Conceptual Model of the effects of terrestrial runoff on the ecology of corals and coral reefs of the GBR

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Summary

Coastal coral reefs, like other marine coastal ecosystems, are exposed to increasing loads of nutrients, sediments and other pollutants discharged from the land. Terrestrial runoff resulting in poor coastal water quality is therefore a growing concern for most nations endowed with coral reefs, and a major factor contributing to a global decline in the condition and diversity coral reefs. The objective of this study was to build a conceptual model to address the specific question: “How are changes in river loads linked to changes in lagoonal water quality and biogeochemical processes, and do these changes alter the condition and ecological properties of coral reefs”? The conceptual model presented here summarises the present understanding of the processes involved the dynamics of nutrients, sediments, and their effect on the condition of inshore coral reefs of the GBR. The model combines published process understanding, budgets and reviews including Furnas et al. (1995); Furnas (2003); Wolanski et al. (2004); Alongi and McKinnon (2005); Fabricius (2005); Schaffelke et al. (2005), and Fabricius et al. (2007). This conceptual model may now be used to populate a process-based numerical model to test scenarios / model risks in relation to changes in water quality, to design conceptual diagrams as communication tools, and to identify future research priorities.

1. Background

Detrimental effects of terrestrial runoff of nutrients and sediments on coral reefs have been documented in a number of regions, including 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 others, as reviewed in Fabricius (2005). Expanding and intensifying land use, deforestation, and a growing human population in catchments adjoining coral reef systems are the principal cause of declining coastal water quality.

On the Great Barrier Reef (GBR), human population density in the adjacent catchments is relatively low, however annual river discharges of fine sediments, nitrogen and phosphorus into the ~1,500 km long GBR lagoon are estimated to average 15×10^6, $4\text{-}8 \times 10^4$ and $7\text{-}11 \times 10^3$ tones, respectively (Furnas 2003; Brodie et al. 2003). This is an estimated five- to tenfold increase in nutrient and sediment discharges compared with pre-European times ~150 years ago, and largely attributed to expanding agriculture that has increased sediment and nutrient runoff to coastal waters (McCulloch et al. 2003). Sediments, nutrients and other materials discharged by river freshwater plumes typically remain within the coastal zone, although large floods can extend all the way across the continental shelf. Most of the sediment carried by rivers is deposited close to the river mouths. The fine fraction is then distributed northward along the coast by wave action and coastal currents, undergoing cycles of resuspension and sedimentation. Some of the sediments may be transported offshore by cyclone events, or in near-bottom nepheloid layers (Wolanski et al. 2003; Brinkman et al. 2004). A large proportion of the nutrients in river water (ca 40-80% of N and 70-80% of P) is initially attached to sediment particles and deposited in sediments near the coast (Furnas 2003). Dissolved inorganic nutrients are rapidly assimilated by phytoplankton and bacteria and converted to organic matter, which is then dispersed within the coastal zone.

On the GBR, the scientific understanding how in detail runoff alters the ecological condition of inshore coral reef communities has substantially improved within the last 10 – 15 years (van Woesik et al. 1999; Koop et al. 2001; Furnas 2003; McCulloch et al. 2003; Fabricius 2005; Fabricius et al. 2005; Haynes et al. (in press)) . Coral reefs in shallow nearshore water grow in habitats that are naturally affected by freshwater runoff and sediment resuspension. Corals in these habitats spend more energy removing settled particles, but some can derive energy by feeding on suspended particulate organic material (Anthony and Fabricius 2000). Enhanced levels of suspended sediment and nutrients, however, change the condition of coral reef communities in a number of ways. The conceptual model depicted in Figure 1 summarises the present-day understanding of the effects of increasing exposure of coral reefs to nutrients and sediment runoff from the land to the ecological balance between main ecosystem components of reefs of the GBR.

2. Conceptual Model

Figure 1 depicts the conceptual link between river discharges and coastal water quality, focusing on four main water quality constituents (blue), and shows how the condition of inshore coral reefs (yellow) is coupled to coastal water quality. The relationships between the most relevant model elements shown in Figure 1 are detailed here:

2.1. Water quality

The four most relevant **water quality drivers** are inorganic nutrients, particulate organic matter, light reduction from turbidity, and sedimentation; these cycle and interact in a complex way (Furnas 1997; Alongi and McKinnon 2005). **Hydrodynamics** determine the direction and distance of the transport of materials (dissolved and particulate matter) and the spread of flood plumes in the coastal waters (King et al. 2001). **Bathymetry** in the coastal water is an essential background driver determining local water quality, as depth, together with the shelter provided by reefs affect the balance between sedimentation and resuspension of materials (Larcombe et al. 1995; Wolanski et al. 2005). There is substantial variation in the long-term average concentrations of nutrients, chlorophyll, sediments and water clarity in the GBR (Furnas 2003; Brodie 2007; De'ath, 2007), hence the exposure of coral reefs to high levels of nutrients and sedimentation varies both spatially and temporally (Appendix, Figures 1 and 2). The main processes of interest are:

a. Land use, together with vegetation cover, soil types, rainfall and hill slope angles, influences river loads of sediments and nutrients (Prosser et al. 2001; Brodie et al. 2003).
b. The main source of **new nutrients** into the inshore water column is river discharge (inshore), additional sources of new nutrients are upwelling (more relevant offshore), nitrogen fixation, and atmosphere (via rain) (Brodie et al. 2003; Furnas 2003).
c. Main sources of **new sediments** into the water column is river discharge (Furnas 2003).
d. Main pathways of nutrient removal from the water column are mineralization, denitrification, biological uptake, and burial (Furnas 2003; Alongi and McKinnon 2005).
e. Dissolved inorganic nutrients are taken up quickly by microalgae and bacteria, entering into the food chain as particulate organic matter, leading to organic enrichment (Furnas 1997).

2.2. Direct ecological effects on corals and other reef-inhabiting organisms

Coral reefs undergo cycles of episodic reef **disturbance** (e.g., by bleaching, storms, and hyposalinity) and recovery (Rogers 1993; Lapointe 1999). The successful recovery of coral reefs, through continued growth of adult corals, and coral recruitment, are therefore fundamental background drivers determining the status of coral reefs. **Hydrodynamics** are also essential background drivers, as currents and waves are essential to determine the flushing or retention of pollutants, and hydrodynamics also determine the connectivity of a reef to external sources of larvae. The main effects of water quality on corals are:

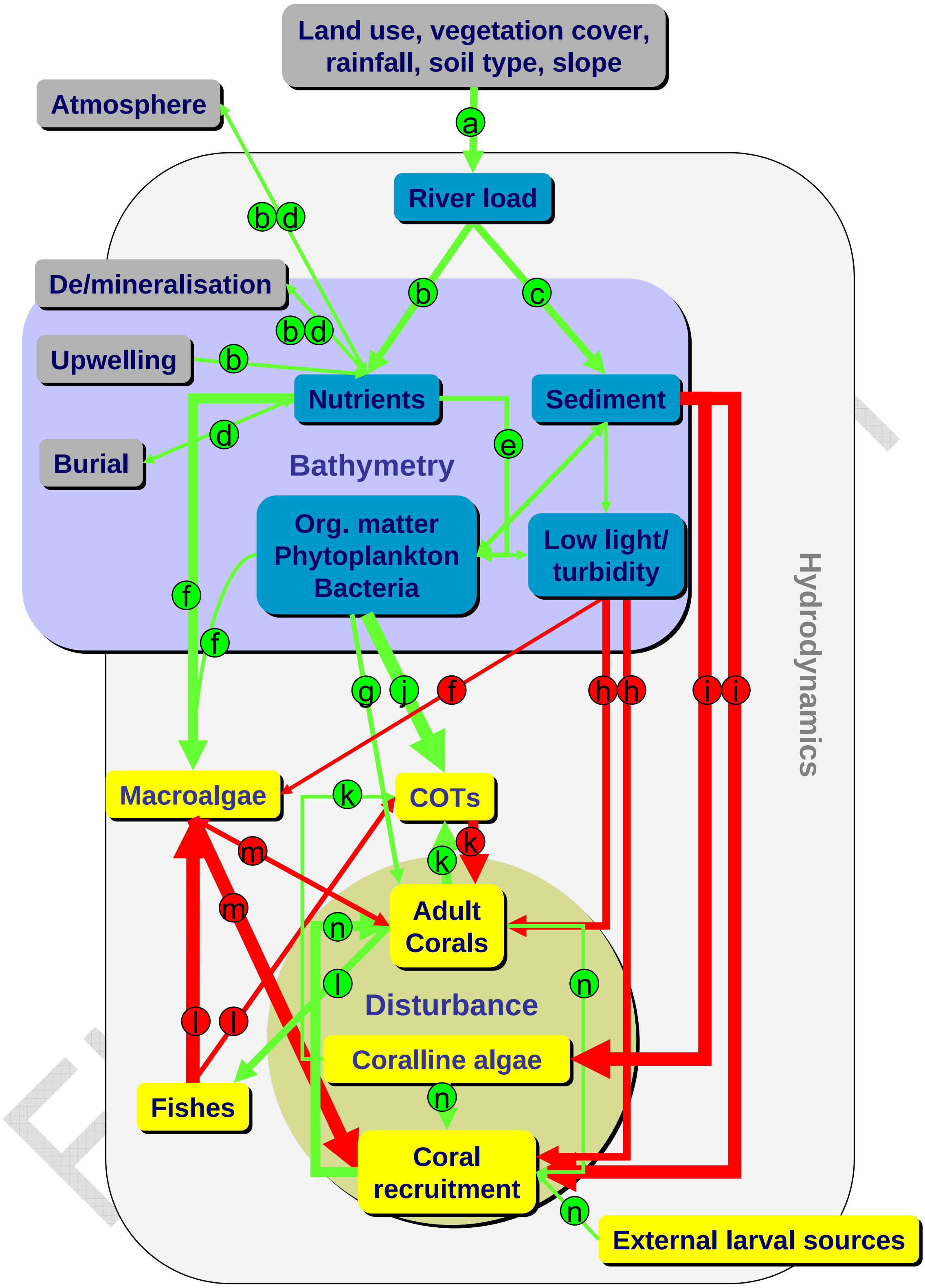


Figure 1: Conceptual model of the relationships between the four main water quality constituents (blue) and biotic responses (yellow). External and physical factors (grey boxes) further shape the relationships. Arrow thickness represents strength of links, their colour the direction of change (green: promote, red: reduce), round letter symbols identify the underlying processes which are explained in Chapter 2 in the main body of text.

f. **Macroalgae** can gain competitive advantage at high concentrations of dissolved inorganic nutrients (Lapointe 1999; Schaffelke et al. 2005). High levels of other organic matter in reef waters also favor the growth of some macroalgae, while light attenuation from turbidity decreases the depth range for some species of macroalgae (Schaffelke 1999).

g. Enhanced particulate organic matter stimulates the growth of some species of **corals** (Anthony 2000).

h. Light reduction from turbidity greatly reduces photosynthesis and recruitment in **corals**, and decreases the depth range within which phototrophic hard and soft corals can grow (Anthony and Fabricius 2000; Yentsch et al. 2002). Although coastal reefs can flourish at relatively high levels of particulate matter and silt, they are restricted to the upper 4 m depth in turbid water, while extending to >40 m in clear waters. Stress by light limitation varies greatly between species, reducing coral biodiversity as light-dependent species disappear. The settlement of coral larvae is also controlled by light intensity and spectral composition, hence reduced light reduces the depth where larvae settle (Baird et al. 2003). The main symptoms of light limitation in the field are therefore reduced **coral recruitment** and biodiversity, and a shallower depth limit for reef growth.

i. **Increased sedimentation** represents a severe disturbance for coral reefs. **Coral recruitment** rates are extremely low on sediment-covered surfaces, and young corals have high mortality rates when exposed to sedimentation, greatly reducing the ability of coral reefs to recover from disturbance (reviewed in Fabricius 2005). In adult **corals**, the sensitivity to sedimentation differs between species (Stafford-Smith and Ormond 1992; Philipp and Fabricius 2003). 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, newly settled corals and other small animals (Fabricius et al. 2003, Weber et al. 2006). Sedimentation also prevents the growth of some species of crustose coralline algae, which are essential for coral larval settlement (Harrington et al. 2005).

2.3. Altered performance of organism groups that interact with corals

j. Increased nutrients can increase chlorophyll concentrations in the coastal waters, particularly during summer (Brodie et al. 2007). Enrichment with particulate organic matter have been linked with an increased survival of filter feeders thriving at high loads of particles. The survival of filter-feeding larvae of the crown-of-thorns (**COT**) starfish *Acanthaster planci* increases ten-fold with each doubling of their phytoplankton food in experimental conditions. Circumstantial and experimental evidence suggests large land runoff events or increased oceanic productivity from phytoplankton blooms may stimulate COT outbreaks (Brodie et al. 2005; Houk et al. 2007). In particular, enhanced biomass of phytoplankton >10 µm coincident with COT spawning increases larval survival and recruitment to start a population outbreak. Models show that a doubled supply of microalgae can explain increases in outbreak frequencies from once in 50 – 100 years to one in 12 –15 years (as presently observed), through a 10-fold increased survival of the filter feeding larvae (De'ath in prep).

k. The crown-of-thorns starfish *Acanthaster planci* predates on corals, and coral loss from COTS predation is greater than coral loss through any other form of mortality (Sweatman et al. 2005). COTS outbreaks, however, collapse when corals are depleted below ~5% (Moran 1988). COTS also require crustose coralline algae as food in their first 6 months after metamorphosis (Moran 1988; Keesing et al. 1997), but it is unknown whether their survival is limited by the food availability at this stage.

l. Fish abundances are reduced at reduced structural complexity after corals die (Wilson et al. 2006). Using high coral cover as a proxy for structural complexity, it may therefore be argued that high coral cover might promote local fish abundances, helping to sustain grazing pressure on algae. It is unclear whether the abundances of herbivorous fish on coral reefs are different in turbid compared with clearer water (Wolanski et al. 2004), as found for some north Australian estuarine fish (Cyrus and Blaber 1993). Reduced abundances of herbivorous fish leads to proliferation of macroalgae (McCook 1999). Reduced abundances of predatory and omnivorous fish have also been associated with enhanced survival of COTS juveniles, although invertebrate infauna rather than fish are the main predators of juvenile COTS (Keesing 1995; Keesing et al. 1996).

m. Some macroalgae compete for space with corals ((Tanner 1995; Jompa and McCook 2003; Lirman 2001), and space occupied by macroalgae is often unavailable for the settlement of coral larvae (Rogers and Miller 2006).

n. The recovery of adult coral populations from disturbances depends on successful coral recruitment. Coral recruitment depends on the availability of larvae from external larval sources further upstream, and from local brood stock (self-seeding). Coral larvae also need crustose coralline algae (or turf algae if sedimentation is low) to settle upon (Harrington et al. 2004).

3. Model Refinement

The conceptual model presented above incorporates the most relevant elements and processes, and may serve as a starting point to develop a simple numerical process-based model of ecosystem responses to environmental change, to separate and quantify the effects of water quality and natural disturbances on the condition of the GBR. The 'HOME' model (Wolanski et al. 2004; Wolanski and De'ath 2005) or a similar model could be used as framework to build upon. A model would focus on the strongest associations (fat arrows in Figure 1) and initially ignore the weaker ones (thin arrows). Future numerical models should be developed and presented in a user-friendly manner so they can be used by researchers and managers to test hypotheses and to help identifying research priorities. The numerical model could be used to test scenarios or model risks in relation to changes in water quality, for example:

- How do effects of large disturbance events (COTS, cyclones, floods) and of climate change differ between reefs with high and low exposure to altered water quality? How different is their speed of recovery from such disturbances?
- What is the likely condition of inshore coral reefs under future land use scenarios at various scales (whole of system, within individual catchments / within-reef scale)? This question may be best addressed through models rather than through monitoring. This is due to the incongruity in location and scales, between the location of restoration efforts (paddock-scale, on land) and of the monitoring sites (regional, within the inshore GBR).
- What are the relative effects of pulsed exposure to poor water quality (flood events) versus chronic water quality changes on the condition of inshore reefs? Again, models populated with real monitoring data may provide the clearest answer to such long-term questions.

The conceptual model may also be converted into a series of conceptual diagrams, to aid communication with the wider public. An example of such conceptual diagram is presented in Figire 2. Such diagrams are useful to translate scientific knowledge and concepts into a language that is easily understood by managers, politicians, farmers, highschool students and other stakeholders.

As more water quality specific monitoring data will become available, a range of additional refinements, including the thin arrows in Figure 1, as well as additional spatial and temporal considerations, and interactions between water quality and biological responses could be built into more detailed numerical models. The model domain could be built nested both biologically and spatially. For example, population data (recruit densities, juvenile growth rates, size-specific mortality etc), could be used for one or few well-described coral species and scaled up to represent coral communities. Detailed data from one specific region (e.g., Tully River – Dunk Island area, or the Whitsundays area) could be used as test area, and scaled up to a regional or lagoon-wide model. The following processes and sub-processes may be incorporated:

3.1. Spatial and temporal considerations

There are substantial differences in the water quality characteristics of the GBR at all spatial and temporal scales (Appendix, Figures A1 and A2). Spatially, the exposure of individual coral reefs to high levels of nutrients varies significantly across and along the continental shelf (De'ath 2007). Furthermore, there is substantial variation within reefs and at even smaller spatial scales. Reefs at greatest risk from degradation by altered terrestrial runoff are:

- Located north of and near a river mouth, and within or near the coastal boundary zone (Appendix, Figure A3).
- Surrounded by a shallow sea floor from which sediments and nutrients are re-suspended by wind waves.
- Within poorly flushed bays, back reefs or lagoons where sediments accumulate.
- On deeper reef slopes where light is limiting and sediments accumulate (Appendix, Figure A4).
- Areas that are frequently affected by other forms of disturbance, including storms, COTS and bleaching. In these areas, population maintenance is particularly dependent on fast recruitment and the growth of remnant colonies.

The more of these characteristics apply to a location, the more likely it is that this location will experience degradation when exposed to terrestrial runoff. Well-flushed shallow reef crests surrounded by deep sea floors are likely to have the lowest exposure to sedimentation and should have the highest level of resistance and resilience, especially when inhabited by healthy populations of herbivores that protect against overgrowth by sediment-trapping macroalgae. In contrast, deeper back reef slopes are most vulnerable to exposure.

Temporal considerations:

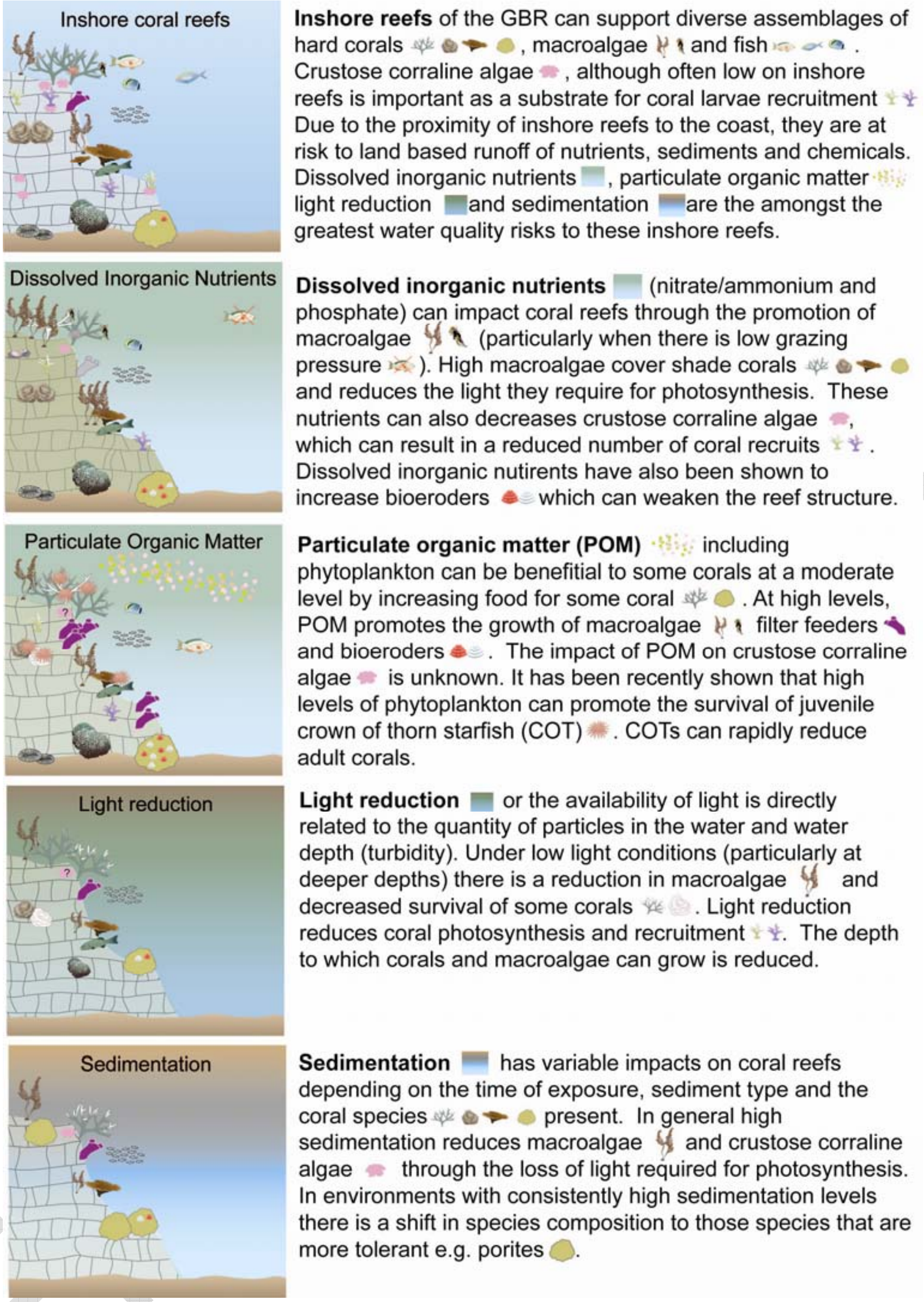
- The effects of episodic exposure events are vastly different from those of chronic exposure (however the differences are poorly understood).
- Both the frequency of episodic exposure, and times between exposures greatly affect the outcome of such disturbances.
- The timing of exposure is highly relevant (e.g., phytoplankton blooms coinciding with time of COTS reproduction when larvae are pelagic filter feeders).

3.2. Water quality and sediments:

- Include river characteristics into model (sediment loads versus nutrient loads versus freshwater volume, and their inter-annual differences)
- Dissolved inorganic nitrogen and phosphorus undergo complex cycling that influences their fate, transport and bio-availability (Appendix, Figures A5a and b).
- Terrestrial runoff may alter marine sediment quality (nutrient contents and grain size). Small particles from river discharges remain suspended for longer than coarse particles, they carry more nutrients and pesticides (Gibbs et al. 1971) and have greater light absorption capacity than coarse ones (Moody et al. 1987).
- The role of nutrient storage and release by the seafloor sediment is highly significant but is presently poorly understood.
- Agrochemicals such as herbicides or insecticides can also play an important role. For example, some herbicides suppress the photosynthesis of corals and macroalgae at low concentrations. The concentrations of agrochemicals currently measured within the GBR are lower than those resulting in physiological effects during short-term exposure experiments, but the effects of chronic exposure is largely unknown and likely to be more relevant. Agrochemicals have not yet been included in the model as the knowledge of environmental concentrations of the numerous and diverse substances, and species-specific responses of the main life stages is still extremely limited.
- Reduced salinity from terrestrial runoff can also kill benthos (below a level of around 20 ppt; naturally, episodically).

3.3. Effects on biota:

- While the four components of water quality (inorganic nutrients, particulate organic matter, light reduction from turbidity, and sedimentation) all negatively affect coral recruitment, they have contrasting effects on coral physiology, coral growth, and on organisms that interact with corals (Figure 2, Appendix, Figures A6a - d).
- Synergistic effects between sediments and nutrients are little understood, but such interactions might be highly relevant e.g., through organic enrichment of sediments and formation of marine snow.
- Dose-response relationships are rarely linear (Appendix, Figure A7a). Such non-linear relationships have to be factored into models assessing the effects of water quality exposure on coral reef organisms.
- The severity of responses is often a combined function of the magnitude and the duration of exposure (Appendix, Figure 7b), and further depends on species tolerance levels. Contrasting species-specific tolerance levels to sedimentation and nutrients in adult corals can lead to altered species composition and perhaps lower biodiversity.
- Coral diseases by bacterial and fungal infections have caused widespread coral mortality in the Caribbean. Infection rates and the spread of infection in Caribbean colonies has been experimentally linked to increased nutrient levels (Bruno et al. 2003), but to date similar associations have not been documented in the GBR.
- Heterotrophic filter feeders proliferate at high nutrient concentrations. Benthic filter feeders may compete for space with phototrophic corals, leading to a shift in trophic guilds, and bioeroding filter feeders thrive and weaken the structural strength of reefs, making them more susceptible to cyclone damage.



Inshore reefs of the GBR can support diverse assemblages of hard corals, macroalgae and fish. Crustose corraline algae, although often low on inshore reefs is important as a substrate for coral larvae recruitment. Due to the proximity of inshore reefs to the coast, they are at risk to land based runoff of nutrients, sediments and chemicals. Dissolved inorganic nutrients, particulate organic matter light reduction and sedimentation are the amongst the greatest water quality risks to these inshore reefs.

Dissolved inorganic nutrients (nitrate/ammonium and phosphate) can impact coral reefs through the promotion of macroalgae (particularly when there is low grazing pressure). High macroalgae cover shade corals and reduces the light they require for photosynthesis. These nutrients can also decreases crustose corraline algae, which can result in a reduced number of coral recruits. Dissolved inorganic nutirents have also been shown to increase bioeroders which can weaken the reef structure.

Particulate organic matter (POM) including phytoplankton can be benefitial to some corals at a moderate level by increasing food for some coral. At high levels, POM promotes the growth of macroalgae filter feeders and bioeroders. The impact of POM on crustose corraline algae is unknown. It has been recently shown that high levels of phytoplankton can promote the survival of juvenile crown of thorn starfish (COT). COTs can rapidly reduce adult corals.

Light reduction or the availability of light is directly related to the quantity of particles in the water and water depth (turbidity). Under low light conditions (particularly at deeper depths) there is a reduction in macroalgae and decreased survival of some corals. Light reduction reduces coral photosynthesis and recruitment. The depth to which corals and macroalgae can grow is reduced.

Sedimentation has variable impacts on coral reefs depending on the time of exposure, sediment type and the coral species present. In general high sedimentation reduces macroalgae and crustose corraline algae through the loss of light required for photosynthesis. In environments with consistently high sedimentation levels there is a shift in species composition to those species that are more tolerant e.g. porites.

Figure 2: Conceptual diagram of some of the main processes summarised in Figure 1. From: Joelle Prange (unpublished).

4. Key Research Priorities

A preliminary review of the data and processes needed to develop a numerical model, and of questions that could be addressed with this model, is given here. The compilation of the conceptual model has highlighted the following knowledge gaps:

Water quality:

- **River load** estimates: Better model estimates of flow vs concentrations, and better estimates of nutrient loads during wet and dry years.
- What are the **retention times** of dissolved nutrients and fine particulate matter in the lagoon? E.g., how long are river discharges retained in the coastal area if biological uptake is factored in,
- What are the **fates of the additional nutrients** originating from terrestrial runoff? How much of these nutrients enter coastal food webs and how quickly, are they removed through sedimentation or biological uptake?
- What are the pathways of **organic matter formation**, and its ecological effects?
- What are the **transport and retention processes of the additional sediment** in river discharges: how to best input/parameterise the dynamics of mud and of wind-induced mud resuspension events? Is turbidity likely to increase/have increased in coastal areas in response to intensive land use or loss of vegetation cover? If yes, how widespread spatially and temporally (after a discharge event)?
- Better knowledge of **nepheloid layers** exporting materials to the offshore
- What are the differences in **sediment quality** (grain size, nutrient, detrital and clay contents etc) between new river sediments and old seafloor sediments?
- What is the spatial and temporal distribution of **light attenuation**?

Ecological responses:

- Link water quality maps to **maps of ecological properties** of reefs (populations, communities and biodiversity (esp. coral and fish): Map of risk for reef degradation due to run-off, controlling for time since last major disturbance or some other form of successional stage.
- What are the **explicit links between changes in river discharge** rates and changes in inshore ecosystems?
- What are environmental **thresholds**, how much is too much? What are the relative merits of reducing sediments vs nutrient vs herbicide discharges?
- What are the links between coastal nutrient enrichment, **macroalgal** dynamics and coral recruitment/re-establishment on coastal reef systems?
- Links between terrestrial nutrient input events and **COT** population dynamics
- Links between **turbidity and fish** abundances, and coral cover and fish abundances
- Effects of **chronic** exposure to agrochemicals and turbidity versus exposure to **episodic** spikes.
- Are **coral pathogens** linked to nutrient availability?
- Better parameterisation of other disturbances such as bleaching from thermal stress. What are the recovery rates of inshore reefs after disturbance? What are the interactions between WQ effects and climate change?

5. Conclusions

The conceptual model presented here shows that the main ecological processes that regulate the condition in coral reefs exposed to changing water quality are:

- **Shifts in trophic webs (top-down and bottom-up effects):**
    - Dissolved nutrients → converted into organic matter including phytoplankton → consumed by COTS larvae → COTS feed on coral → coral consumption induces COTS starvation
    - Dissolved nutrients → converted into organic matter → consumed by corals
    - Dissolved nutrients → taken up by and proliferate macroalgae
    - Fishes → consume and control macroalgae
    - Fishes → consume COTS juveniles
- **Space competition** between macroalgae and coral, especially after disturbance
- **Positive interaction** between corals that provide shelter to fishes, and fish that remove space competitors (macroalgae) for corals
- **Disturbance and recovery dynamics** (recruitment, resilience, connectivity)

In conclusion, from the perspective of inshore coral reefs of the GBR, the four most relevant water quality drivers are inorganic nutrients, particulate organic matter, light reduction from turbidity, and sedimentation. Agrochemicals may also be important, but their exposure levels and ecosystems effects are still poorly understood. The severity of water quality effects depend both on exposure and on the sensitivity which varies between species groups and between life stages. Gradients of exposure are found in the field along water quality gradients both naturally and in places where nutrient and sediment exposure levels are enhanced by human activity. The main processes of direct impact are the inhibition of coral recruitment by even moderate levels of sedimentation and light attenuation from turbidity. Coral larvae and newly settled juvenile stages, rather than adults, are at greatest risk from poor water quality. Sediment layers covering otherwise suitable hard substratum inhibit the successful recruitment of juvenile corals, either directly, or through negative effects on crustose coralline algae which are a preferred settlement substratum. The two main indirect effects are (a) potentially increased frequencies of outbreaks of crown-of-thorns starfish (COTs) in response to phytoplankton availability, resulting in enhanced predation pressure on corals, and (b) the proliferation of macroalgae in response to increased nutrient levels, resulting in more severe space competition especially after disturbance has removed corals.

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Appendix

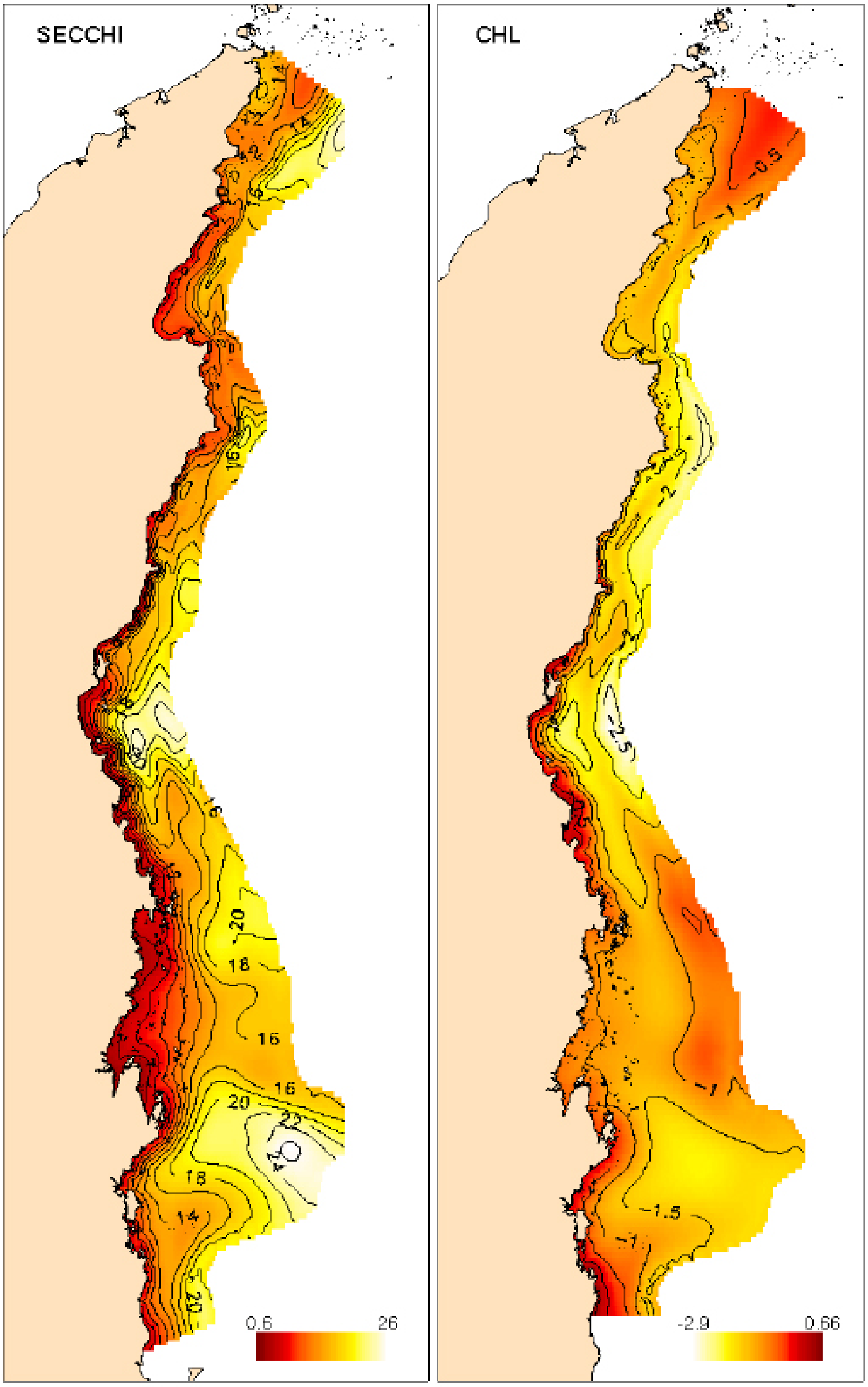


Figure A1: Estimated spatial trends of secchi disk visibility and water column chlorophyll (log base 2 – i.e., a change of one unit represents a doubling or halving). From De'ath (2007).

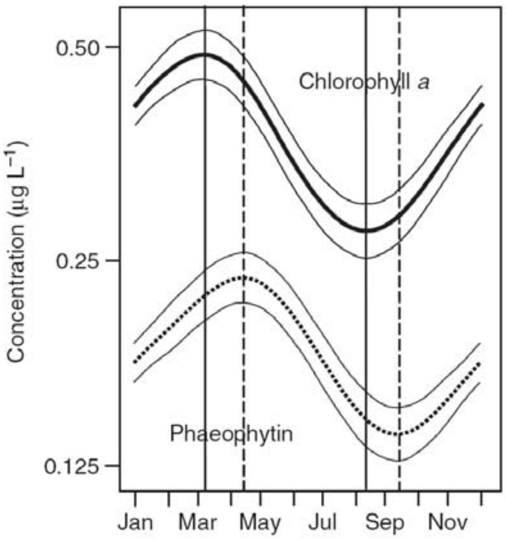


Figure A2: Seasonal changes in chlorophyll on the Great Barrier Reef. From Brodie et al. (2007)

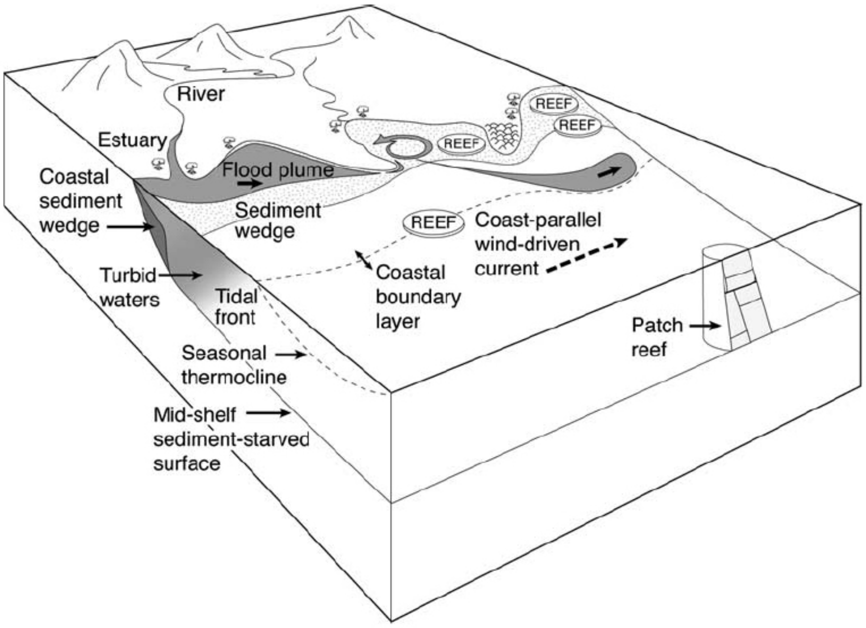


Figure A3: Schematic representation of the GBR coastal zone, with some key oceanographic features. It encompasses tidal rivers, estuary and adjacent inner shelf, and a dynamic seaward limit which often coincides with the 20m isobath. The coastal boundary zone is formed when river waters mixed with turbid inshore waters are trapped along the coast. It can encompass an area of 30,000 km^2 (15% of the shelf area) and a water volume of 300 km^3 (4% of total shelf water volume) (Furnas, 2003). River floods, typically lasting only a few days, enter the shelf as plumes, which rapidly break up into patches due to the presence of headlands and capes. From Alongi and McKinnon (2005).

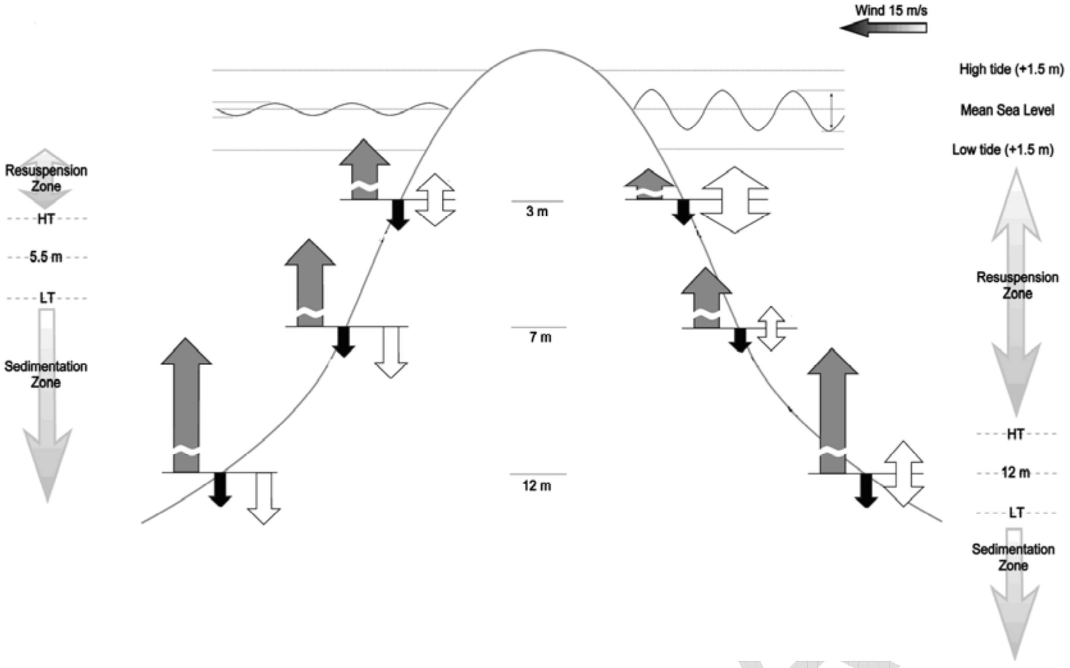


Figure A4: Schematic representation of the observed fine sediment budget at High Island, northern GBR. The windward side is to the right, the lee side to the left. Black downward arrows = sedimentation rates (mg cm^{-2} d^{-1}) in calm weather. Dark grey upward arrows = potentially resuspendable fine sediment (1000 × mg cm^{-2}). White arrows, pointing downward if only sedimentation occurs; both upward and downward if resuspension also occurs = storm sedimentation/resuspension rates. Wave characteristics, and the resuspension and sedimentation zones at high tide (HT) and low tide (LT) are also shown. Modified from Wolanski et al. (2005).

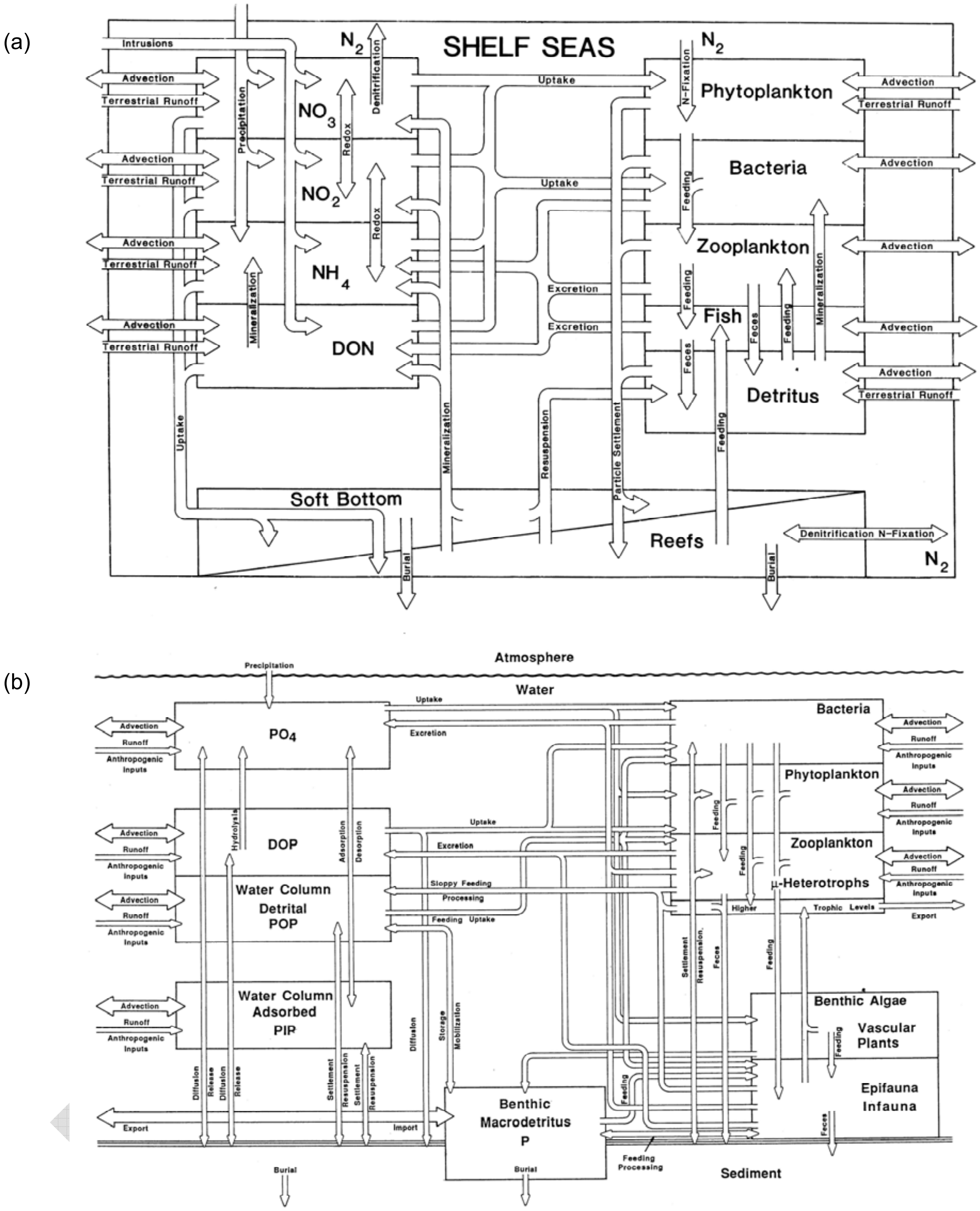


Figure A5a and b: Conceptual model of the water column nitrogen and phosphorus budget and cycling in the GBR. From: Furnas et al. (1995); Furnas (1997).

	Dissolved inorg. nutr.	POM	Light reduction	Sedimentation
Fecundity	↓		↓	↓
Fertilization	⬇	↓	—	—
Embryo develop./ larval surv.	⬇	↓	—	—
Settlement / metamorphosis	↓	↓	⬇	⬇
Recruit survival			↓	⬇
Juvenile growth / survival			↓	↓

(a)

	DIN	DIP	POM	Light reduction	Sedimentation
Calcification	↓	↓	↑	⬇	⬇
Tissue thickness	—	—	↑	↓	⬇
Zooxanthellae density	⬆	—	↑	↑	↓
Photosynthesis	↑	↑	↑	⬇	⬇
Adult colony survival	—	—	↑	↓	⬇

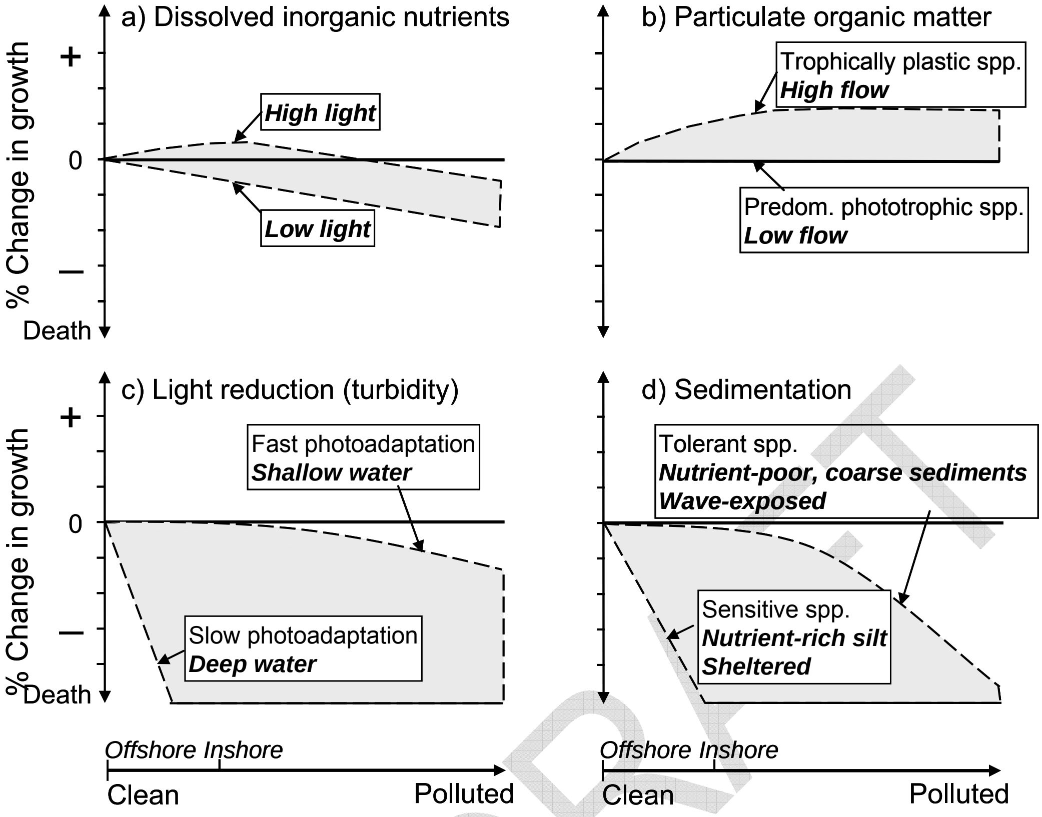
(b)

	Dissolved inorg. nutr.	POM*	Light reduction	Sedimentation
Crustose coralline algae	↓			⬇
Bioeroders	↑	⬆		↓
Macroalgae	⬆	↑	⬇	↓
Heterotrophic filter feeders		⬆	⬆	↓
Coral diseases	↑			↑
Coral predators		⬆		

(c)

* including phytoplankton

Figure A6: Effects of the four main water quality variables on (a) coral recruitment; (b) physiological measures in corals, (c) organisms within coral reefs that interact with corals, and (d) coral growth (page 25). From Fabricius (2005).



(d)

Figure A6 (continued).

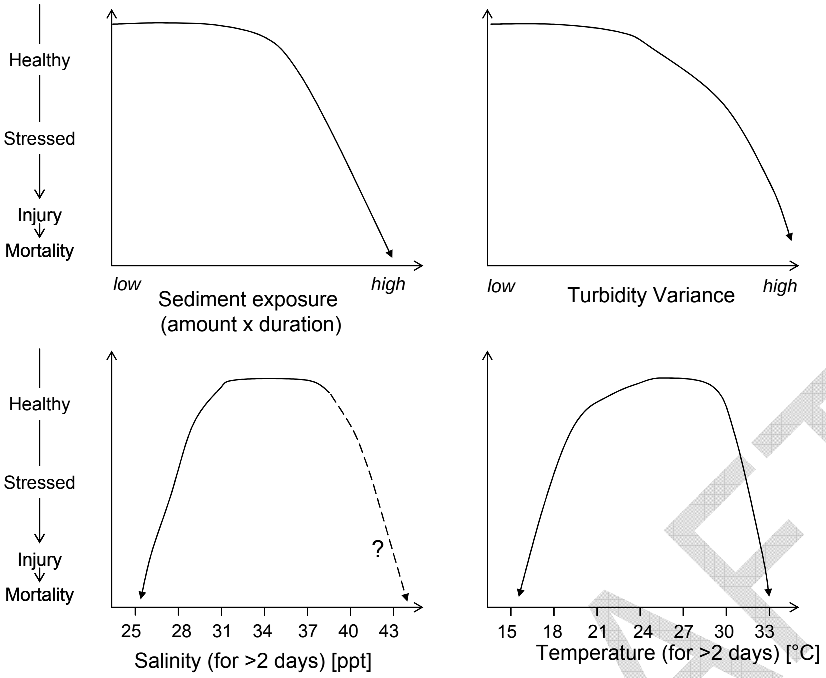


Figure A7a. Schematic representation of the responses of corals to changes in water quality. Note that responses are often non-linear. From Gilmour et al. (2006).

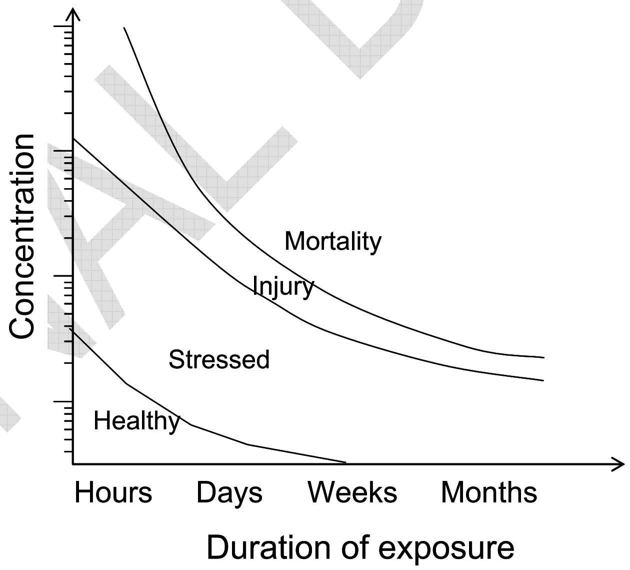


Figure A7b. Schematic representation of the responses of corals to changes in water quality. Responses are generally a combined function of the duration of exposure, and the amount (concentration, or load) of exposure (Philipp and Fabricius 2003). Modified from Gilmour et al. (2006).