Coral Reefs: An Ecosystem in Transition

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Factors determining the resilience of coral reefs to eutrophication: a review and conceptual model

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1. Introduction

Eutrophication and increased sedimentation have severely degraded many coastal coral reefs around the world. This chapter reviews the main impacts of eutrophication on the ecology of coral reefs, and the properties of reefs that determine their exposure, resistance and resilience to it. It shows that eutrophication affects coral reefs by way of nutrient enrichment, light loss from turbidity, and the smothering and alteration of surface properties from sedimentation. These changes lead to changes in trophic structures, reduced coral recruitment and diversity, the replacement of corals by macroalgae, and more frequent outbreaks of coral-eating crown-of-thorns starfish. The reefs and areas most susceptible to degradation from pollution are deeper reef slopes, reefs located in poorly flushed locations and surrounded by a shallow sea floor, frequently disturbed reefs, and reefs with low abundances of herbivorous fishes. The chapter concludes with a conceptual model of the main links between water quality and the condition of inshore coral reefs.

The term ‘eutrophication’ defines the increase in nutrient concentrations (especially nitrogen or phosphorus) in a water body, which can increase the production of algae, turbidity, sedimentation of particulate matter, and in severe cases hypoxia. A ‘contaminant’ is a substance (including nutrients and sediments) that occurs at above ‘natural’ concentrations, while a ‘pollutant’ is defined as a substance that occurs at a concentration causing environmental harm (GESAMP 2001). Minor nutrient enrichment may therefore be considered contamination, while major eutrophication constitutes pollution.

Eutrophication degrades reefs through three mechanisms (Rogers 1990; Dubinsky and Stambler 1996; Szmant 2002; Fabricius 2005):

(a) nutrient enrichment causes trophic changes
(b) turbidity causes light loss, which affects photosynthesis in deeper water
(c) sedimentation causes reduced larval settlement and mortality

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The main source of new dissolved and particulate nutrients and sediments that enter coastal marine systems is rivers. How much nutrient and sediment rivers carry is determined by geography (e.g. rainfall, soil type and slope) and land management (e.g. degree of vegetation cover, fertilizer application etc; (Bourke et al. 2002). Other sources of nutrients and particulate matter are aquaculture and sewage outfall sites (Loya et al. 2004), diffuse coastal runoff, groundwater seepage, the upwelling of nutrient-rich water from greater depths, nitrogen fixation by benthic and pelagic cyanobacteria and algae, and the atmosphere (e.g. rain; settling dust; Dumont et al. 2005; Duce et al. 2008).

Marine coastal ecosystems, including coastal coral reefs, are exposed to increasing amounts of soil, fertilizer and pesticide washed from cleared land, and discharged from sewage and fish farms and other point sources (Vitousek et al. 1997, Tilman et al. 2001; Smith et al. 2003). Globally, an additional 1% of the earth's surface is being cleared every year; nitrogen fertilizer use has increased more than sixfold since 1960 (Matson et al. 1997); and human population along the coast is growing even faster than elsewhere. All this contributes to a rapidly intensifying exploitation of coastal resources, and increasing losses of nutrients from the land (Crossland et al. 2005). Oxygen-depleted seafloor zones, attributable to runoff of agricultural nitrogen and phosphorus, have doubled in area in the last few decades – indicating that many marine water bodies are becoming more eutrophic (Diaz 2001, GESAMP 2001; Vaquer-Sunye and Duarte 2008).

New nutrients that enter coral reefs cycle rapidly and in extremely complex ways. It is useful to differentiate between dissolved and particulate, and between organic and inorganic forms of nutrients, because the biological effects of the four differ fundamentally. *Dissolved inorganic nutrients* (especially phosphate, nitrate or ammonium) are highly bioavailable; they are incorporated into benthic and pelagic food webs within hours to days, and, thereafter, are found as particulate organic matter (especially detritus, bacteria, phytoplankton and marine snow). *Dissolved organic nutrients* often occur in relatively high concentrations, but a large proportion cannot be used as food by any organism, including bacteria. *Particulate organic matter* is dominated by detritus and plankton, while particulate inorganic nutrients are often bound to suspended sediment grains. Concentrations of particulates are typically determined by measuring proxies – chlorophyll, particulate nitrogen, particulate phosphorus, and total suspended solids. Uptake, excretion and decomposition in benthic and pelagic food webs ensure continuous conversions between dissolved and particulate, and between organic and inorganic forms of nutrients.

Both the concentration and type of suspended particles strongly determine water clarity, which in turn determines *benthic irradiance* at a given water depth. While coastal coral reefs can flourish at relatively high levels of turbidity (Kleypas 1996; DeVantier et al. 2006), in turbid water they tend to be restricted to the upper 4–10 m because of reduced coral photosynthesis and growth at greater depth. In comparison, in clear oceanic waters coral reefs can be found at depths of over 40 m (Yentsch et al. 2002). Water clarity is strongly governed by the degree to which waves resuspend sediments in shallow shelf seas (Larcombe and Woolfe 1999). Water clarity can also be affected by increased phytoplankton productivity, such as recorded in the past around a sewage outfall site in Kanehoe Bay, Hawaii (Hunter and Evans 1995), and fish farms in the Northern Red Sea (Loya et al. 2004). Historic data on water clarity in marine systems are, however, sparse, and the conditions leading to long-term changes in water clarity in tropical coastal systems are poorly understood.

Altered *sedimentation* regimes are often linked to eutrophication, as particulate matter eventually settles onto the seafloor and onto benthic organisms. Larger grain sizes are deposited within a few kilometers of the source, but the smallest grain fractions (clay and silt particles) remain suspended for prolonged periods of time, and are often distributed over tens to hundreds of kilometers, undergoing several cycles of deposition and resuspension. Such small particles carry more nutrients and pesticides (Gibbs et al. 1971), absorb more light (Moody et al. 1987) and cause greater stress and damage to corals than do sediments that are coarse and poor in organic matter (Weber et al. 2006). Not only the amount of sedimentation but also its type and organic contents thus determine the extent of damage caused by sedimentation to coral reefs.

Although degradation or damage from elevated nutrients and sediments has been reported from reefs around the world, it has often been difficult to distinguish whether human activities have contributed to cause the damage. Comprehensive reports documenting damage include studies from Hawaii (Hunter and Evans 1995), Indonesia (Edinger et al. 1998), Costa Rica (Cortes and Risk 1985; Hands et al. 1993), Barbados (Tomascik and

Sander 1987; Wittenberg and Hunte 1992), St Croix (Hubbard and Scaturo 1985), Kenya (McClanahan and Obura 1997), and the Great Barrier Reef (van Woesik et al. 1999; Koop et al. 2001; McCulloch et al. 2003; Fabricius et al. 2005a). Most of these studies assessed spatial and/or temporal variation at control and impact sites. By their nature, such assessments based on associations cannot assert causal relationships between pollution and reef degradation, because historical data are often missing and other disturbances (e.g. overfishing, coral bleaching, storms and floods) tend to co-occur. In shallow nearshore waters, nutrient concentrations and water clarity can vary – both spatially and temporally – by up to two orders of magnitude. Even without increased terrestrial runoff and eutrophication, reef communities change along water quality gradients: from terrestrially influenced conditions (characterised by fluctuating salinity, more variable or higher nutrient load, siltation and turbidity) to oceanic conditions (where nutrients, siltation and turbidity are typically low) (Fig. 1). Epidemiological tools originally developed to assess the weight of evidence that smoking causes lung cancer (U.S. Department of Health 1964), have now been applied to coral reef studies to assess causal links between reef degradation and increased levels of nutrients and sediments in the central Great Barrier Reef (Fabricius and De'ath 2004).

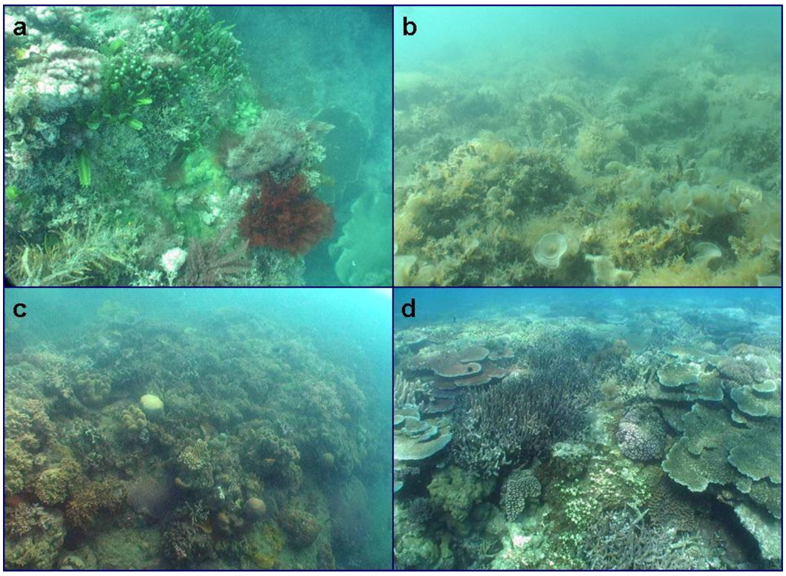

Fig. 1 Shallow-water coral reef communities can change visibly along water quality gradients, as shown by these photographs from reefs near the mouths of the Proserpine and O'Connell Rivers, central Great Barrier Reef. (a) 20 km from the rivers: reef assemblages in the shallow water are dominated by green and red macroalgae and have few coral colonies; assemblages at greater depths are dominated by heterotrophic filter-feeders (not shown); (b) 40 km from the rivers: communities are dominated by macroalgae and low coral cover; (c) 60 km from the rivers: octocoral and hard coral dominate communities; (d) 70 km from the rivers: diverse *Acropora*-dominated communities. (Photos: K. Fabricius).

2. Responses of reef organisms to eutrophication

The following section of this chapter reviews the available information on two things: first, how eutrophication directly and indirectly effects corals and other reef-associated organisms; and, second, how the ecological balances of coral reef ecosystems changes with nutrient enrichment, light loss and sedimentation.

2.1. Hard corals

Hard corals are competitive in low-nutrient environments for three reasons. First, they are remarkably efficient in internally recycling nutrients between the host and its endosymbiotic unicellular algae (zooxanthellae; Stambler 2010 this book Chapter 7). Second, they have the capacity to occupy most trophic levels simultaneously. This is because they are efficient phototrophs (due to their endosymbiotic algae), they take up dissolved inorganic and organic nutrients, graze on primary producers (such as large phytoplankton), capture and prey upon herbivorous and predatory zooplankton, and feed on decompositional material such as detritus (Rosenfeld et al. 1999). Third, many hard coral species are able to phenotypically adapt to varying light and food availability within days, and such plasticity helps maximizing energy gains throughout their lifetime (Anthony and Fabricius 2000).

Studies of the impacts of eutrophication have often focused on *dissolved inorganic nutrients* (e.g. Stambler et al. 1994; Dubinsky and Stambler 1996 ; Koop et al. 2001; Szmant 2002). Most studies show that high levels of dissolved inorganic nitrogen and phosphorus can cause significant physiological changes in corals, but do not kill or greatly harm individual coral colonies (reviewed in Fabricius 2005). However, exposure to dissolved inorganic nitrogen can lead to declining calcification, higher concentrations of photopigments (affecting the energy and nutrient transfer between zooxanthellae and host; Marubini and Davies 1996), and potentially higher rates of coral diseases (Bruno et al. 2003). In areas of nutrient upwelling or in heavily polluted locations, chronically elevated levels of dissolved inorganic nutrients may so alter the coral physiology and calcification as to cause noticeable changes in coral communities (Birkeland 1997). However, dissolved inorganic nutrients are generally quickly removed from the water column by way of biological uptake by bacteria, phytoplankton and the benthos; hence, concentrations will often not increase greatly along pollution gradients. The main way in which dissolved inorganic nutrients affect corals appears to be by enriching organic matter in the plankton and in sediments.

Particulate organic matter is used by corals as food, and tissue thickness, photosynthetic pigment concentrations and calcification in corals increase. At higher levels of particulate organic matter, some hard coral species can increase rates of heterotrophy – and, thus, partly or fully compensate for energy losses resulting from light attenuation – while other species show feeding saturation and are unable to compensate for light loss (Anthony and Fabricius 2000). At even higher levels of particulate organic matter, gross photosynthesis and respiration, tissue thickness and calcification start to decline in all species as light attenuation outweighs further energy gains from particulate organic matter feeding. Photosynthesis, tissue thickness and calcification therefore change in a modal fashion along eutrophication gradients (Tomascik and Sander 1985; Marubini and Davies 1996). However, photosynthetic pigment concentrations further increase with increasing particulate organic matter, and have, therefore, been suggested as one of the most useful early-warning indicators of eutrophication (Marubini 1996; Cooper et al. 2009). While corals are not greatly harmed by dissolved inorganic nutrients – and may even benefit from particulate organic matter – macroalgae and heterotrophic filter-feeders benefit more from dissolved inorganic and particulate organic nutrients than do corals (see below). As a result, corals that can grow at extremely low food concentrations may be out-competed by macroalgae and/or more heterotrophic communities that grow best in high nutrient environments.

Benthic irradiance is a crucial factor for reef corals. Shading reduces photosynthesis, leading to slower calcification and thinner tissues (Anthony and Hoegh-Guldberg 2003; Allemand et al., 2010 this book). Few corals can grow when surface irradiance is less than about 4% – as encountered at ~40 m in clear water or at ~4 m in highly turbid water – and reef development tends to cease at around this light level (Yentsch et al. 2002; Cooper et al. 2009). Phototrophic species are more severely affected by light limitation than are other species, with the result that species richness declines at high turbidity in deeper depths, due to the loss of sensitive species. On the other hand, slower-growing species may be out-competed at high irradiance by fast-growing phototrophic species and by macroalgae; hence, species richness is often highest at intermediate light levels (Cornell and Karlson 2000). Corals acclimatise to low irradiance by increasing their pigment density. However full photoacclimation takes about 5–10 days, and is too slow to compensate for energy losses if turbidity fluctuates (Anthony and Hoegh-Guldberg 2003).

Sedimentation reduces coral recruitment rates and coral biodiversity, with many sensitive species being under-represented or absent in sediment-exposed communities. Small colonies and species with thin tissues and flat morphologies are often more sensitive to sedimentation than are large colonies or those with thick tissues or branching growth forms (Rogers 1990; Stafford-Smith and Ormond 1992). In coral colonies, sedimentation stress increases linearly with the duration and amount of sedimentation: for example, a certain amount of sediment deposited on the coral for one time unit exerts the same measurable photophysiological stress as twice the amount deposited for half the time (Philipp and Fabricius 2003). High sedimentation rates (up to >100 mg dry weight cm^{-2}) can kill exposed coral tissue within a few days, while lower rates reduce photosynthetic yields in corals within ~24 h (Philipp and Fabricius 2003). Exposure to a few days of sedimentation can cause long-term damage to coral populations, by removing whole cohorts of small and sensitive corals. Some suggest a sedimentation threshold of 10 mg cm^{-2} d^{-1}, with reefs being severely damaged at higher sedimentation rates (Rogers 1990).The damage to tissue under a layer of sediment further increases with increasing organic content and bacterial activity, and with decreasing grain size of the sediment (Hodgson 1990; Weber et al. 2006). Levels of ~12 mg cm^{-2} d^{-1} can kill newly settled corals with <48 h exposure if sediments are rich in organic contents; but such levels can be tolerated if organic content is low (Fabricius et al. 2003). These and similar data demonstrate the critical, but as yet poorly understood, effects of organic enrichment of sediments.

2.2. Coral recruitment

It is during their recruitment stages that corals are the most sensitive to pollution. While adult corals can tolerate prolonged periods of low light, competition with macroalgae and moderate levels of sedimentation, the settlement of coral larvae and the survival of newly settled young and small colonies are extremely sensitive to them (Fabricius 2005). Indeed, very little settlement occurs on sediment-covered surfaces, and the tolerance of coral recruits to sediment is at least one order of magnitude lower than that of adult corals. Settlement of coral larvae is also controlled by light intensity and spectral composition; reduced light reduces the depth at which larvae settle (Baird et al. 2003). Because successful coral recruitment is essential if reefs are to recover from bleaching, storms or other disturbances – and because recruitment is one of the main factors determining speed of recovery from disturbances – reduced coral recruitment is one of the most deleterious effects of eutrophication on coral reefs.

2.3. Crustose coralline algae

Certain species of crustose coralline algae are essential for coral settlement (Harrington et al. 2004). Experiments and field data suggest that high nutrient levels do not greatly alter the physiology of crustose coralline algae, but high sedimentation rates are related to low abundances of corallines in coral reefs (Kendrick 1991; Fabricius and De'ath 2001). Some crustose coralline algae associated with coral reefs survive burial under coarse inorganic sediments for days to weeks, but their survival rates rapidly decline if the sediments contain traces of herbicides (Harrington et al. 2005). Turf algae often out-compete coralline algae (Steneck 1997), and, because turf algae can trap large quantities of sediments (Purcell 2000), they make the surrounding substratum less suitable for coralline algae and for coral settlement (Birrell et al. 2005).

2.4. Macroalgae

Macroalgal communities are an integral and often diverse component of inshore reef systems. They use photosynthesis to satisfy their carbon demand, while their nutrient demand is met by uptake of dissolved inorganic nutrients plus, in some species, by demineralisation of particulate organic matter deposited on their fronds (Schaffelke 1999). In the absence of grazing, the growth and productivity of some – but not all – groups of macroalgae are nutrient-limited, and increase with minute increases in dissolved inorganic nutrients and particulate organic matter (Littler and Littler 2007). Macroalgae can be dominant around point sources of nutrients (Smith et al. 1981; Lapointe et al. 2004,Lapointe and Bedford 2007). On the Great Barrier Reef, total macroalgal cover increases several-fold along gradients of declining water clarity and increasing nutrients (van Woesik et al. 1999; Fabricius and De'ath 2004; Fabricius et al. 2005b). Long-term data have also shown that expansion (Cuet et al. 1988) or decline (Smith et al. 1981) in macroalgal cover over time coincide with increasing and declining nutrients, respectively. These time series data indicate a causal link between macroalgal abundances and nutrient availability. Macroalgae also tend to flourish in areas of nutrient upwelling, on eastern sides of continents or large islands, where more rivers originate than in the west (Birkeland 1988), and with latitude, as do nutrient concentrations (Johannes et al. 1983). These large-scale geographic data all add evidence that the availability of nutrients controls macroalgal biomass. However, increases in macroalgal biomass are only observed in areas where grazing by herbivorous fishes or invertebrates is low (McCook 1999; Littler and Littler 2007), and where light is not limiting.

Macroalgae that form low ephemeral mats tend to overgrow, damage or even kill understorey corals by shading, restricting gas exchange, and creating hypoxia when mats collapse (Loya et al. 2004). In contrast, tall perennial species, such as *Sargassum* spp., do not usually kill corals, but they can reduce coral growth by shading (Littler and Littler 2007). All dense macroalgal assemblages (low ephemeral mats *and* tall perennial stands) suppress coral recruitment through space occupancy, allelopathy, silt-trapping or shading (Connell et al. 1997 ; Szmant 2002).

2.5. Crown-of-thorns starfish (*Acanthaster planci*)

Another severe consequence of eutrophication is the apparent increase in frequencies of outbreaks of crown-of-thorns starfish (Birkeland 1982; Brodie et al. 2005). *A. planci* is corallivore – it feeds on coral tissue – and has been the most common cause of coral mortality throughout many tropical Indo-Pacific regions in the last five decades. The pelagic larvae of this starfish filter-feed on large phytoplankton, and experiments suggest that these larvae are food limited: their survivorship in the laboratory increases steeply with increasing availability of suitable food at environmentally relevant concentrations (Lucas 1982). In the field, increased nutrient availability can increase the abundance of large phytoplankton cells: a strong temporal and spatial relationship exists between drought-breaking floods from high continental islands and outbreaks of this starfish (Birkeland 1982). New research further strengthens the evidence that more frequent outbreaks of *A. planci* are linked to high nutrient levels, while acknowledging that the removal of predators of *A. planci* can further increase the likelihood of outbreaks (Brodie et al. 2005 ; Houk et al. 2007). After primary *A. planci* outbreaks have formed in a region with high phytoplankton concentrations, many of their numerous larvae may be transported by currents to remote regions, hence secondary *A. planci* outbreaks may form far away from areas of eutrophication.

2.6. Filter-feeders, macro-bioeroders and suspension feeders

Benthic filter feeders – such as sponges, bryozoans, bivalves, barnacles and ascidians – are important components of reef ecosystems. Most of them live hidden in crevices or drill or etch their own holes within coral skeletons (so called internal bioeroders). Far fewer live on the reef surface where they would compete with hard corals and with algae for space. Most filter-feeders are heterotrophic (i.e. not associated with photosynthetic symbionts), and are specialised to feed on a narrow spectrum of planktonic particles. Due to these trophic constraints, they are often unable to obtain a positive carbon balance in oligotrophic waters (Birkeland 1988), and their densities increase in response to nutrient enrichment (Smith et al. 1981; Costa Jr et al. 2000). Literature suggests that, unlike macroalgae – that directly compete with corals for well-lit habitats – surface-inhabiting heterotrophic filter-feeders tend to monopolise space in poorly lit, highly productive environments, i.e., conditions that are marginal for corals. Filter-feeders therefore rarely out-compete corals directly (Aerts and Van Soest 1997), with the few observed exceptions all occurring in areas of low light, high plankton productivity and organic enrichment (Smith et al. 1981; Brock and Smith 1983). The demise of corals and the establishment of filter-feeders therefore appear largely as independent symptoms of eutrophication, with the fate of each group determined by altered trophic conditions rather than by altered balances in their competition for space.

Many internal macro-bioeroders are filter-feeders that actively bore into or chemically erode the calcium carbonate skeletons of live corals and dead reef substrata. The main groups of macro-bioeroders are boring sponges (e.g. *Cliona* spp.) and bivalves (e.g. *Lithophaga* spp.). In high densities they can substantially weaken the structure of coral reefs and increase their susceptibility to storm damage. Several studies have documented abundances of internal macro-bioeroders increasing in response to increased nutrient availability (Hallock 1988; Cuet et al. 1988). For example, abundances of the boring sponge *Cliona delitrix* increased five-fold in an area exposed to untreated sewage (Rose and Risk 1985), and abundances of most internal macro-bioeroders are higher in productive inshore environments than they are offshore. Increased bioerosion in areas of nutrient enrichment, combined with reduced coral growth, diminished skeletal densities and lower recruitment rates, can lead to conditions in which reef erosion exceeds calcium carbonate accretion (Pari et al. 2002).

Octocorals (soft corals and sea fans), are passive suspension feeders rather than internal filter-feeders, with the more abundant genera all containing photosynthetic endosymbionts (Fabricius and Alderslade 2001). Very few studies report photosynthetic soft corals monopolizing space after hard coral disturbance, and a shift from hard corals to octocorals appears to be a rare occurrence and restricted to productive and high-irradiance, high-current and wave-protected waters. Indeed, octocorals appear to be more strongly affected by declining water quality than are hard corals: octocoral species richness declines by up to 60% along a gradient of increasing turbidity, due to the disappearance of zooxanthellate octocorals (Fabricius and De'ath 2004).

2.7. Fishes

Fishes play an essential role in the ecology of coral reefs. The abundances of many taxa is related to the structural complexity of reefs (Wilson et al. 2006). High coral cover – a proxy for structural complexity – promotes local fish abundances, thus sustaining grazing pressure on algae. Reduced abundances of herbivorous fish lead to proliferation of macroalgae (McCook 1999). However, it is unclear whether the abundances of herbivorous fish on coral reefs decline with increasing turbidity (Wolanski et al. 2004), as they do in some estuarine areas (Mallela et al. 2007). It has also been argued that increased fishing pressure may lead to complex and largely unpredicatble trophic cascades. For example, the overfishing of large carnivores could lead to higher densities of small carnivores, which in turn may reduce the number of invertebrates that feed on juvenile crown-of-thorns starfish (*Acanthaster planci*), and therefore an increased survival of this coral-eating starfish (Dulvy et al. 2004).

3. Factors influencing the susceptibility of reefs to eutrophication

Reefs differ significantly in their exposure, resistance and resilience to pollution – and the identification of coral reef areas with low exposure and high resistance and resilience is a high management priority (West and Salm 2003).

Exposure to a pollutant is typically a function of the amount (concentration or load) of pollutant and the length of time it is in contact with a coral (Fig. 2). A coral that is exposed to a high concentration of a pollutant for a short period of time may suffer a similar fate to one that is exposed to lower concentrations for longer periods (Philipp and Fabricius 2003). Peak concentrations are only a relevant measure of pollutants if the onset of damage or mortality is rapid (Fig. 2). For example, dredging may kill benthic organisms by acute sedimentation within a few hours to days, but prolonged dredging can also cause damage through cumulative physiological changes due to light loss from turbidity (Bak 1978).

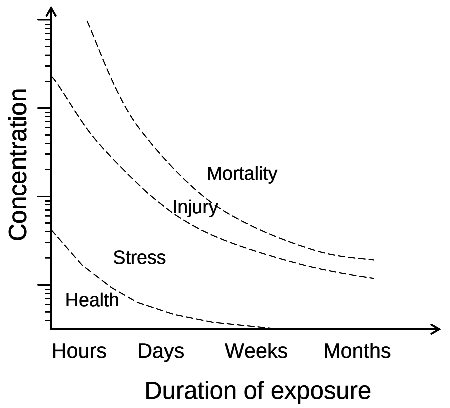

Fig. 2: Schematic representation of responses of coral exposed to a pollutant. The severity of response is typically a combined function of the duration and amount (concentration or load) of exposure.

Resistance of an ecosystem is defined as the ease or difficulty with which it can change in response to a disturbance (Pimm 1984). Resistance can arise from environmental (extrinsic) or biological (intrinsic) factors (Done 1999; West and Salm 2003). For example, a coral reef composed of coral communities adapted to naturally turbid settings may be low in species richness and dominated by the turbidity-tolerant genera *Turbinaria* and massive *Porites*. Such communities are more resistant to pollution than communities adapted to clearwater environment which contain many sensitive species.

Ecological *resilience* is defined here as the time it takes an ecosystem to return to a stable equilibrium point after being disturbed (Pimm 1984; Tilman and Downing 1994). Note that several definitions of resilience are in use (Nyström et al. 2008). Notably, resilience has sometimes been defined as the *capacity* of an ecosystem to recover after some acute disturbance without undergoing a phase shift into an alternate state (West and Salm 2003), a definition of resilience that is more difficult to quantify and hence not employed here.

The factors that predict exposure, resistance and resilience of reefs to degradation are listed in Table 1, derived from a qualitative review of some of the better-described case studies in the literature (Fabricius 2005). A formal risk analysis will be required to quantify the relative contributions of these properties.

Currents, waves and tides are extremely important properties of coral reefs, and key predictors of exposure, resistance and resilience at both local and regional scales. At local scales, current-swept reef fronts, flanks and channels and reef crests with moderate wave exposure are the least likely to retain pollutants; they support high recruitment, and have the fastest coral growth (Sebens 1991). Ideally, wave exposure is sufficient to remove sediment deposits without causing frequent coral breakage (in inshore waters, coral skeletons are, typically, very brittle). As fast currents and waves also facilitate macroalgal growth, competition between corals and macroalgae is intense if nutrient levels are high. At regional scales, currents determine where and how far pollutants are being transported. Where currents are predominantly tidal, very low and very high tidal ranges affect transport and resuspension and the ability of reefs to withstand pollution. A strong connectivity to upstream populations that produce pelagic larvae also decreases the time for recovery from a disturbance, and is a strong predictor of resilience.

Spatial factors are the simplest predictors of exposure: the closer downstream a coral reef is to a pollution source, and the higher the mean annual load of this source, the greater is its exposure to a pollutant. Geospatial models of the global scale of pollution around coral reefs have been developed based on the distance of reefs to pollution sources (Bryant et al. 1998). These models estimate that 22% of all coral reefs worldwide are classified as at high (12%) or medium (10%) threat from inland pollution and soil erosion. They also classify 12% of reefs at threat from marine pollution (distance from ports, oil tanks, oil wells and shipping areas), and 30% of reefs as threatened from coastal development such as cities, mines and resorts (Bryant et al. 1998). At regional scales, the percentage of reefs at risk is a direct function of the extent of land clearing, and up to 50% of reefs are at risk in the countries with the most widespread land clearing (Bryant et al. 1998). At local scales, such as downstream from well-defined point sources, or in coastal reefs fringing eroding land, terrestrial runoff can be the single most significant pressure for selected coral reefs (Bourke et al. 2002). However, such geospatial models do not factor in additional indirect effects that may occur hundreds of kilometres away from areas of eutrophication, such as increasing outbreak frequencies of crown-of-thorns starfish populations.

Topography/geomorphology and bathymetry can modify exposure enormously: pollutants are retained for prolonged periods in poorly flushed embayments and lagoons, but may rapidly disappear from a well-flushed headland surrounded by a deep water body (Hopley et al. 2007). Around the world, most severely polluted and hypoxic marine sites appear to be located in shallow and poorly flushed semi-enclosed waterbodies such as gulfs, bays, fjords or bights (e.g. Kaneohe Bay, the Baltic Sea, Chesapeake Bay, Irish Sea; Diaz 2001). Bathymetry also modifies exposure, by affecting the balance between sedimentation and resuspension of materials. Materials are easily washed away from shallow, upper reef slopes, but accumulate below the reach of surface waves in deeper areas (Wolanski et al. 2005). Upper reef slopes are also less affected by turbidity than are deeper areas, where light becomes limiting for photosynthetic organisms. Repeated wave resuspension and deposition of materials is worst at sites surrounded by a wide, shallow continental shelf, whereas pollutants are flushed away into deeper waters if no shelf retains them. For example, the Great Barrier Reef is located on a 50–200 km-wide shallow continental shelf with >2000 barrier reefs between the land and the open ocean. Retention times here are unknown, but some estimate them to be up to 300 days for dissolved materials (Luick et al. 2007). Particulate materials are likely to be retained for even longer periods of time, as they are repeatedly deposited and resuspended from the shallow sea floor. So, although nutrient enrichment is less severe on the Great Barrier Reef than in many other more densely populated regions, symptoms such as macroalgal dominance and low coral diversity on numerous inshore reefs (Fig 1) have been attributed to enhanced terrestrial runoff (van Woesik et al. 1999; Fabricius and De'ath 2004; Fabricius et al. 2005b).

Lastly, *biological processes* are believed to modify the resistance and resilience of coral reefs, but many of these processes are as yet poorly understood. For example, abundant herbivorous fish strongly control macroalgal abundances, thereby promoting resilience (Littler and Littler 2007). It is also still unresolved to what extent resistance and resilience are co-determined by biodiversity; regions of low biodiversity have fewer species to replace the loss of sensitive species, and may be more likely to undergo structural and functional changes in their communities (Bellwood et al. 2004). For example, the loss of the dominant coral species *Acropora palmata* and *Acropora cervicornis* and the one remaining important algal grazer, *Diadema antillarum,* in the Caribbean, has led to a widespread collapse of reef ecosystems there. It is also unknown whether or not the resistance and resilience of reefs varies along latitudinal gradients, as reefs in higher latitudes naturally have lower calcification rates, higher macroalgal biomass and lower coral biodiversity than do low latitude reefs. Lastly, regions that are prone to severe or frequent disturbances (e.g. from coral bleaching, storms, cold water upwelling, or outbreaks of crown of thorns starfish) are more likely to be prone to degradation than rarely disturbed regions. This is because poor water quality often does not directly kill the adult coral populations, but retards coral recruitment and hence the speed of recovery from unrelated disturbances. It has also been shown that exposure to one form of stress may decrease the resilience of an ecosystem to another stressor (Hughes et al. 2003; Wooldridge et al. 2005).

In summary, Table 1 suggests that degradation from poor water quality is most likely to occur in poorly flushed locations with weak currents, on deeper reef slopes, in places where fish abundances are low, and in regions that are frequently affected by other forms of disturbance. In contrast, reefs with strong currents, well-flushed locations, shallow reef crests surrounded by a deep water body, and reefs inhabited by healthy populations of fishes are likely to have the highest levels of resistance and resilience.

Table 1 Spatial, geophysical and biological properties that predict the exposure, resistance and resilience of coral reefs to degradation by eutrophication.

Factor	Property	Highest risk, lowest resistance and resilience

Hydrodynamics	Currents and waves determine exposure to pollutants (through dilution, mixing, and removal), and resistance of organisms (growth rates and photosynthesis are high at strong currents).	Weak currents, weak or extreme wave exposure.
Connectivity	Connectivity to region with large brood stock determines larval supply and rates of self-seeding.	Low connectivity to region with large brood stock, and low self-seeding.
Location	Downstream distance from source, and discharge load of source, determines exposure.	Near to and downstream of point of discharge.
Local topography	Local: steepness of reef slope determines the accumulation or downward transport of settled pollutants.	Terraces, gradual slopes.
Geomorphology	Geomorphology determines sediment retention vs flushing: retention is greatest in lagoons, embayments and on leeward reefs sides, while sediments and pollutants are flushed away from headlands, channels, or reef flanks.	Lagoons, semi-enclosed embayments, leeward areas.
Bathymetry	Depth of area, and depth and nature of surrounding seafloor determine the rate of wave resuspension and removal of sediments, and light limitation in turbid water.	Lower reef slopes, areas surrounded by shallow sea floor.
History	Exposure history facilitates adaptation to local conditions, and determines successional stage.	Large and fast changes from historical to present conditions.
Ecology	Substrata suitable for coral recruitment.	Low coral recruitment success.
	Fish abundances balance community structures (herbivores controlling macroalgal biomass, predators controlling invertebrate populations).	High fishing pressure, low abundances of herbivores and predators.
	Biodiversity (functional redundancy, presence of more tolerant taxa)	Low biodiversity.
	Additional coral disturbances (coral predators, diseases, bleaching, storms) determine cumulative stress.	Frequent and severeadditional disturbances, synergistic stressors.

4. The conceptual model

So far, we have seen that corals, and many groups that interact with corals, are either inhibited or promoted by eutrophication, especially through (a) trophic shifts resulting from greater availability of dissolved and particulate inorganic and organic nutrients, (b) light limitation in deeper water, and (c) sedimentation. We have also seen that the severity of response to eutrophication varies spatially – with reefs located in poorly flushed locations at greatest risk of damage – and depends on a number of environmental and biological conditions at a site.

A qualitative model (Fig. 3) may help to summarise the numerous links between water quality (blue) and the condition of inshore coral reefs (yellow) in the context of external environmental processes and parameters that determine exposure, resistance and resilience (grey). At first sight, the model could appear daunting– but it is easily deconstructed into a set of causal links, many of which are explained in the text above, and briefly summarised here:

a. *Pollutant loads* are typically determined by geographic conditions (vegetation cover, rainfall, soil type, slope etc) and land management.

b. *The main sources of new dissolved nutrients* are rivers, point sources, upwelling and the atmosphere via rain; de/mineralization and biological uptake and release (see below at d, e) affect both nutrient gains and losses.
c. *The main sources of new particulate matter, particulate nutrients and sediments* entering coastal marine systems are rivers and point sources; burial is the main pathway of removal, whilst biological uptake and release (see below at d, f) affect both gains and losses.
d. *Cycling:* Dissolved and particulate matter enter into complex cycles of conversions by way of biological uptake and release, chemical absorption and desorption, and sedimentation and resuspension. Dissolved inorganic nutrients can increase concentrations of phytoplankton and other forms of particulate organic matter, leading to higher turbidity, reduced light and increasing rates of sedimentation.
e. *Dissolved inorganic nutrients* release nutrient limitation in some m*acroalgae*, which may thus gain a competitive advantage over corals.
f. High levels of *particulate organic matter* in reef waters favor the growth of some macroalgae; some species of coral also gain advantage at moderate levels of particulate organic matter. High phytoplankton loads are also linked to an increased survival of filter-feeders that thrive when particle loads are high. Crown-of-thorns starfish have filter-feeding pelagic larvae that appear to be limited by the availability of large phytoplankton. Circumstantial and experimental evidence suggest large terrestrial runoff events and/or increased oceanic productivity resulting from phytoplankton blooms stimulate outbreaks of this starfish. Higher fish biomass is also often associated with increasing marine productivity.
g. *Light reduction* resulting from turbidity leads to greatly reduced photosynthesis and recruitment in corals, and a shallower depth limit for reef development. Stress from light limitation varies greatly between species, and after light-dependent species disappear a reef will have fewer species and suffer a decline in biodiversity. Settlement of coral larvae is also controlled by light intensity and spectral composition. It also decreases the depth range for some species of macroalgae. In contrast, many heterotrophic filter-feeders can only live at low light conditions. The main symptoms of light limitation in the field are, therefore, reduced coral recruitment and biodiversity, a shallower depth limit for reef growth, and a shift from phototrophic to heterotrophic processes.
h. Increased *sedimentation* **s**everely disturbs most aspects of for coral reefs. Settlement rates are low, and young corals have high mortality rates on sediment-covered surfaces. The effects of increased levels of sedimentation are, therefore, slower recovery from disturbance, altered species composition and reduced coral diversity. Sediment coated or mixed with organic matter is more difficult to remove than clean calcareous sediments, and is particularly detrimental to small organisms including newly settled corals. Sedimentation also inhibits the growth of some species of crustose coralline algae.
i. Some *macroalgae* compete for space with corals, and space occupied by macroalgae is often unavailable for the settlement of coral larvae.

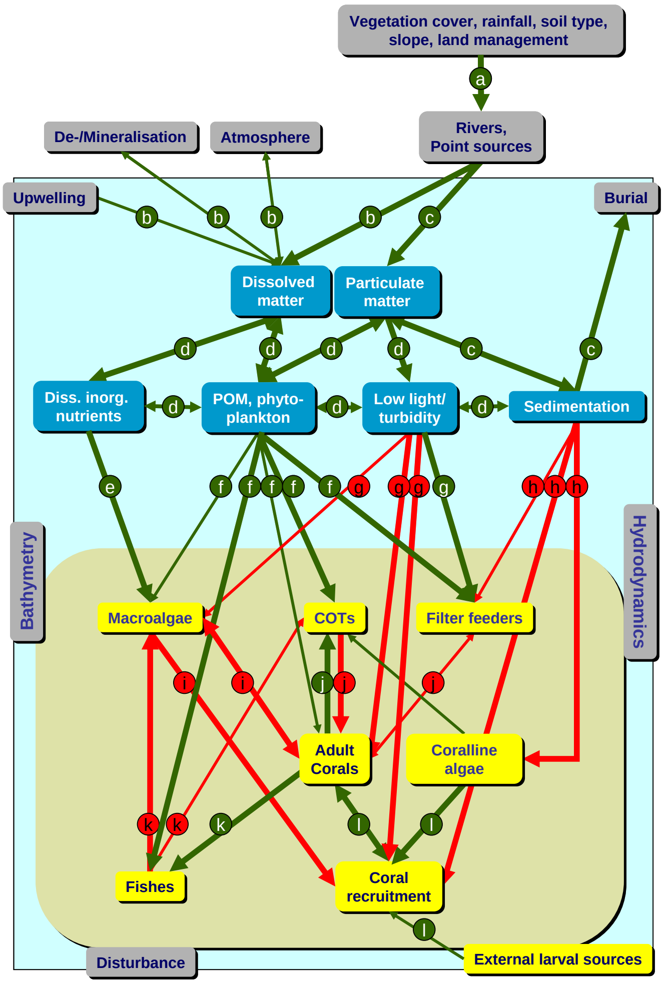

Fig. 3 Conceptual model of the relationships between the main water quality constituents (blue) and biotic responses (yellow) on coral reefs (pale yellow box) within their marine setting (light blue box). External and geophysical factors (grey boxes) are additional drivers further shaping the relationships. Thick arrows indicate strong effects, thin arrows, weaker effects. Arrow colours indicate the direction of change (green: promote, red: reduce), round letter symbols identify the main processes and relationships explained in the text. Minor links are omitted for clarity. Abbreviations: POM, particulate organic matter; COTS, crown-of-thorns starfish.

j. *Fishes* directly interact with corals and macroalgae. Grazing fishes can control macroalgae, and a reduction in grazing by fishes can leads to their proliferation at high nutrient levels. High coral cover leads to high structural complexity, promoting local fish abundances, and sustaining grazing pressure on algae. Predatory and omnivorous fish have also been associated with controlling abundances of juvenile crown-of-thorns starfish and numerous other invertebrates, playing an immensely important role to protect the integrity of numerous ecological functions. It remains to be investigated to what extent herbivorous fishes are directly affected by turbidity.

k. *Crown-of-thorns starfish*: coral loss from predation by crown-of-thorns starfish is greater than coral loss through any other cause of mortality. However, adult crown-of-thorns starfish are also controlled by food availability as outbreaks collapse at less than 5% coral cover. Crown-of-thorns starfish also require crustose coralline algae for settlement and as food in their first 6 months after metamorphosis, but it is unknown whether their survival is food limited at this stage.

l. Successful coral recruitment is a prerequisite for the recovery of corals from disturbances. Coral recruitment depends on the availability of larvae, either from external larval sources upstream or from local brood stock (self-seeding). Coral larvae also need crustose coralline algae on which to settle.

Lastly, models need to include the factors that determine exposure, resistance and resilience to changing water quality. As has been shown above, the main factors are hydrodynamics, spatial location (distance to a point source, to upwelling etc), bathymetry, and the propensity to disturbance; all of which strongly determine the fate of a specific reef system exposed to eutrophication.

5. Discussion

This study has shown that increased abundances of macroalgae, reduced recruitment success in corals, and increased frequencies of outbreaks of *A. planci*, are arguably the most significant effects of eutrophication on coral reefs. While variations in nutrients, light and sediment are naturally found in pristine conditions, they are often exacerbated by human activity, such as land clearing, agriculture and urban activities, and aquaculture. With severe exposure, reefs will suffer shallower reef development, changed coral community structure and greatly reduced species richness. Hence, increasing exposure to terrestrial runoff causes reef ecosystems to become less diverse, and compromises their ability to maintain essential ecosystem functions and to recover from disturbances.

The study has also shown that the severity of eutrophication effects is strongly determined by a relatively small number of environmental properties and biotic conditions. Several of these factors are identical to those that determine the resistance and resilience of coral to bleaching caused by warming oceans from greenhouse gas emitted by the burning of fossil fuels and deforestation. For example, fast currents, topography, proximity to deep water and a diverse community with abundant herbivores are considered reliable factors in predicting the likelihood of coral communities dying as a result of bleaching (West and Salm 2003) – as they are in predicting death arising from eutrophication. However, reefs in shallow waters are – relative to deeper reef slopes – tolerant of the turbidity associated with eutrophication but sensitive to bleaching. A better understanding of the additive or interactive effects between eutrophication and climate change is clearly needed.

The conceptual model presented here incorporates the main factors associated with coral reefs exposed to changing water quality. It may serve as a starting point to develop quantitative models to predict how specific coral reefs would respond to environmental change. Such models could be used to assess degradation and recovery prospects due to deteriorating or improving water quality, and to identify research gaps.

Although disturbances are a normal and important aspect of their environment, coral reefs are inherently quite stable over time, with coral cover and composition often not changing for many years, or even decades (Connell 1997). After severe acute and short-term disturbances, coral in shallow, well-lit and well flushed windward reefs can recover within 10 to 15 years if larvae are plentiful (Connell 1997). Recovery takes longer (possibly up to 50 years) on deeper reef slopes, and in poorly flushed settings (such as lagoons) and areas with poor connectivity. Recovery from chronic and human-induced disturbances that alter the physical environment is also slower and less commonly observed than recovery from fast and acute disturbances (Connell et al. 1997).

In most Indo-Pacific coral reefs including the Great Barrier Reef (GBR), coral cover has been declining at a rate of 0.2 – 1.5% per year since the 1960s (Bruno and Selig 2007). To avoid further reef degradation, it is essential that the disturbance frequency does not exceed the average recovery time in anyone location, and that chronic disturbances are minimised. In recent times, the frequency and nature of major disturbances such as outbreaks of crown-of-thorns starfish, coral bleaching, and severe storms, have exceeded the capacity of many reefs around the world to recover (Bruno and Selig 2007; Wilkinson 2004). Such large-scale events are typically not controllable by management action. In contrast, eutrophication is much more manageable – and can often be prevented by preserving vegetation cover on land, reducing fertiliser loss into the sea, and restricting aquaculture facilities to well-flushed locations where dilution is rapid and the resistance and resilience of reefs is greatest. With increasing reef disturbances as a result of global warming and seawater acidification, management of water quality and healthy fish abundances will be critically important to the future of coral reef ecosystems (Wooldridge et al. 2005).

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