

Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis

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Abstract

This paper reviews and evaluates the current state of knowledge on the direct effects of terrestrial runoff on (1) the growth and survival of hard coral colonies, (2) coral reproduction and recruitment, and (3) organisms that interact with coral populations (coralline algae, bioeroders, macroalgae and heterotrophic filter feeders as space competitors, pathogens, and coral predators). The responses of each of these groups are evaluated separately against the four main water quality parameters: (1) increased dissolved inorganic nutrients, (2) enrichment with particulate organic matter, (3) light reduction from turbidity and (4) increased sedimentation. This separation facilitates disentangling and understanding the mechanisms leading to changes in the field, where many contaminants and many responses co-occur. The review also summarises geographic and biological factors that determine local and regional levels of resistance and resilience to degradation. It provides a conceptual aid to assess the kind of change(s) likely to occur in response to changing coastal water quality.

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1. Introduction

Around the world, water quality in coastal areas is changing in response to rapidly increasing fertiliser use and land clearing (Vitousek et al., 1997; Tilman et al., 2001; Smith et al., 2003). Annual nitrogen fertiliser use has increased globally more than sixfold since 1960 (Matson et al., 1997), land clearing continues at a rate of 1% of the earth's surface per year (GESAMP, 2001), and coastal urbanisation is expanding disproportionately to human population growth. Oxygen-depleted seafloor zones, caused primarily by river-borne agricultural nitrogen and phosphorus, have doubled in number and expanded in size since 1990, presenting clear evidence that many coastal waters are becoming more eutrophic (GESAMP, 2001). Coastal coral reefs, like other marine coastal ecosystems, are increasingly exposed to growing

loads of nutrients, sediments and pollutants discharged from the land. Terrestrial runoff is therefore a growing concern for most of the 104 nations endowed with coral reefs (Bryant et al., 1998; Spalding et al., 2001).

Field studies have provided a large body of information showing that sedimentation, nutrient enrichment and turbidity can degrade coral reefs at local scales (Table 1). At regional scales, it has often been difficult to assess causal relationships between increasing terrestrial runoff and reef degradation, because pollution effects and other disturbances are typically confounded, historical data are often missing, and reef communities change naturally along gradients from oceanic conditions (low siltation, high water clarity, generally low nutrient levels except during upwelling periods) to terrestrially influenced conditions (fluctuating salinity, variable or high silt and nutrient levels, variable or reduced water clarity). As nutrients increase, coral reef communities change from dominance of nutrient-recycling symbiotic organisms such as corals (in oligotrophic oceanic waters), to

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Table 1

List of some of the more comprehensively documented field assessments on the effects of enhanced terrestrial runoff, and other forms of pollution, on the ecology of coral reefs

Location	Agent	Response	Source
Northern Gulf of Aqaba (Eilat), Red Sea	50% increase in nutrients from floating fish farms	50% coral mortality from benthic algal blooms, 3–4 fold reduced reef calcification, 50% increased P/R ratio	Loya (2004)
	Sewage discharge, spillage of phosphate dust	Increased algal growth trapping sediment; fourfold increased mortality in <i>Stylophora pistillata</i> , possibly from reduced light, inhibition of calcification, and increased sedimentation	Walker and Ormond (1982)
Reunion Island, Indian Ocean	Coastal urbanisation, groundwater enriched with nutrients from untreated sewage	Higher coral cover, coral diversity, fish diversity and density of sea urchins, and lower macroalgal density on reefs away from nutrient enrichment and in the 1970s before nutrient enrichment, than on nutrient-enriched reefs. High bioerosion, calcification slower than reef erosion on nutrient enriched reefs	Cuet et al. (1988), Montaggioni et al. (1993), Naim (1993) and Chazottes et al. (2002)
Hong Kong	Excess pollutants, nutrients, sediment dredging	Low coral recruitment, few zooxanthellate octocorals, disappearance of giant clams (<i>Tridacna</i> spp.), high bioerosion	Morton (1994) and Hodgson and Yau (1997)
Japan	Eutrophication and sedimentation	Declining coral cover	Shimoda et al. (1998)
	Gradients away from rivers	Change in coral community composition away from source	West and Van Woesik (2001)
Philippines	Excess sedimentation from logging	Declining coral cover, declining biodiversity due to disappearance of sediment-sensitive species over 12 months, inhibition of coral settlement	Hodgson (1990a) and Hodgson and Walton Smith (1993)
Indonesia	Excess nutrients and sedimentation	Low coral cover, reduced coral diversity, unaltered vertical extension but low skeletal density in massive corals, increased bioerosion	Edinger et al. (2000), Tomascik et al. (1997), Edinger et al. (1998) and Holmes et al. (2000)
Great Barrier Reef	Gradient in nutrients and turbidity	Increased macroalgal cover and richness (esp. red and green macroalgae), reduced octocoral richness	Fabricius et al. (in press) and Fabricius and De'ath (2004)
	Gradient away from river	Reduced coral cover, richness; increased filter feeders and macroalgae near source	van Woesik et al. (1999)
	Turbidity	Decreasing richness of zooxanthellate octocorals	Fabricius and De'ath (2001b)
	Inshore–offshore gradient, terrestrial runoff Sedimentation gradient	Increasing density of internal macrobioeroders towards the coast Decreasing cover of crustose coralline algae	Hutchings et al. (in press) Fabricius and De'ath (2001a)
Kanehoe Bay, Hawaii	Nutrients	Reduced coral cover, increased filter feeders, increased macroalgal cover	Smith et al. (1981), Hunter and Evans (1995), Stimson and Larned (2000) and Stimson et al. (2001)
Barbados	Eutrophication gradient	Photosynthetic pigments increase with increasing nutrient enrichment. Convex modal responses in gross photosynthesis, respiration, linear extension, calcification (enhanced by nutrients, depressed by turbidity)	Marubini (1996), Tomascik and Sander (1985) and Tomascik (1990)
		Reduced species diversity, probably due to differences in sediment rejection abilities, combined with feeding and reproductive strategies, altered community structure; increased bioerosion in coral rubble	Tomascik and Sander (1987b) and Holmes (2000)

Table 1 (continued)

Location	Agent	Response	Source
		Reduced gamete formation, larval development and settlement, reduced recruit and juvenile density and diversity, juveniles larger, increased juvenile mortality	Tomascik and Sander (1987a), Tomascik (1991), Hunte and Wittenberg (1992) and Wittenberg and Hunte (1992)
Grand Cayman Island	Untreated fecal sewage, sixfold increased bacterial biomass	Fivefold increased internal bioerosion by the boring sponge <i>Cliona delitrix</i>	Rose and Risk (1985)
Costa Rica (2 sites)	Sedimentation	Low live coral cover, low species diversity, and large average colony diameters, high acid-insoluble residues incorporated in skeleton on exposed reef	Cortes and Risk (1985)
Brazil (2 sites)	Eutrophication	High macroalgal abundances, high density of heterotrophs	Costa Jr et al. (2000)

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increasing proportions of macroalgae (on eastern continental margins naturally exposed to river runoff), and further to heterotrophic filter feeders (in nutrient-enriched areas of upwelling or lagoons) (Birkeland, 1987). Although coastal coral reefs can flourish at relatively high levels of particulate matter and siltation (Anthony, 1999), they tend to be restricted to the upper 10 m depth (in extreme cases 4 m depth) in turbid water, while extending to >40 m in clear oceanic waters (Yentsch et al., 2002).

This review compiles the current state of knowledge on runoff-specific responses in coral reefs, in order to aid assessment of the effects of terrestrial runoff at regional scales. Inorganic nutrients and particulate material, although not 'classical' pollutants, are arguably the most important contaminants at national and regional levels (GESAMP, 2001), and this review will focus on assessing the effects of these materials on reef communities. However, contamination by pesticides, heavy metals, hydrocarbons or other human-made pollutants can also significantly affect the health of reefs at local scales (Guzman and Holst, 1993). For example, heavy metals such as copper and zinc and some hydrocarbons have been linked to reduced fertilization, fecundity and growth in adult corals (Heyward, 1988; Brown, 1987; Loya and Rinkevich, 1987; GESAMP, 2001). Some herbicides (e.g., diuron and atrazin) cause rapid (but reversible) photophysiological stress in corals after short-term exposure at environmentally relevant concentrations of $1 \mu\text{g l}^{-1}$ (Owen et al., 2003; Jones and Kerswell, 2003; Jones et al., 2003; Negri et al., in press); their effects at chronic low-level exposures are still largely unknown. Other studies, too numerous to be listed here, document the uptake of a variety of human-made pollutants by

adult corals; the effects of these substances on coral reefs are beyond the scope of this review.

This paper systematically reviews and synthesises the available information on the direct effects of terrestrial runoff on (1) calcification, tissue growth, zooxanthellae populations and photosynthesis in adult hard corals, (2) the six main stages of coral reproduction and recruitment, and (3) six groups of other reef organisms that affect hard coral abundances. The latter group includes those organisms that affect coral larval settlement, bioeroding filter feeders that weaken the structural strength of reefs, macroalgae, heterotrophic filter feeders and octocorals competing for space with corals, disease pathogens, and coral predators. Responses of each of these groups are assessed separately against exposure to the four main water quality parameters, namely: (1) dissolved inorganic nutrients, (2) suspended particulate organic matter, (3) light reduction from turbidity and (4) sedimentation. This separation disregards additive or synergistic effects, but helps to understand the mechanisms for change in the field where many contaminants and responses co-occur. Furthermore, the paper identifies geographic and biological properties influencing the level of resistance and resilience of reefs to degradation.

2. Direct effects of terrestrial runoff on hard corals

2.1. Colony calcification, tissue growth and symbiosis

2.1.1. Dissolved inorganic nutrients

Considerable effort has gone into experiments studying the direct effects of elevated dissolved inorganic

Table 2

List of some representative studies of direct effects of terrestrial runoff on adult corals (see also Figs. 1 and 2)

Parameter	Response	Source
(a) <i>Enrichment with dissolved inorganic nutrients</i>		
NH ₄ , NH ₄ plus PO ₄ ³⁻	Increased zooxanthellae density, increased protein synthesis by zooxanthellae	Muscatine et al. (1989)
NH ₄ (15 μM)	After 8 weeks, increased zooxanthellae density, increased chlorophyll and N per zooxanthella	Snidvongs and Kinzie (1994)
NO ₃ (0, 1, 2, 5, 20 μM)	Calcification decreases with increasing NO ₃ to 50% of controls, effects significant at ≥ 1 μM. After 30–40 days: at ≥ 1 μM, increased N per zooxanthellae, increased zooxanthellae density. At ≥ 5 μM NO ₃ , increased zooxanthellae size, chlorophyll per zooxanthellae, photosynthesis, increased coral protein through greater zooxanthellae biomass. At 20 μM NO ₃ , 30% increased chlorophyll and zooxanthellae density, reduced respiration per unit protein	Marubini (1996)
NH ₄ (10 μM and 20 μM)	After 9 weeks: unaltered buoyant weight gain at 10 μM, reduced buoyant weight gain (–60%) at 20 μM	Ferrier-Pages et al. (2000)
NO ₃ (2 μM)	No change in zooxanthellae density or rate of photosynthesis. Reduced buoyant weight gain (–34%) after 3 weeks	Ferrier-Pages et al. (2001)
NH ₄ (10 or 20 μM)	Inconsistent effects on linear extension and buoyant weight after 1 year: 10–20% reduction, or no effect, or slight increase. Reduced lipids	Koop et al. (2001)
NH ₄	Increased zooxanthellae density, chlorophyll concentration. Decreased linear extension	Stambler et al. (1991)
NO ₃ (15 μM)	After 2 weeks, reduced primary production, unaltered zooxanthellae density and chlorophyll concentrations. Temperature effects enhanced by presence of nitrate	Nordemar et al. (2003)
PO ₄ ³⁻ (2 μM)	Increased photosynthesis, reduced calcification	Kinsey and Davies (1979)
PO ₄ ³⁻	No effect on zooxanthellae density or their protein production	Muscatine et al. (1989)
PO ₄ ³⁻ (1.2 μM)	Slowed calcification, unaltered zooxanthellae density, lower C and P per zooxanthella	Snidvongs and Kinzie (1994)
PO ₄ ³⁻ (0, 0.2, 1, 5 μM)	After 30 days: no change in photosynthesis, organic productivity, zooxanthellae density or size, tissue biomass; calcification up to 20% decreased in one species with increasing PO ₄ , unaltered in another	Marubini (1996)
PO ₄ ³⁻ (2 μM)	After 9 weeks, reduced buoyant weight gain (–60%), increased gross photosynthesis (up to +150% increase)	Ferrier-Pages et al. (2000)
PO ₄ ³⁻ (2 or 4 μM)	Inconsistent effects on growth rates after 1 year: increased calcification, linear extension and/or reduced skeletal density in some species. Increased lipids	Koop et al. (2001)
PO ₄ ³⁻	No effects on zooxanthellae density or linear extension	Stambler et al. (1991)
NH ₄ (10 or 20 μM) plus PO ₄ ³⁻ (2 μM)	Reduced buoyant weight gain (–60%), increased gross photosynthesis (up to +150% increase)	Ferrier-Pages et al. (2000)
NH ₄ plus PO ₄ ³⁻ (20 and 4 μM)	Increased mortality in <i>Pocillopora damicornis</i> after 1 year	Koop et al. (2001)
(b) <i>Enrichment with suspended particulate matter</i>		
Increased particulate and dissolved nutrients from fish excretions	Increased linear extension	Meyer and Schultz (1985)
<i>Artemia</i> food	No effect on density of zooxanthellae	Muscatine et al. (1989)
Particulate and dissolved nutrients released from fish farm	In adult corals, increased growth, oocyte and testes numbers, unaltered survival. In small coral fragments, reduced growth probably due to physical effects (burial by settled particulate matter, light reduction)	Bongiorni et al. (2003b) and Bongiorni et al. (2003a)
Suspended particulate matter (SPM), sedimentation, eutrophication gradient	Increased linear extension at moderate SPM, reduced linear extension at high SPM due to smothering, reduced light levels and reduced zooxanthellae photosynthesis. Small average colony size. No effect on partial mortality	Tomascik and Sander (1985) and Lewis (1997)

Table 2 (continued)

Parameter	Response	Source
1–32mg l ⁻¹ SPM	Increased SPM feeding, covering up to 50% carbon and 30% nitrogen required for tissue growth at high particle concentrations. No effect on calcification	Anthony (1999)
1–16mg l ⁻¹ SPM	After 4 weeks exposure: unaltered calcification. Increased tissue biomass but unaltered lipids in one species; convex modal change in tissue biomass and lipids in response to SPM in a second species	Anthony and Fabricius (2000)
Cross-shelf gradient	Increased linear extension, reduced skeletal density towards inshore environments. Highest annual calcification inshore, lowest offshore	Lough and Barnes (1992)
<i>(c) Light reduction from turbidity</i>		
Reduced light, excess phosphate, sedimentation	Reduced calcification, increased mortality	Walker and Ormond (1982)
Turbidity	Changed coral community structure and life forms, reduced species richness, compressed depth zonation	Loya (1976), Acevedo and Morelock (1988), Fabricius and De'ath (2001b) and Crabbe and Smith (2002)
Shading	After 5 weeks, reduced growth, net primary productivity and respiration. Altered community structure after bleaching and death in several coral species	Rogers (1979)
Turbidity	High turbidity (28–30 NTU) increased mucus production, depressed P:R ratio to below 1.0, possibly due to increased respiration	Telesnicki and Goldberg (1995)
Shading (plus 1–16mg l ⁻¹ SPM)	After 4 weeks exposure: reduced calcification, reduced tissue biomass, reduced lipids in 2 species. In 1 species, feeding on 16mg l ⁻¹ SPM annulled shading effects	Anthony and Fabricius (2000)
<i>(d) Sedimentation</i>		
Low sedimentation	Increased respiration, reduced net photosynthesis; Species-specific rejection efficiency	Abdel-Salam et al. (1988)
Sedimentation	Coral cover and coral species diversity increase with distance from the sediment source Partial or total burial of colonies, bleaching and surface colonisation by filamentous blue-green algae	Acevedo and Morelock (1988)
Sedimentation	Low or brief sedimentation: reduced photosynthetic yield; high or prolonged sedimentation: loss of zooxanthellae, partial mortality, but species-specific tolerances	Philipp and Fabricius (2003)
Sedimentation (30 mg cm ⁻²)	Species-specific rejection efficiency	Hodgson (1990b)
Sedimentation (50–1000mg cm ⁻² of four particle sizes, and 200mg cm ⁻²)	Species-specific rejection efficiency: rejection rates positively correlated with calice size, and faster for medium-fine (63–250 μm) than for coarse (500–1000 μm) sediment. Bleaching and partial mortality within 48 h in some species, but clearance times generally <2 days	Stafford-Smith and Ormond (1992) and Stafford-Smith (1993)
Sedimentation (up to 14mg cm ⁻² d ⁻¹)	Passive sediment removal more successful for fine grain sizes, tall polyps, and convex colonies, active removal independent of colony morphology	Lasker (1980)
Heavy sedimentation (>10mg cm ⁻² d ⁻¹ and >10mg l ⁻¹)	Reduction in coral species richness, live coral cover, coral growth rates, calcification, net productivity of corals, and rates of reef accretion; increased proportion of branching forms. Species-specific capabilities for particle rejection and for surviving lower light levels	Rogers (1990)
High sedimentation	Reduced linear extension: growth inversely related to sediment resuspension	Cortes and Risk (1985) and Dodge et al. (1974)
Sedimentation	Loss of zooxanthellae, reduced calcification	Bak (1978)
Sedimentation	Reduced mean colony sizes (through stunted growth and/or reduced life expectancy)	Van Woesik and Done (1997)

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Table 2 (continued)

Parameter	Response	Source
Sedimentation	Increased mean colony sizes (through reduced recruitment)	Wesseling et al. (2001), Cortes and Risk (1985) and Tomascik and Sander (1985)
Terrestrial runoff and sedimentation	Partial mortality: High proportion of injured or algae infested corals, and/or high soft coral cover, and/or high proportion of rocky substrate suitable for, but unoccupied by, living corals	van Katwijk et al. (1993)
Sedimentation	Partial mortality: colony lesion densities increase with sedimentation, wave exposure, colony size, and intensity of human reef exploitation. Colony size, live coral cover and <i>Acropora</i> cover decrease with intensity of human reef exploitation	Wesseling et al. (2001)
Sedimentation	Reduced coral cover	Loya (1976), Cortes and Risk (1985), Acevedo and Morelock (1988), Brown et al. (1990), Chansang et al. (1981) and Morelock et al. (1983)
Sedimentation	Changed coral community structure and life forms, reduced species richness	Loya (1976), Morelock et al. (1983), Pastorok and Bilyard (1985), Acevedo and Morelock (1988), Rogers (1990), Brown et al. (1990), Edinger et al. (1998) and West and Van Woesik, 2001

nitrogen (DIN, as nitrate or ammonium) and phosphate (DIP) on coral calcification, tissue growth and zooxanthellae. Table 2a, and detailed reviews by Dubinsky and Stambler (1996) and Szmant (2002) show that most experiments were conducted at environmentally unrealistically high levels, and that significant inconsistencies exist across studies that are as yet unresolved. Many studies found that high levels of DIN and DIP both reduce calcification up to 50%, while other studies found no change in growth rates, or reported slightly increased rates of calcification and linear extension but reduced skeletal densities (Table 2a). Effects of DIN on tissue growth and composition vary across studies, with some reporting reduced lipids (Koop et al., 2001), and others finding enhanced zooxanthellae protein but unaltered host protein (Marubini, 1996). Increased DIP appears to have little effect on tissue growth. Most studies found that increased DIN increases zooxanthellae density, increases the contents of nitrogen and chlorophyll *a* per zooxanthellae, and increases photosynthetic rates. In contrast, high levels of DIP did not affect zooxanthella densities. In experimental studies, colony survival was generally unaffected by DIN and DIP, while coral mortality increased, for unknown reasons, in one species after a 1-years field exposure to high daily pulses of both DIN and DIP (Koop et al., 2001); however, such high and frequent nutrient pulses are unlikely to be encountered in nature for sustained periods except near sewage outfall sites.

Zooxanthellae are typically nitrogen-limited at high irradiance when ample photosynthetically fixed carbon is available (C/N ratios are up to 30), whereas they

may not be nitrogen-limited at lower irradiance (C/N ratios about 10; Falkowski et al., 1984; Dubinsky and Jokiel, 1994). Zooxanthellae densities increase in response to enhanced DIN availability because this nutrient is preferentially used for zooxanthellae growth rather than the growth of host tissue (in contrast to nutrients derived from zooplankton feeding which increase both tissue and zooxanthellae growth; Dubinsky and Jokiel, 1994). Reduced calcification at elevated DIN has been explained as follows: zooxanthellae populations increase after release of N limitation, these cells have preferential access to the available CO₂ which they use for photosynthesis, hence less CO₂ is available for calcification and CO₂ becomes a limiting factor (Marubini and Atkinson, 1999; Marubini and Thake, 1999). Evidence for this hypothesis is provided by data that show that DIN causes no growth reduction in the presence of high levels of bicarbonate (Marubini and Thake, 1999). Reduced calcification at higher DIP availability seems to be caused by another, as yet not fully understood mechanism (Marubini and Davies, 1996). Hypotheses focus on the reduced chemical CaCO₃ crystal formation in the presence of phosphate (Simkiss, 1964), or experimental artifacts based on lowered pH from using unbuffered PO₄. Possibly due to the presence of two different mechanisms, simultaneous increases of DIN and DIP generally do not result in interactive effects on calcification rates (Table 2a, Marubini and Davies, 1996).

In the field, both DIN and DIP are quickly taken up by phytoplankton and bacteria and benthic food webs. Hence elevated nutrients are available in their dissolved inorganic form only for short periods of time

over relatively limited areas. Severe direct effects of dissolved inorganic nutrients on corals appear restricted to heavily polluted, poorly-flushed locations such as semi-enclosed lagoons and bays, where they are linked to reduced reef calcification, coral cover and biodiversity (Table 1). Away from the coast, regions that regularly experience the upwelling of cool waters (i.e., rich in dissolved inorganic nutrients but no sedimentation or light reduction) have also been used to assess the effects of DIN and DIP on calcification. Coral calcification can be up to 50% reduced in upwelling regions, which has been attributed to elevated nutrients as well as to cool temperatures (Kinsey and Davies, 1979; Wellington and Glynn, 1983). Reef formation is noticeably restricted in places where upwelling is a common occurrence, such as along western tropical and subtropical land masses (Birkeland, 1987; Achituv and Dubinsky, 1990). This has led to the conclusion that reduced calcification from exposure to periodic or chronically elevated dissolved inorganic nutrients can substantially alter coral populations and communities (Kinsey and Davies, 1979; Hallock, 1988; Wilson et al., 2003); however cool temperatures may to a large part explain such low calcification (e.g., calcification declines by 50% with every 3° temperature in massive *Porites*; Lough and Barnes, 2000).

In summary, the available information suggests that short-term exposure to high levels of unprocessed DIN and DIP does not kill or greatly harm individual coral colonies, however chronically increased levels of dissolved inorganic nutrients may alter reef metabolism and reef calcification sufficiently to cause noticeable changes in coral communities. Existing data indicate (Fig. 1) that: (a) there is strong evidence that zooxanthellae numbers, chlorophyll per unit surface area, and photosynthetic rates increase with increasing DIN (but not DIP), affecting the transfer of energy, CO₂ and nutrients between zooxanthellae and host; (b) there is little evidence that dissolved inorganic nutrients alter tissue thickness, lipids or coral protein per unit surface area; and (c) while some studies found increased or unaltered skeletal growth (measured as linear skeletal extension, skeletal density and/or calcification), many controlled experimental studies found a reduction in growth at elevated levels of DIN and/or DIP. Combining the few existing physiological data with environmental data leads to the suggestion that coral growth (calcification) declines gradually with increasing dissolved inorganic nutrient availability (Fig. 2a), but levels of dissolved inorganic nutrients will often not greatly increase along pollution gradients. In reality, the response curves are likely to be more complex, for the following reasons: (1) there are complex interactions between the growth of tissue, zooxanthellae and calcification, (2) nutrient limitation occurs predominantly at high irradiance where carbon is available in overabundance, hence nutrient addition may be only of conse-

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

Fig. 1. Synthesis of documented direct effects (Tables 1 and 2) of the four main parameters of terrestrial runoff on the growth and survival in adult corals, based on published studies or known biological properties and processes. The arrows indicate the relative strength and direction of the response (arrows pointing up or down = increasing or decreasing, thick arrow = strong, medium = moderate, thin = weak effect); a dash indicates that a response is unlikely; empty cells indicate that insufficient data are available.

quence in highlight environments; (3) other limitations such as that of CO₂ co-occur; and (4) nutrient uptake rates are partly mass transfer limited, hence not only a function of concentrations but also of water currents (Hearn et al., 2001). All these factors are insufficiently considered in most experimental studies, and may contribute to explaining the inconsistencies between results.

2.1.2. Particulate organic matter

Particulate organic matter (POM) greatly contributes to nutrient availability in many coastal regions, because a majority of nutrients are discharged to the marine environment in particulate form, and much of the dissolved inorganic nutrients can be taken up and converted into particulate form within hours to days (Furnas, 2003). Suspended particulate matter in areas of high sediment resuspension can have a nutrient content of >5%, either contained in the bacteria, phytoplankton, zooplankton and detritus, or absorbed to the surfaces of fine inorganic particles; the nutrient content is even higher offshore where less inert material is suspended from the seafloor. POM can be used by a range of benthic organisms including corals (Lewis, 1976; Anthony, 1999). However the ability to utilize POM varies widely between coral species, and a number of species are naturally restricted to clear water habitats (Veron, 2000). Depending on species, feeding saturation may occur at low to moderately high levels of POM: some species become mixotrophic at high turbidity, while others remain mostly phototrophic and gain a small proportion of their energy demand from particle feeding (Anthony and Fabricius, 2000). Rates of POM intake furthermore depend on water current speeds, with intake rates being generally higher at moderate to fast flow than in sheltered locations.

Moderate loads of POM have been linked to increases in tissue thickness in some species (Tables 1 and 2b). Linear skeletal extension may double, while

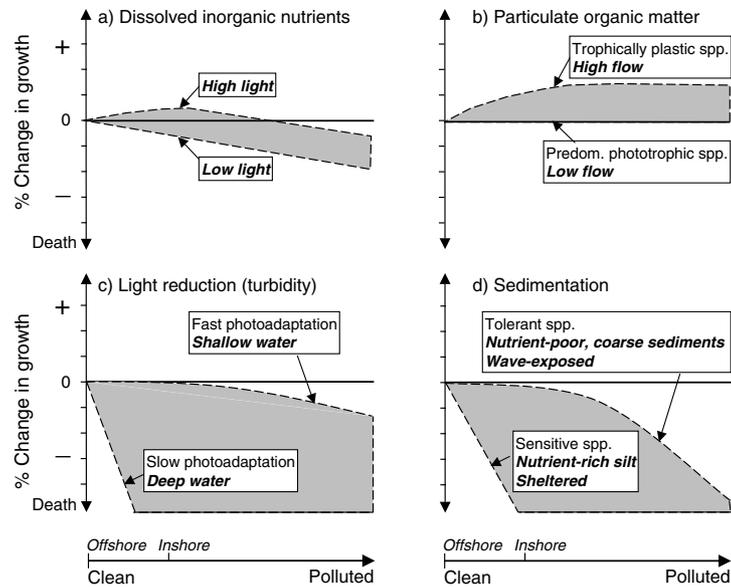


Fig. 2. Schematic representation of direct effects of terrestrial runoff on coral growth (measured as change in calcification and/or linear extension, i.e., addition of skeletal biomass) and survival along environmental gradients. Plotted are changes in coral growth in response to (a) uptake of dissolved inorganic nutrients, (b) feeding on suspended particulate organic matter, (c) light reduction from turbidity, hence reduction in gross photosynthesis, and (d) disturbance by sedimentation. The x -axis represents a hypothetical water quality gradient from offshore water quality to polluted conditions, also indicating the relative positions of offshore and inshore conditions unaltered by human activities. The y -axis scale represents relative units of changes in growth, with severe long-term reduction in growth effectively representing 'colony death'. Grey shading is used to approximate typical response envelopes due to species-specific differences (normal font) and local environmental conditions (bold italic font).

skeletal density may be up to 20% reduced in response to POM feeding, with varying effects on overall calcification rates. In fragile branching species, increased linear skeletal extension may be partly offset by greater breakage due to reduced skeletal density. Zooxanthellae densities appear to increase to a lesser extent in response to organic enrichment than in response to dissolved inorganic nutrients, possibly because POM promotes the growth both of host and zooxanthellae, in contrast to dissolved inorganic nutrients that are preferentially used for zooxanthellae rather than host tissue growth (Dubinsky and Jokiel, 1994).

In the field, coral calcification and growth appears to change in a modal fashion along eutrophication gradients: in areas of intermediate turbidity where particulate and dissolved nutrient loads were high, corals had higher concentration of photosynthetic pigments, calcification, gross photosynthesis and respiration compared to a cleaner site (Tomascik and Sander, 1985; Marubini, 1996). At the most eutrophic site, pigment concentration was even higher than at the intermediate site, however light reduction from turbidity annulated the growth advantages from POM feeding, consequently calcification, gross photosynthesis and respiration was lower at the most eutrophic site than at the intermediate site (Marubini, 1996). Photosynthetic pigment concentrations in corals have therefore been suggested as the most linear and hence most useful early-warning indicator for nutrification (Marubini, 1996).

In summary, the limited existing data suggest that moderate concentrations of POM can provide substantial energy and growth benefits for some, but not all coral species, especially at high water flow and high irradiance (Fig. 2b). Overall, of the four parameters of terrestrial runoff considered, POM is the one parameter that can enhance growth in some species, at moderate levels compensating for growth reduction from the other three parameters. At higher levels of POM, feeding saturation prevents additional energy gains, while losses from the associated light reduction, dissolved inorganic nutrients and sedimentation outweigh the benefits of POM feeding.

2.1.3. Light reduction

The availability of light decreases directly as a function of particle concentration and water depth, but also depends on the nature of the suspended particles (Te, 1997). Fine clays and organic particles are easily suspended from the sea floor, reducing light for prolonged periods while undergoing cycles of deposition and resuspension. Increased nutrient runoff into semi-enclosed seas accelerates phytoplankton production to the point that it also increases turbidity and reduces light penetration (Abal and Dennison, 1996). In areas of nutrient-enrichment, light for benthic organisms can be additionally severely reduced by dense stands of large frondose macroalgae (see below), and to a minor extent by particles settling on colony surfaces.

Shading temporarily reduces photosynthesis by zooxanthellae, leading to lower carbon gain, slower calcification and thinner tissues (Table 2c; Rogers, 1979; Telesnicki and Goldberg, 1995; Anthony and Hoegh-Guldberg, 2003). Within 5–10 days, many corals can adjust to somewhat lower light by increasing the size and amount of chloroplasts in zooxanthellae (not altering zooxanthellae densities per unit area), a process known as photoacclimation. However, light exposure on inshore reefs fluctuates through a fivefold range on a time scale of days to weeks as a result of tides, resuspension and clouds (Anthony and Hoegh-Guldberg, 2003). Under such variable conditions, photoacclimation does not significantly enhance gross productivity, because delays in upward- and downward-regulation of photosynthesis in response to altered light are symmetrical and compensate for each other over longer periods (Anthony and Hoegh-Guldberg, 2003). Therefore, the maximum depth for photocompensation (the depth range within which corals can survive or maintain active reef growth) diminishes as a direct function of turbidity from >40m to <4m depth (Birkeland, 1987; Yentsch et al., 2002).

In the field, the effects of light reduction on species richness are strongly depth-dependent, as light requirements greatly vary between species. Few species can tolerate the low light levels at deep depths or at high levels of turbidity. On the other hand, in high-irradiance conditions many slower-growing species are out-competed by fast-growing phototrophic species, hence species richness is often highest at intermediate light levels (Cornell and Karlson, 2000).

Historic data on water clarity in coastal marine systems are sparse. Indeed, only few records of changes in water clarity exist, and these are from places where research stations are located, or in areas of extreme pollution. Reduced visibility has been linked to phytoplankton blooms around a sewage outfall site in Kaneohe Bay, Hawaii (Hunter and Evans, 1995), and around floating fish farms in the Northern Red Sea (Loya, 2004). Some researchers argue that resuspension, governed by water depth and wave height, is the best predictor of turbidity over a sediment-covered seafloor, and nearshore water clarity therefore would not substantially increase due to increased sediment discharges from the land (Larcombe and Woolfe, 1999). In contrast, other researchers point out that biological processes such as water column productivity can also reduce water clarity, and that nepheloid layers can form and reduce water clarity offshore at regional scales, such as described off a mud-enriched coastline along the central Great Barrier Reef (Wolanski et al., 2003). Given the strong link between turbidity, light reduction and lower depth limits for coral reefs, more research is needed to understand conditions leading to long-term changes in water clarity in tropical coastal systems.

In summary, the effects of shading from turbidity are minimal in shallow water and progressively increase with increasing depth, but effects greatly vary between species (Fig. 2c). The main symptoms in the field are more compressed depth distribution zones, low biodiversity at deeper depths, and an overall more shallow lower depth limit for reef growth.

2.1.4. Sedimentation

Enhanced levels of sedimentation from coastal erosion have severely degraded many coastal reefs around the world (Table 2d, Rogers, 1990). Most sediments are imported into coastal marine systems via rivers, with >95% of the larger sediment grain fractions being deposited within a few kilometres of the river mouth, while fine grains may be transported over longer distances. Near the source, benthic communities are easily smothered by sedimentation (e.g., Golbuu et al., 2003), as high sedimentation rates (accumulating to >100mg dry weight cm^{-2} deposits) can kill exposed coral tissue within a period of a few days (Riegl and Branch, 1995). Lower (<100mg cm^{-2}) sedimentation levels reduce photosynthetic yields in corals (Philipp and Fabricius, 2003), and the removal of settled particles increases metabolic costs (Telesnicki and Goldberg, 1995). 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).

Coral damage appears to not only depend on the amount and duration of sedimentation, but also strongly depends on the sediment type. For example, tissue damage under a layer of sediment increases with increasing organic content and bacterial activity, and with decreasing grain sizes (Hodgson, 1990b; Weber et al., 2004). Low-level sedimentation ($\sim 12\text{mg cm}^{-2}$) when combined with transparent exopolymer particles (polysaccharides possibly exuded by bacteria and diatoms, called 'marine snow') kills newly settled coral recruits, whereas the same amount of sediment without the addition of marine snow does not reduce their short-term survival (Fabricius et al., 2003). Marine snow aggregates are found in high concentrations in coastal and inshore areas of the central Great Barrier Reef. These and similar data demonstrate the critical (but as yet poorly understood) interactions between sediment quality and quantity on coral damage (Fabricius and Wolanski, 2000). They also show that short exposure to sediments (few days) can cause long-term effects in populations, by removing cohorts of young corals and thus retarding reef recovery after a disturbance.

In the field, sedimentation is greatest on sheltered, wave-protected lagoons, bays or deeper reef slopes,

whereas sediment deposition is minimal in wave-exposed shallow-water areas. Sedimentation has been linked to profound changes in coral population structures, such as altered size frequencies, declining mean colony sizes, altered growth forms, and reduced growth and survival (Table 2d; Rogers, 1990). However, sedimentation tolerances greatly vary among coral species. Large colonies or those with branching growth forms or thick tissues are more tolerant of sedimentation, whereas small colonies or species with thin tissues and flat surfaces are often highly sensitive (Rogers, 1990). Some species with thick tissues can remove particles from their surfaces by tissue extension, mucus production or ciliary movement (such as found in *Fungia*) and are therefore quite sediment tolerant (Stafford-Smith and Ormond, 1992). As tolerance of sedimentation varies widely among species, a reduction in biodiversity is a common outcome of sedimentation stress, with fewer sensitive species and persistence of more tolerant species (such as massive *Porites*) in the coral communities (Table 2d).

In summary, sedimentation effects greatly vary between coral species, but also between sediment types and between environmental conditions (Fig. 2d). Only few species can persist in wave-protected regions where silt-sized, nutrient-enriched sediments are deposited. In contrast, more wave-exposed areas, or areas with nutrient-poor or coarse-grained sediments will support a wider range of species even at moderate levels of sedimentation.

2.2. Reproduction and recruitment

In most cases where terrestrial runoff causes reef degradation, disturbances other than eutrophication were the proximate causes of coral mortality, and runoff effects only became obvious when hard corals failed to reestablish after such disturbances (see Tables 1 and 3 for references). This indicates that coral reproduction and/or recruitment are affected by terrestrial runoff. Indeed, sedimentation and eutrophication have commonly been related to decreased juvenile densities on reefs (for references see Table 3). This section presents a brief literature overview to resolve how the four main parameters of terrestrial runoff affect the six main pre- and post-settlement processes, namely (1) gamete production, (2) egg fertilisation, (3) embryo development and larval survival, (4) larval settlement and metamorphosis, (5) recruit survival, and (6) juvenile growth and survival.

The limited available experimental data suggest that the three main pre-settlement stages of coral reproduction (gamete production, egg fertilization, and larval development and survival), as well as larval settlement rates, are sensitive to dissolved inorganic nutrients (Table 3). In acroporid corals, fecundity, egg sizes, egg

fertilisation rates and embryo development are all reduced, and the occurrence of irregular embryos increased, at slightly elevated levels of dissolved inorganic nutrients (from $1 \mu\text{M NH}_4$ and $0.1 \mu\text{M PO}_4$, i.e., at <10% of concentrations that detrimentally affect adult corals; Ward and Harrison, 2000; Harrison and Ward, 2001). Furthermore, spat densities were reduced at elevated levels of nitrogen (Ward and Harrison, 1997). Other observed effects include failed planulation in the brooding coral *Pocillopora damicornis*, and reduced egg sizes in *Montipora* that releases zooxanthellate eggs, after four months of exposure to elevated ammonium levels (Cox and Ward, 2002). The underlying mechanisms for such surprisingly high levels of sensitivity are presently not understood.

Laboratory experiments show that POM can inhibit egg fertilization rates, larval development, larval survival, settlement and metamorphosis (Gilmour, 1999). It is unknown to what extent juveniles (like adult colonies, see above) benefit from feeding on POM. Light affects both reproduction and recruitment, as coral fecundity decreases in low-light conditions, and coral larvae use light quantity and quality to choose their settlement site. At low light levels, corals preferentially settle on upper surfaces, where the risk of sedimentation damage is high, rather than on vertical or downward facing surfaces (Birkeland et al., 1981). At highly turbid conditions, coral recruits may undergo reverse metamorphosis, indicating conditions are unsuitable for continued development and growth (Te, 1992). Light reduction from turbidity is therefore likely to result in compressed depth zonations. Finally, sedimentation also strongly inhibits successful coral reproduction, especially coral settlement and recruit and juvenile survival. Sedimentation mortality thresholds for coral recruits are an order of magnitude lower than those for larger colonies (loads of tens rather than hundreds of mg cm^{-2} ; Fabricius et al., 2003). Few coral larvae settle on sediment-covered surfaces, and survival on such surfaces is minimal. At moderate to high rates of sedimentation, successful larval settlement is restricted to downward-facing surfaces where growth and survival are negatively affected by low light.

In summary, existing data suggest that coral reproduction and recruitment are far more sensitive to changes in water quality than adult corals, and are highly dependent on clean water and low sedimentation. Each of the four water quality parameters affect different stages of coral recruitment, and each of the effects is a negative one (Fig. 3): dissolved inorganic nutrients inhibits fecundity, fertilization, embryo and larval development, and possibly larval settlement; suspended particulate matter reduces pre-settlement survival; shading alters larval settlement, and sedimentation inhibits settlement and increases post-settlement mortality. Cer-

Table 3

Summary of reported effects of water quality on coral reproduction and early life stages in corals (see also Fig. 3)

Agent	Response	Source
$\geq 1 \mu\text{M NH}_4$ and/or $\geq 1 \mu\text{M PO}_4$	Reduced egg fertilisation rates in <i>Acropora</i> , increased rate of abnormally formed embryos	Harrison and Ward (2001)
NH_4 (11–36 $\mu\text{M m}^{-3}$) and/or PO_4 (2–5 $\mu\text{M m}^{-3}$)	Reduced spat densities on tiles in NH_4 enriched, but not in PO_4 enriched treatments	Ward and Harrison (1997)
NH_4 (11–36 $\mu\text{M m}^{-3}$) and/or PO_4 (2–5 $\mu\text{M m}^{-3}$)	Smaller and fewer eggs per polyp, reduced egg fertilization, increased proportion of irregular embryos	Ward and Harrison (2000)
20 $\mu\text{M NH}_4$ for 4 months	Failed planulation in <i>Pocillopora damicornis</i> . Reduced egg size, but no difference in fecundity and fertilisation in <i>Montipora</i> with zooxanthellate eggs	Cox and Ward (2002)
Increased nutrients from floating fish farms Eutrophication gradient	Reduced coral planulation Reduced gametogenesis, larval development, larval settlement, recruit and juvenile density and diversity, increased juvenile mortality	Loya et al. (2004) Tomascik and Sander (1987a), Tomascik (1991), Hunte and Wittenberg (1992) and Wittenberg and Hunte (1992)
Suspended sediment (50 and 100 mg l^{-1})	Reduced fertilisation, uninhibited post-fertilisation embryonic development, reduced larval survival and larval settlement	Gilmour (1999)
Turbidity by SPM (0, 10, 100, 1000 mg l^{-1})	Unaltered settlement rates, but increased rates of reversed metamorphosis after settlement (“polyp bail-out”) at 100 and 1000 mg l^{-1}	Te (1992)
Turbidity, sedimentation	Reduced fecundity	Kojis and Quinn (1984)
Shading	Reduced fecundity	Carlson (2002)
Shading	Species-specific effects on settlement and metamorphosis	Mundy and Babcock (1998) and Babcock and Mundy (1996)
Sedimentation	Reduced larval settlement on upper surfaces, especially when sediments are trapped by thick turf algae	Hodgson (1990a), Babcock and Davies (1991), Te (1992), Babcock and Mundy (1996), Babcock and Smith (2002) and Birrell et al. (in press)
Sedimentation (1–11.7 $\text{mg cm}^{-2} \text{d}^{-1}$)	Reduced recruit survival	Babcock and Smith (2002)
Muddy marine sediments (14 mg cm^{-2}), with and without enrichment with marine snow	After 48 h, reduced recruit survival in sediments enriched with marine snow	Fabricius et al. (2003)
Sedimentation	Increased juvenile mortality (abrasion, smothering, competition with algae)	Birkeland (1977), Sato (1985), Sammarco (1991) and Wittenberg and Hunte (1992)
Eutrophication, sedimentation	Increased mean colony sizes (interpreted as sign of low recruitment rates)	Cortes and Risk (1985) and Tomascik and Sander (1985)
Terrestrial runoff, heavy sedimentation (> 10 $\text{mg cm}^{-2} \text{d}^{-1}$ and > 10 mg l^{-1})	Reduced coral recruitment	Pastorok and Bilyard (1985), Rogers (1990) and Richmond (1997)
Water from creek runoff (28 ppt salinity)	Reduced fertilisation (–86%), reduced larval development (up to –50%)	Richmond and Walton Smith (1993)
Gradient in exposure to terrestrial runoff	Reduced recruit and juvenile density	Smith et al. (in press)

tainly more experimental studies are needed to verify and complement the data synthesis of Fig. 3.

3. Effects of terrestrial runoff on benthic organisms that affect corals and coral communities

Abundances of a large number of invertebrates and algae in coral reef communities change along environmental gradients influenced by terrestrial runoff. This section focuses on the responses of those organism groups that profoundly affect health and abundance of corals; hence changes in their abundances in response to terrestrial runoff induce secondary or indirect effects

on corals. The six main groups of organisms are those that (1) facilitate coral settlement (especially crustose coralline algae), (2) alter the structural strength of the reef substratum (internal bioeroders), (3) compete for space with corals (macroalgae), (4) do not contribute to reef calcification (heterotrophic filter feeders and octocorals), (5) infect corals with diseases, and (6) predate on corals (the crown-of thorns starfish *Acanthaster planci*).

3.1. Organisms that determine coral settlement

Substratum availability, and especially the presence of certain species of crustose coralline algae (CCA) and the absence of sediment layers are essential for coral

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

Fig. 3. Synthesis of documented direct effects (Table 3) of the four main parameters of terrestrial runoff on the six main processes associated with coral reproduction and recruitment (Table 3). Symbols as in Fig. 1.

settlement (Harrington et al., in press a). Few experimental data exist to assess the effects of terrestrial runoff on substratum availability and suitability for coral settlement. Some experiments and field data suggest that sedimentation may be a major factor influencing CCA abundances. CCA cover on reefs is negatively related to sedimentation (Kendrick, 1991), with cover decreasing from >30% in some low sedimentation habitats to 1% at high sedimentation on the Great Barrier Reef (Fabricius and De'ath, 2001b). Laboratory experiments suggest that some coral reef associated CCA survive burial under coarse inorganic sediments for days to weeks, but their survival is compromised if sediments are fine-grained (<0.63 m) or organically enriched (Harrington et al., in press b). The responses of CCA to sediments is complicated by their interaction with turf algae that efficiently trap sediments (Purcell, 2000), and by this means not only smother and replace CCA (Steneck, 1997) but also make the surrounding substratum less suitable for coral settlement (Birrell et al., in press). Light also affects CCA abundances, however responses are species-specific, with high-irradiance species being replaced by low-light species as light availability decreases. Laboratory studies show that elevated levels of orthophosphate can reduce calcification in tropical CCA (Brown et al., 1977; Björk et al., 1995), but field experiments found no responses by either CCA or turf algae to enrichment with dissolved inorganic nutrients (Koop et al., 2001).

3.2. Organisms that determine structural strength of the substratum

By far the largest proportion of filter feeders lives below the reef surface. Some types, especially sponges, bryozoans, ascidians, molluscs and some polychaetes, colonise existing cracks and crevices of the substratum. Others actively bore into or chemically erode the inorganic reef substratum and the calcium carbonate skeletons of live corals. These are internal macrobioeroders

that can reach densities of thousands of individuals m^{-2} reef area, weakening the structure of coral reefs and affecting their susceptibility to storm damage (Rose and Risk, 1985). The main groups are sponges such as the boring sponge *Cliona* spp., and bivalves such as the date mussel *Lithophaga* spp., the latter known to redissolve up to 40% of skeletons of living coral by direct boring and by changing alkalinity around the bore holes (Loya, 1991). The boring activity of these filter feeders is complemented by internal microboring green and blue-green microalgae. Several studies have documented increased abundances of internal macro- and microbioeroders in response to enhanced nutrient availability (Rose and Risk, 1985; Hallock and Schlager, 1986; Hallock, 1988; Cuet et al., 1988; Holmes, 2000; Chazottes et al., 2002). For example, abundances of the boring sponge *Cliona delitrix* increased fivefold in an area exposed to untreated fecal sewage (Rose and Risk, 1985). Similarly, erosion by boring microalgae and other microbes is enhanced 10-fold by fertiliser application (Carriero-Silva et al., in press). While certain borers are detrimentally affected by sedimentation (Hutchings et al., in press), abundances of most internal macrobioeroders are highest in the more productive in-shore environments than offshore (Sammarco and Risk, 1990; Edinger and Risk, 1996). Of greatest concern is that increased bioerosion in areas of nutrient enrichment, combined with reduced coral growth, skeletal densities and recruitment rates, can lead to conditions where reef erosion exceeds calcium carbonate accretion (Montaggioni et al., 1993; Edinger et al., 2000; Pari et al., 2002; Carriero-Silva et al., in press).

3.3. Organisms in competitive interaction with corals: macroalgae

Hard corals are competitive in low-nutrient environments because of efficient internal recycling of nutrients and energy between host and zooxanthellae, and because they occupy almost all available trophic levels simultaneously: they are efficient in photosynthesis, they take up dissolved inorganic and organic nutrients, feed on primary producers such as large phytoplankton, capture and prey upon herbivorous and predatory zooplankton, and also feed on decompositional material such as detritus (Lewis, 1976; Rosenfeld et al., 1999). Additionally, corals show considerable trophic plasticity in response to light and food availability. Such remarkable ability to gain energy at most trophic levels simultaneously allows hard corals to grow in nutrient-poor as well as quite productive environments. This trophic flexibility contrasts with the more specialised feeding strategies of other major benthic groups on coral reefs, the most important ones being macroalgae and heterotrophic filter feeders.

Macroalgal communities are an integral and often diverse component of inshore reef systems. However at certain environmental conditions, some macroalgal species can form dense mats that overgrow or damage large areas of coral by trapping sediment, restricting gas exchange, and creating anoxic conditions when mats age and collapse. For example, mats of the ephemeral green filamentous *Enteromorpha* sp. can smother adult corals by depleting oxygen at night. A 50% local increase in nutrients in the northern-most part of the Red Sea (Eilat, Gulf of Aqaba) has led to such blooms, reducing coral cover by 50% and reef ecosystem calcification by a factor of 3–4 since 1990 (Loya, 2004). Other, fleshy perennial species such as *Sargassum* spp. seasonally grow to form up to 2 m tall forests. Such forests shade corals underneath and their fronds can cause some tissue abrasion in coral. Rather than directly smothering adult corals, they tend to establish after corals are killed by other disturbance, however once established, they can become a major factor retarding coral recovery (Schaffelke et al., in press). Both types of macroalgae (low ephemeral mats and fleshy perennial stands) inhibit coral recruitment by space occupancy, allelopathy, silt trapping or shading (Sammarco, 1980; Connell et al., 1997; Hughes and Tanner, 2000; Szmant, 2002; Schaffelke et al., in press).

Macroalgae cover their carbon demand by photosynthesis, and their nutrient demand by uptake of dissolved inorganic nutrients, plus in some species by decomposing particulate organic matter deposited on their fronds (Schaffelke, 1999b). In the absence of grazing control, the growth and productivity of certain groups of macroalgae is nutrient limited and increases with slight increases in dissolved inorganic nutrients and POM (Schaffelke, 1999a, Schaffelke et al., in press). High standing biomass of fleshy, silt-trapping macroalgae has been reported around many point nutrient sources (Table 1), such as Kaneohe Bay (Smith et al., 1981), Brazil (Costa Jr et al., 2000) or the Bahamas (Lapointe et al., 2004). On inshore reefs of the central and northern Great Barrier Reef, total macroalgal cover (especially red and green algae) increases by up to 50% from reefs in water with lowest nutrient and particle loads to those in least clean water (van Woerik et al., 1999; Fabricius and De'ath, 2004; Fabricius et al., in press). Time series data of sites where macroalgal cover expanded with increasing nutrients from coastal runoff on Reunion Island (Cuet et al., 1988), and where macroalgal cover decreased after sewage diversion in Kaneohe Bay (Smith et al., 1981), add evidence for a causal link between increasing macroalgal abundances with increasing nutrient availability. The prevalence of macroalgae on eastern sides of large land masses from which most rivers originate (Birkeland, 1987), the increase of both macroalgal biomass and nutrients with latitude (Johannes et al., 1983), and the high abundances of macroalgae found

in areas of nutrient upwelling (Birkeland, 1988), add further strong evidence to the conclusion that nutrients can limit macroalgal biomass, and that they can have a negative effects on reef development. However, interactions between macroalgae and nutrients are complicated by the fact that macroalgal biomass is co-limited by grazing (McCook, 1997; Hughes et al., 1999), and in turbid or deeper water by light availability. The link between nutrients and macroalgal productivity is further complicated by the fact that nutrient uptake is mass transfer limited and increases with water flow (such as in wave zones) as well as with nutrient concentrations.

3.4. Surface occupying organisms that do not calcify: heterotrophic filter feeders and octocorals

Filter feeders (predominantly sponges, bivalves, ascidians, bryozoans and barnacles) that occupy the reef surface also increase in densities in response to nutrient enrichment (Birkeland, 1977; Smith et al., 1981; Costa Jr et al., 2000). Most actively pumping benthic filter feeders are asymbiotic, feeding on a narrow size range of plankton particles, and are often unable to obtain a positive carbon balance in oligotrophic waters (Birkeland, 1988). Again, heterotrophic filter feeders contribute to the biodiversity of coral reefs, and indeed only few examples exist of filter feeders (in particular some sponges; Aerts and Van Soest, 1997; Aronson et al., 2002) directly competing with corals for space, replacing corals and preventing further reef growth. Such takeover seems restricted to areas of low light, high phytoplankton concentrations and organic enrichment (Smith et al., 1981; Brock and Smith, 1983). Other filter feeders are sensitive to sedimentation and therefore disadvantaged by terrestrial runoff. Unlike macroalgae that directly compete with corals for well-lit habitats, surface-inhabiting heterotrophic filter feeders are generally low in profile, and tend to monopolise space only in poorly lit, highly productive environments that are per se marginal or unsuitable for corals. It therefore seems that, with few locally restricted exceptions involving one or few fast-growing species, the decline of corals and the spread of filter feeders are largely independent symptoms of high nutrient loads in the water, driven by organic enrichment rather than by competition between the two disparate groups.

Octocorals are also suspension feeders, however most of the more abundant genera with larger colonies tend to be zooxanthellate and therefore depend on light. There are some reports of zooxanthellate soft corals monopolizing space in productive waters (Fabricius and Dommissie, 2000) or after hard coral disturbance (Nishihira, 1981), but this is probably not a widespread phenomenon (Fabricius, 1998). Exceptions are found in some species of the families Alcyoniidae (especially the genus *Simularia*), Briareidae and Clavulariidae that can

locally establish space dominance at moderate concentrations of suspended particulate matter (Fabricius, 1998; Fabricius and Dommissie, 2000), but their success in space competition with hard corals tends to be restricted to high-irradiance, high-current and wave-protected inshore reefs. Indeed, octocorals appear to be overall more strongly affected by declining water quality than hard corals are (Fabricius et al., in press): octocoral species richness declines by up to 60% along a gradient of increasing turbidity, mostly due to the disappearance of zooxanthellate octocorals (Fabricius and De'ath, 2001a). Some octocorals are also more sensitive to sedimentation than hard corals (Riegl and Branch, 1995).

3.5. Organisms that cause diseases in corals

Bacteria, cyanobacteria, fungi and protists cause diseases in coral reef organisms, and some of these are now major factors threatening coral and octocoral populations in the Caribbean (Linton et al., 2002). Slow-release fertiliser experiments have demonstrated that infection rates and the spread of certain coral and octocoral diseases are accelerated by experimentally enhancing concentrations of inorganic nutrients (Bruno et al., 2003). On regional scales, disease prevalence has been attributed to increasing seawater temperatures as well as to sedimentation, pathogens transported via airborne dust from expanding deserts, eutrophication and pollution (Sutherland et al., 2004). Overall, more data are needed to test for the potential links between water quality and disease prevalence and virulence in coral reef organisms.

3.6. Organisms that predate on corals

Another indirect, and particularly severe effect of water quality on the status of the wider coral reef ecosystem is the apparent link between frequencies of population outbreaks of the coral eating crown-of-thorns starfish *Acanthaster planci*, and terrestrial runoff. A strong spatial and temporal relationship exists between drought-breaking floods around high continental Indo-Pacific islands and outbreaks of *A. planci* (Birkeland, 1982). Experimental studies document faster development and enhanced survival of the planktotrophic larvae of *A. planci* when concentrations of large phytoplankton are sufficiently high (Lucas, 1982; Okaji et al., 1997). Large phytoplankton groups tend to be nutrient-limited and bloom in response to nitrification events. New research further strengthens the evidence that higher outbreak frequencies of *A. planci* are linked to terrestrial runoff, while acknowledging that the removal of predators of *A. planci* can further enhance the likelihood of outbreaks (Brodie et al., in press; De'ath et al., unpublished data). The offsprings of the

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

* including phytoplankton

Fig. 4. Synthesis of effects of the four main parameters of terrestrial runoff on the five main groups of organisms that affect coral cover. High abundances crustose coralline algae as settlement substrata promote coral populations, whereas high abundances of the other groups are assumed to negatively affect coral populations. Symbols as in Fig. 1.

primary *A. planci* outbreak that formed in a region with high phytoplankton concentrations are moved by currents to more remote offshore reefs, hence new *A. planci* outbreaks can form even in areas that are far away from sources of terrestrial runoff.

In summary, the different groups of organisms that interact with corals are inhibited or promoted in diverse ways by the four water quality variables (Fig. 4). Dissolved inorganic nutrients affect at least four of the six groups, especially macroalgae. However, dissolved inorganic nutrients are also converted to organically enriched suspended particulate matter, and hence in this way, promote the growth of filter feeding bioeroders, larvae of *A. planci* and heterotrophic filter feeders. Sedimentation strongly inhibits some crustose coralline algae, but can also interfere with certain bioeroders and space competitors. Overall, two of these indirect effects, namely increased abundances of macroalgae and increased frequencies of outbreaks of *A. planci*, arguably affect adult corals more than do the direct effects of nutrient enrichment.

4. Reef properties related to resistance, resilience and risk

Inshore reefs vary considerably in their resistance against detrimental effects from terrestrial runoff and their resilience after exposure. Understanding properties of reefs or regions that contribute to their resistance and resilience could underpin management decisions, e.g., by prioritizing protection of reefs that have the greatest chance of withstanding degradation by terrestrial runoff. This section provides an assessment of the physical, hydrodynamic, spatial and biological properties that may contribute to protecting coral reefs from deterioration at local and regional scales (Table 4). This list of risk factors is preliminary and qualita-

Table 4

Spatial, physical and hydrodynamic, and biological properties of coral reefs, affecting reef resistance and resilience to degradation by exposure to poor water quality from terrestrial runoff

Most affected reef areas	Mechanism	Least affected reef areas
<i>(a) Spatial, physical and hydrodynamic properties</i>		
Short distance and/or downstream location relative to discharge source	More frequent exposure to less diluted discharges	Far away or upstream of source of discharge
Shallow surrounding seafloor on wide continental shelf	Resuspension, retention	Deep or precipitating surrounding seafloor
Small (< 2m) tidal range; or very large (> 4m) tidal range	Retention of pollutants and sedimentation, esp. in bays at small tides; or chronic resuspension/turbidity and low capacity for photoacclimation at very large tidal ranges	Intermediate tidal range (2–4m)
Low current area	Retention of pollutants, sedimentation, slow dilution	Current-swept front reef, flank or channels
Embayment, lagoon	Small water volume hence low dilution	Large, open water body
No waves; or high wave exposure	Retention of pollutants, sedimentation; or storm damage and bioerosion due to low skeletal densities in corals	Moderate wave exposure
Deeper reef slope	Low light, slow growth rates, high sediment deposition	Reef crest, upper reef slope
<i>(b) Biological properties</i>		
Overfished area	Reduced macroalgal grazers and predators of <i>A. planci</i>	Healthy abundances of herbivores and predators (fish, molluscs)
Region prone to frequent or severe disturbances	Removal of adult populations, slow recovery	Region with low disturbance regime
Poor connectivity to larval pools	Low recruitment, slow recovery	High connectivity to larval pools
Region of low biodiversity	Low species redundancy, less functional replacement	Region of high biodiversity

tive, based on previously discussed ideas as well as commonalities that emerged by comparing the better-described regions (Tables 1–3); a formal risk analysis is needed to confirm the contributions of the properties identified.

An important factor that has been previously identified to determine the risk of degradation is the level of exposure (concentration and duration) to terrestrial runoff of a reef system. This exposure is spatially determined by the downstream distance between a reef and the major sources of discharge, the mean annual pollutant load from the source, and dilution processes (West and Van Woessik, 2001; Bourke et al., 2002; Devlin et al., 2003). Exposure is also determined by the rate of retention of pollutants in the ecosystem: any mechanism that promotes retention will enhance exposure and hence the risk of degradation. Retention and removal depend on hydrodynamic processes (flushing rates, dilution), hydrology (e.g., accumulation and slow discharge via groundwater) as well as biological processes (e.g., absorption and storage of pollutant spikes in tissues, altering the organisms' physiology throughout a whole growing season).

At regional scales, tides are important factors determining rates of pollutant removal. Estuarine areas with <2m tidal amplitudes are more vulnerable to eutrophication

than those with large tides (Monbet, 1992). However, extreme tidal ranges also inhibit reef growth by causing continuous sediment resuspension and chronic turbidity (Kleypas, 1996). A shallow and wide continental shelf is also likely to enhance retention and hence susceptibility of reefs to degradation. This is because material undergoes cycles of deposition and resuspension from a shallow sea floor, whereas the same material is rapidly removed from reefs surrounded by deep water. For example, the shallow and wide northeast Australian continental shelf may play an important role in determining the level of susceptibility of the Great Barrier Reef to terrestrial runoff. A large proportion of the imported material remains in its inshore system for prolonged periods of time due to wave-driven currents and the Coriolis force, and the fine particle fraction (which carries most of the nutrients) is repeatedly resuspended from the shallow sea floor. Possibly as a consequence, although nutrient enrichment on the Great Barrier Reef is less severe than in many other regions, reef communities clearly change along water quality gradients (van Woessik et al., 1999; Fabricius et al., in press; Fabricius and De'ath, 2004).

At local scales, current-swept reef fronts, flanks and channels are likely to experience relatively low levels of retention, as pollutants are rapidly carried away

and diluted. In contrast, poorly flushed bays and lagoons with small water volumes are most likely to be damaged by terrestrial runoff (e.g., Kaneohe Bay, [Smith et al., 1981](#)). Upper reef slopes and crests are also less affected by turbidity and sedimentation than deeper areas ([Fig. 2](#)). This is because light becomes limiting for corals at greater depths, and sediment deposition is normally greater below the reach of surface waves than on reef crests (except in sheltered bays). Locations with moderate wave action also facilitate coral growth, as waves prevent sediment retention, but strong wave action may result in coral breakage in nutrient-rich areas where coral skeletal densities are weak. Current-swept areas and well-lit reef crests with moderate wave action are therefore likely to be the locations with best coral growth and fastest recovery from disturbance. For example, reef development on the most turbid inshore reefs of the Great Barrier Reef is naturally restricted to sheltered bays, whereas exposed headlands and depositional back reef areas do not support reef accretion. However, current flow, waves and light also facilitate macroalgal growth, as nutrient uptake is flow-dependent, and areas with high light and wave-enhanced nutrient fluxes are also the zones where competition with macroalgae is likely to be most intense.

Biological properties of reefs can also enhance the resistance and resilience of coral reefs. In particular, healthy populations of herbivores help controlling algal or prey populations, hence regions that have high grazer abundances are less likely to respond to deteriorating water quality with macroalgal dominance ([McCook, 1999](#)). Importantly, 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 also likely to be more prone to degradation than less frequently disturbed regions. This is because poor water quality often does not directly kill the adult coral populations (see above), but retards coral recruitment and hence the speed of recovery from such unrelated disturbances. Consequently, connectivity due to lateral transport by currents will contribute to enhancing resilience, as reefs that are well connected to upstream larval sources will recover more quickly from disturbance than reefs that are poorly connected. The role of biodiversity in supporting resistance and resilience is comparatively less understood and needs further research. It appears plausible that regions of high biodiversity have more functional redundancy, and structural changes in diverse regions may be prevented by species replacement when some species disappear in response to changing water quality. In contrast, regions of lower biodiversity may not have suitable species to replace the loss of sensitive species, and are more likely to undergo structural and functional change in their communities ([Bellwood et al., 2004](#)). At present it is unknown whether marginal reefs at high latitudes, with their

higher macroalgal biomass, lower coral biodiversity and low calcification rates differ in their resistance and resilience to degradation by poor water quality to those at low latitudes.

In summary, reefs that are surrounded by a shallow sea floor, reefs in poorly flushed bays or lagoons, deeper reef slopes, and frequently disturbed reefs are likely to experience changes even at low levels of pollution, in particular when populations of herbivores are low. In contrast, well-flushed shallow reef crests surrounded by deep sea floors or in areas of moderate tides are likely to have the highest level of resistance and resilience, especially when inhabited by healthy populations of herbivores that protect against overgrowth by sediment-trapping macroalgae.

5. Conclusions

Models of the global scale of pollution around coral reefs estimate that 22% of all coral reefs worldwide are classified as at high (12%) or medium (10%) threat from inland pollution and soil erosion ([Bryant et al., 1998](#)). The percentage of reefs at risk is highest in countries with widespread land clearing, such as Taiwan and Vietnam with 50% of their reefs at risk from terrestrial runoff, or the Philippines with 35% ([Bourke et al., 2002](#)). The models also classify 30% of reefs as threatened from coastal development (proximity to cities, mines and resorts), and 12% at threat from marine pollution (distance to ports, oil tanks, oil wells and shipping areas; [Bryant et al., 1998](#)). On a global scale, pollution is therefore rated as a threat to coral reefs similar in severity and scale to coral bleaching, overfishing and destructive fishing ([Spalding et al., 2001](#)). On local scales, it can be the single most significant pressure on coastal and inshore coral reefs ([Table 1](#)).

This literature review indicates that four fundamentally different processes have to be distinguished when assessing the effects of terrestrial runoff on coral reefs:

1. Dissolved inorganic nutrients can reduce coral calcification and fertilization rates, and increase macroalgal abundances ([Figs. 2a, 3 and 4](#)). In the field however, dissolved inorganic nutrients disappear so quickly that their main role may be that of curbing organic enrichment of benthos, sediments and suspended POM, except in areas of upwelling and near sewage outfalls.
2. Enrichment with POM enhances feeding rates and growth in some corals, providing a growth advantage that can partly or fully compensate for light reduction, especially in high-flow environments ([Fig. 2b](#)). However, while some corals can benefit from POM, heterotrophic filter feeders will benefit even more than corals do, hence the competitive advantage

shifts from corals that can grow at extremely low food concentrations to simpler, more heterotrophic communities. A promotion of the growth and survival of filter feeding larvae of *A. plani* has also profound negative consequences for coral populations (Fig. 4).

3. Turbidity-related light limitation reduces gross photosynthesis (Fig. 2c). Light limitation increases with depth and under macroalgae, but will not occur in shallow water, even in very turbid environments. The effects of light limitation are more severe for phototrophic than mixotrophic species, while heterotrophic species such as filter feeders may be promoted. Light limitation also greatly reduces coral recruitment (Fig. 3).
4. Sedimentation represents a severe disturbance for coral reefs. It reduces growth and survival in a wide range of coral species, although responses differ substantially between species and also between different sediment types (Fig. 2d). Smothering by sedimentation or sediment-trapping macroalgae is the main factor affecting recruitment and the survival of early life stages in corals: settlement rates are near-zero on sediment-covered surfaces, and sedimentation tolerance in coral recruits is at least one order of magnitude lower than for adult corals (Fig. 3). Some of the bioeroding and space-competing groups of organisms are also sensitive to sedimentation by fine silt, and so are crustose coralline algae, with negative consequences for coral recruitment (Fig. 4).

The type and severity of response to terrestrial runoff at any particular location depends on whether changes occurred predominantly in sedimentation, turbidity, POM or dissolved inorganic nutrients, and also depend on the physical, hydrodynamic, spatial and biological properties of a location. In most places, reduced recruitment success in corals, together with the promotion of macroalgae and *A. plani*, arguably represent the most significant direct effect of terrestrial runoff on coral reefs. In severe conditions, the overall outcome is reduced reef calcification, shallower photosynthetic compensation points, changed coral community structure, and greatly reduced species richness. Hence reef ecosystems increasingly simplify with increasing exposure to terrestrial runoff, compromising their ability to maintain essential ecosystem functions at the presently increasing frequencies of human-induced disturbances.

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