[26].

The origin of the GBR and its subsequent geological history are well documented (eg Davies and Hopley[67], Davies[65]). 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-Pleistocene[222]. Reef growth initiated on the Marion Plateau post–early Miocene (23 million years ago) (Davies[66] 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 Kelley[43] 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 present[222].

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 species[257], 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 absent[140].

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 *Cerithideopsilla cingulata* in subtropical mudflats[152]. 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 minute[160]. Since filtration rates largely depend on body size[160], *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 shells[299], as architects through their boring behaviour that provides habitat for cryptofauna[186], 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 Haliotidae[210].

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 fish[111]. Burrowing decapods, particularly thalassinideans and alpheid shrimps are significant bioturbators[189]. Peracarids and other

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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 scavengers[284]. Stomatopods and many decapods can be high-level predators in all habitats[2], 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 nudibranchs[4] and flat worms[191].

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 sea[188] and therefore have been the prime target for research[84]. 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 reef[83]. 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 variations[265] 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 species[217] 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 region[244]. 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 depths[9]. In addition, recent evidence suggests that climate change may delay recovery of the ozone layer[245], and ozone depletion may be linked to more rapid climate change[117], 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 clams[75], sponges[122], anemones[278,75] and those spawning in intertidal habitats exposed to full sun[218].

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 intense[192] (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

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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 beaches[294]. 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 depth[16]. For the temperate reef sponge *Cymbastella concentrica*, increased siltation led to a reduction in weight and a lower reproductive activity[230]. 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 1988[298].

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 skeletons[206]. 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 ocean[206]. 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 temperature[162]. 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 coral[138].

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 time[52]. 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 2010 (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 time[205]. 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 saxatalis*, 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 (Johannesson[148] 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], molluscs[268], and polychaetes[98]. 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 Sea[239]). 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 night[216].

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 populations[195]. 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 skeletons[85]. The biota most sensitive to ocean acidification includes a broad suite of calcifying organisms including molluscs[184], echinoderms, crustaceans, bryozoans, serpulid polychaetes, foraminifera[119] 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 predators[145], 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 (CO_2) in sea water adversely affected growth[250].

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 clams[75] and anemones[278]). 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 attenuation[8].

Sponge-zooxanthellae associations appear to be more stable than coral-zooxanthellae associations, at least in some hadromerid sponges[122]. Although sponges bleach less frequently than adjacent corals[281], completely bleached individuals ultimately die[91]. 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 diet[249].

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 area[17]. 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 invertebrates[11]. Bioeroders, such as boring sponges[228], 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 Wilson[294]).

11.2.2.7 Rainfall and river flood plumes

Marine benthic invertebrates can be highly sensitive to changes in salinity (eg encapsulated molluscs[216]) and many species have, at best, a limited ability to osmoregulate in the presence of freshwater[194]. 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 activity[230]. In addition, the size of the banana prawn harvest in the Gulf of Carpentaria and eastern Queensland strongly correlates with rainfall[263], 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 larvae[182]. 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 feeders[287], 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 group[279].

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 changes[121]. Some species have extended their range during warmer periods (eg Australian species introductions to New Zealand during the Pleistocene[17], northward extension of *Venericardia procera* in the southwestern Atlantic during the late Quaternary[1]. 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 Quaternary[1] or completely extinct (eg many molluscs in the southern hemisphere during the Cretaceous-Tertiary extinction event and associated climate change[264]. In contrast, Jackson and Sheldon[147] 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 GBR[201], associated benthic invertebrates have not. Jackson and Johnson[146] 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 Johnson[146] 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 maximum[90]. 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 stress[219]. 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 species[34]. 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 change[118]. 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 Current[233]. 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 Podolsky[87] found that increasing temperatures impacted negatively on reproductive success of the barnacle *Chthalmus 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 molluscs[1]). Temperature also affects key metabolic enzymes in littorinid molluscs, with variations found in populations at different latitudes and shore levels[259] 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 change[283]. 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 temperature[243].

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 amphipods[272]), and others by reducing their metabolism (eg ascidians[15]). 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 changes[262]. 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 invaders[262].

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 variability[206]. It is expected that the impacts of ocean acidification will be greatest in surface and shallow water[41]. 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 invertebrates[162]. The larval skeleton of gastropods, sea urchins and other benthic invertebrates are particularly fragile and may not be produced under acidic conditions[162]. 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 acidosis[184].

Increased carbon dioxide in surface waters has also been shown to lower metabolic rate in benthic invertebrates[184]. 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 heterotrophy[8], reduced growth[300], or even expulsion of zooxanthellae[286]. 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 polychaetes[177].

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 lagoon[94]. 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. Ben[17] 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 levels[17]. 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 level[256]. 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 ocean[256].

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 beaches[248]. 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 organisms[141], 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 changes[288] (see section 11.2.3.4). Octocorals are susceptible to abrasion, dislodgement by storm waves, movement of sand and rubble[80], 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 plumes[80]. 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 *Botrylloides 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 differences[10], and zooplankton volume decreased during the wet season[213].

Increased levels of sedimentation can negatively affect rates of photosynthesis in octocorals[223] 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 loads[95] 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 colonies[80]. 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 habitat[264]. Suspension-feeding molluscs, on the other hand, exhibited the highest extinction rate[264]. 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 speciation[264]. 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 recruits[80].

Several sponge species that occur on the GBR range further south to the subtropics (eg calcarean *Leucetta chagosensis*[297]). Recent analyses[128] 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) species[64]. 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 Wales[237] (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 phase[54]. *Ophiocoma scolopendrina* seems to be an opportunistic species but, as a specialist of the intertidal, is a heat-tolerant (eurythermal) species[193].

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 rates[80]. 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 record[241]. 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 nutrition[8]. 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 waters[46].

In the fossil record there are many examples of dramatic changes in faunal composition following major shifts in circulation, the formation of the circumpolar current[242] 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 crustaceans[205] 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 colonies[80].

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 field[96].

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 extinct[1].

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 unknown[179]. External gamete production is often highly synchronous and putatively controlled by diverse exogenous and endogenous events, often shortly before the peak summer temperature is reached[89]. 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 observed[179]. 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 rapidly[178].

Temperature and developmental rates positively correlate in many marine invertebrates[195]. 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, Frank[88] found that shell growth and temperature were not related within a single population. However, shell growth preceded reproduction in some species[88], 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 corals[12]. 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 swamp predators and increases the survivorship potential of each species[12]. 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 pollution[258]. 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 coral[138]. 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 research[159].

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 symbionts[75] (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 crabs[45]).

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 Smith[32]). 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 behind[67]. 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 input[20].

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 structures[143]. 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 GBR[199]. 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 (Przeslawski[216] 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 merguiensis*) 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 availability[170]. 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 UVR[218]. 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 desiccation[217]. 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 salinity[266], each of which will be modified by global climate change.
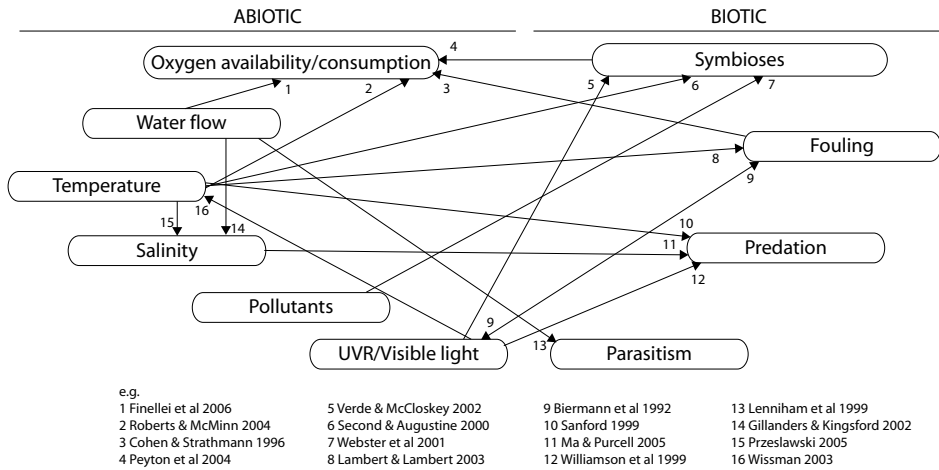
The invasive ability of marine invertebrates should also be considered in a multifactor context[234]. Single-factor studies are relatively simple with easily interpreted results, but they may underestimate 'real-world' effects. Such studies are most appropriate as a baseline or platform for further multifactor research. Some data suggest that impacted communities are more susceptible to invasion by introduced species[59]. 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 complex[125] and have both acute and chronic effects[256]. Some stressors may even have different effects on the same species, depending on the history of the assemblage or environment[135]. 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 Przeslawski[216]). Variables listed do not include events associated with them (eg flooding, runoff and storms), rather only the specific stressors are included[e]*

e.g.

1 Finellei et al 2006	5 Verde & McCloskey 2002	9 Biermann et al 1992	13 Lenniham et al 1999
2 Roberts & McMinn 2004	6 Second & Augustine 2000	10 Sanford 1999	14 Gillanders & Kingsford 2002
3 Cohen & Strathmann 1996	7 Webster et al 2001	11 Ma & Purcell 2005	15 Przeslawski 2005
4 Peyton et al 2004	8 Lambert & Lambert 2003	12 Williamson et al 1999	16 Wissman 2003

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 conditions[124] 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.
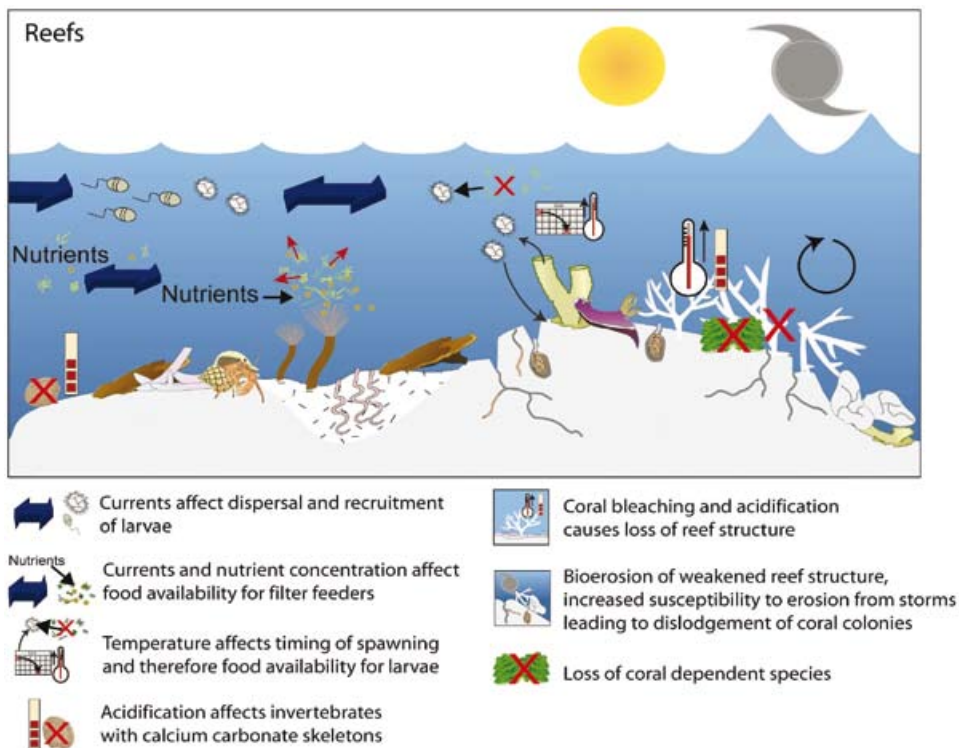
11.4 Summary and recommendations

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.

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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*

Currents affect dispersal and recruitment of larvae

Currents and nutrient concentration affect food availability for filter feeders

Temperature affects timing of spawning and therefore food availability for larvae

Acidification affects invertebrates with calcium carbonate skeletons

Coral bleaching and acidification causes loss of reef structure

Bioerosion of weakened reef structure, increased susceptibility to erosion from storms leading to dislodgement of coral colonies
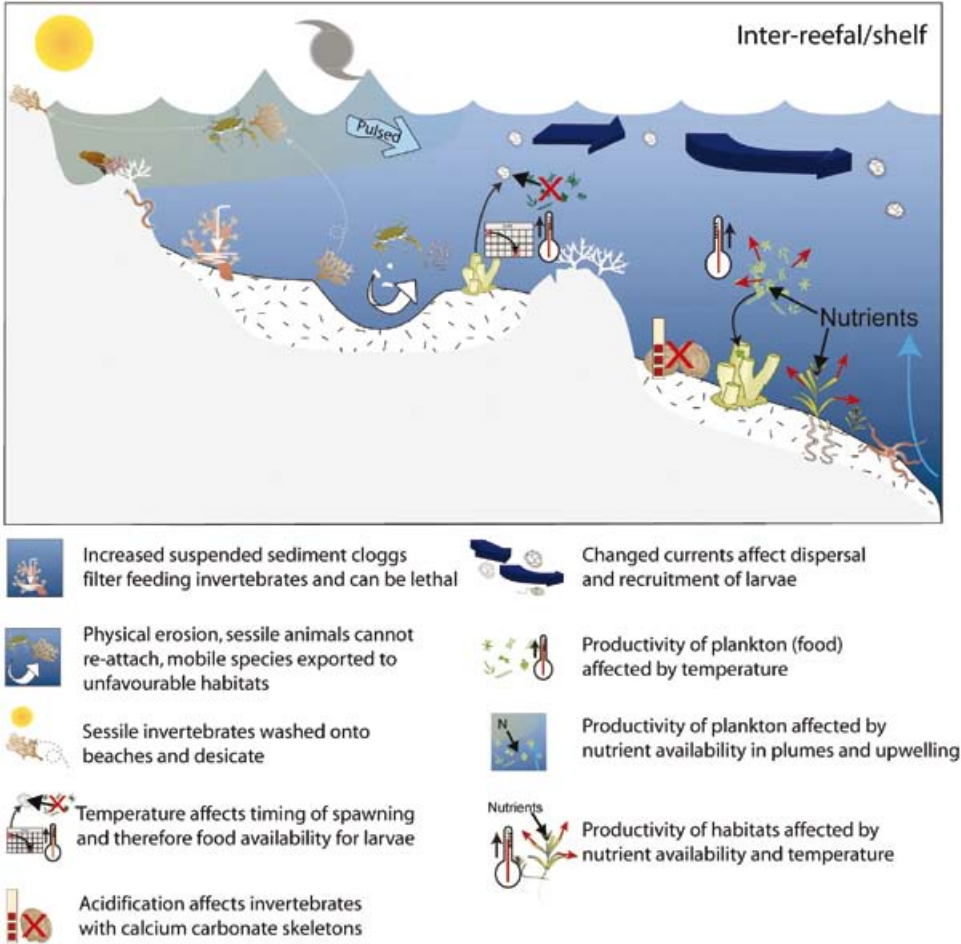
Loss of coral dependent species

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 scenarios[267]. 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 Tomanek[269] and Sorte and Hofmann[261] 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 temperature[269]. 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 extinction[17]. However, Indo–West Pacific coral and mollusc species had a lower rate of extinction then their Caribbean counterparts[256], 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*

Increased suspended sediment cloggs filter feeding invertebrates and can be lethal

Changed currents affect dispersal and recruitment of larvae

Physical erosion, sessile animals cannot re-attach, mobile species exported to unfavourable habitats

Productivity of plankton (food) affected by temperature

Sessile invertebrates washed onto beaches and desicate

Productivity of plankton affected by nutrient availability in plumes and upwelling

Temperature affects timing of spawning and therefore food availability for larvae

Productivity of habitats affected by nutrient availability and temperature

Acidification affects invertebrates with calcium carbonate skeletons

communities in the Pacific changed during these periods of sea level rise, there was little evidence of large-scale or permanent loss of overall diversity[256].

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 Kennedy[129] and Hooper and Ekins[128] 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*
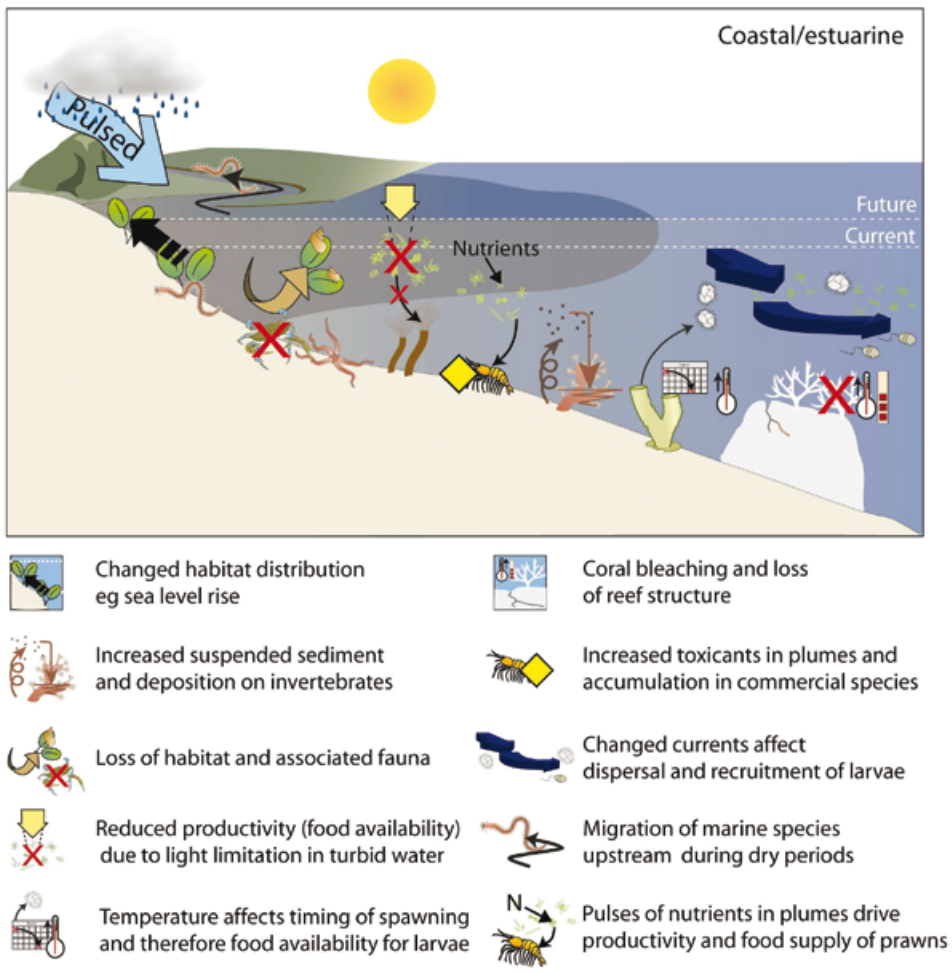
Increased rates of coral death following bleaching and other physiological stresses result in increased rates of bioerosion leading to loss of reef framework[202]. If scleractinian corals do not readily adapt to rising sea surface temperatures and if frequency of bleaching events increases, increasing 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 Alectonidae) will increase and further weaken the structural framework of the reef[239]. 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], hapalocarcinid and trapeziid crabs[45], polychaete worms[255] and coral-associated barnacles[6]. Similarly, many sponges are niche specialists on reefs, found only in particular habitats such as in caves, overhangs and coral interstices[127], 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 starfish[78].

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 change[7]. In Tasmania this urchin has contributed to a phase shift from a kelp-dominated community to a barren seascape[7]. Another example is the recent invasion of the clam *Potamocorbula amurensis* in San Francisco Bay. This species has greatly contributed to the regional CO_2 source through its respiration and calcification, with associated implications for ocean acidification[50]. 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 species[262].

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 decades[23]. 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 to1976, 1979 to 1991 and 1993 to the present[31]. 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 to15 years[61]. 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-1980s[139]. 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 structure[7]. 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 biomass[295]. 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 molluscs[232] and polychaetes[138] 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 dramatically[302], 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 biodiversity[202].

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 studies[269]. 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.

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