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Review

Environmental impacts of dredging and other sediment disturbances on corals: A review

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ABSTRACT

A review of published literature on the sensitivity of corals to turbidity and sedimentation is presented, with an emphasis on the effects of dredging. The risks and severity of impact from dredging (and other sediment disturbances) on corals are primarily related to the intensity, duration and frequency of exposure to increased turbidity and sedimentation. The sensitivity of a coral reef to dredging impacts and its ability to recover depend on the antecedent ecological conditions of the reef, its resilience and the ambient conditions normally experienced. Effects of sediment stress have so far been investigated in 89 coral species (∼10% of all known reef-building corals). Results of these investigations have provided a generic understanding of tolerance levels, response mechanisms, adaptations and threshold levels of corals to the effects of natural and anthropogenic sediment disturbances. Coral polyps undergo stress from high suspended-sediment concentrations and the subsequent effects on light attenuation which affect their algal symbionts. Minimum light requirements of corals range from <1% to as much as 60% of surface irradiance. Reported tolerance limits of coral reef systems for chronic suspended-sediment concentrations range from <10 mg L^{-1} in pristine offshore reef areas to >100 mg L^{-1} in marginal nearshore reefs. Some individual coral species can tolerate short-term exposure (days) to suspended-sediment concentrations as high as 1000 mg L^{-1} while others show mortality after exposure (weeks) to concentrations as low as 30 mg L^{-1}. The duration that corals can survive high turbidities ranges from several days (sensitive species) to at least 5–6 weeks (tolerant species). Increased sedimentation can cause smothering and burial of coral polyps, shading, tissue necrosis and population explosions of bacteria in coral mucus. Fine sediments tend to have greater effects on corals than coarse sediments. Turbidity and sedimentation also reduce the recruitment, survival and settlement of coral larvae. Maximum sedimentation rates that can be tolerated by different corals range from <10 mg cm^{-2} d^{-1} to >400 mg cm^{-2} d^{-1}. The durations that corals can survive high sedimentation rates range from <24 h for sensitive species to a few weeks (>4 weeks for high sedimentation or >14 days complete burial) for very tolerant species. Hypotheses to explain substantial differences in sensitivity between different coral species include the growth form of coral colonies and the size of the coral polyp or calyx. The validity of these hypotheses was tested on the basis of 77 published studies on the effects of turbidity and sedimentation on 89 coral species. The results of this analysis reveal a significant relationship of coral sensitivity to turbidity and sedimentation with growth form, but not with calyx size. Some of the variation in sensitivities reported in the literature may have been caused by differences in the type and particle size of sediments applied in experiments. The ability of many corals (in varying degrees) to actively reject sediment through polyp inflation, mucus production, ciliary and tentacular action (at considerable energetic cost), as well as intraspecific morphological variation and the mobility of free-living mushroom corals, further contribute to the observed differences. Given the wide range of sensitivity levels among coral species and in baseline water quality conditions among reefs, meaningful criteria to limit the extent and turbidity of dredging plumes and their effects on corals will always require site-specific evaluations, taking into account the species assemblage present at the site and the natural variability of local background turbidity and sedimentation.

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1. Introduction

Coastal construction, land reclamation, beach nourishment and port construction, all of which involve dredging, are increasingly required to meet the growing economic and societal demands in the coastal zone worldwide. In tropical regions, many shorelines are not only home to people but also to coral reefs, one of the most biodiverse ecosystems on earth (Hoeksema, 2007). World-wide, ∼3 billion people depend more or less directly on coral reefs for a significant part of their livelihood, obtaining their protein needs or other essential commodities (Bryant et al., 1998). Even if not necessarily sustaining human life in many wealthier regions of the world, the economic value of the realised tourism potential of coral reefs can be enormous. For example, three southern Florida counties (Miami-Dade, Broward and Palm Beach) derive ∼6 billion dollars annually from reef-oriented tourism and fisheries (Johns et al., 2001). Clearly, coral reefs are a biologically as well as economically valuable resource worth protecting. Unfortunately, coastal construction and dredging is frequently unavoidable in their immediate vicinity (Salvat, 1987).

The excavation, transportation and disposal of soft-bottom material may lead to various adverse impacts on the marine environment, especially when carried out near sensitive habitats such as coral reefs (PIANC, 2010) or seagrass beds (Erftemeijer and Lewis, 2006). Physical removal of substratum and associated biota from the seabed, and burial due to subsequent deposition of material are the most likely direct effects of dredging and reclamation projects (Newell et al., 1998; Thrush and Dayton, 2002). Dredging activities often disturb sediments reducing visibility and smothering reef organisms (Dodge and Vaisnys, 1977; Bak, 1978; Sheppard, 1980; Fortes, 2001). Coastal engineers and conservation officials need to balance the needs of a healthy economy, of which construction and dredging are often an integral part, with those of a healthy environment. Managing these potentially conflicting priorities can at times be a formidable challenge, particularly where coral reefs are concerned (Smith et al., 2007).

In many cases, dredging operations have contributed to the loss of coral reef habitats, either directly due to the removal or burial of reefs, or indirectly as a consequence of lethal or sublethal stress to corals caused by elevated turbidity and sedimentation. Dredging activities potentially affect not only the site itself, but also surrounding areas, through a large number of impact vectors (e.g. turbid plumes, sedimentation, resuspension, release of contaminants, and bathymetric changes) (Wolanski and Gibbs, 1992). Effects can be immediate or develop over a longer time frame and they may be temporary or permanent in nature. Some coral species appear to be more sensitive than others to increases in turbidity or sedimentation that are commonly associated with dredging operations. Their responses to such increases may depend on typical local conditions and vary between seasons. In general, the impact from dredging on corals and coral reef ecosystems is complex and far from fully understood. Yet there is an extensive body of experience to learn from. This experience lies with dredging contractors, in assessment reports, in monitoring data and in scientific literature derived from field-based and laboratory studies.

In this review we examine the environmental impacts of dredging on corals. We outline the type and level of dredging operations near coral reefs; provide an overview of the general impacts of sediment disturbances on corals; examine the current state of knowledge regarding sensitivity among and within coral species, tolerance limits and critical thresholds; and, finally, discuss mitigating factors and the potential for recovery. Where appropriate, these findings are illustrated with case studies. The focus of this review is limited to the effects of dredging on corals. The nomenclature of the coral species discussed in this review has been updated according to the most recent taxonomic revisions. The effects of dredging on other reef-associated organisms were not considered, except those depending on corals as specific host organisms. A similar analysis for seagrasses can be found in Erftemeijer and Lewis (2006). Information sources for the review included peer-reviewed scientific literature, "grey" literature in the form of environmental impact assessments, consultancy and technical reports, and additional information obtained from members of Working Group 15 of the Environmental Commission of the World Association for Waterborne Transport Infrastructure (PIANC, 2010). While the emphasis of this review is on the impacts of dredging, the findings and implications presented here are equally applicable to other sediment disturbances as sources of elevated turbidity or sedimentation (rivers, natural resuspension, flood plumes, bottom-trawling, etc.).

2. Dredging near coral reefs

An overview of 35 selected case studies of documented dredging operations in, near or around coral reef areas is presented in Table 1, which provides an indication of the scale and type of impact that dredging operations can have on corals and coral reefs. Undoubtedly, there are many more cases of coral damage associated with dredging operations worldwide, some of which are reported in confidential documents or in local languages, to which access is limited. Many of the historical dredging operations and port developments near coral reefs have never been documented and effects on corals were rarely quantified. The actual scale of dredging damage to coral reefs worldwide can therefore be assumed to be much greater than the available literature may suggest. Not all dredging projects near coral reefs lead to mortality of corals and not all observed changes in coral health in the immediate vicinity of dredging sites are necessarily the result of dredging-induced turbidity. Indeed, distinguishing the effects of anthropogenic disturbances from natural dynamics in the marine environment can be a challenge and calls for an appropriate monitoring design (Underwood, 2000; Stoddart et al., 2005). Nevertheless, the cumulative effects of dredging, filling and other coastal construction activities in coral reef environments have collectively resulted in major adverse ecological impacts on many reefs (Maragos, 1993).

Coral reefs are generally recognised as biogenic structures, but it is rarely appreciated that over half of the material in most coral reef complexes is actually made up of sediments (Hubbard et al., 1990; Dudley, 2003). Over 90% of the sediments on most coral reefs consist of carbonate (aragonite, high-magnesium calcite and calcite) produced by the growth and subsequent destruction of reef organisms as well as pre-existing reef rock through physical, chemical and biological erosion processes. Only on nearshore fringing reefs do silicate mineral grains from weathered and eroded igneous or metamorphic rocks (terrigenous sediments) constitute a significant part of the sedimentary material (Dudley, 2003). With time, the skeletons of primary and secondary reef organisms and loose sediments may be changed into a firm sedimentary rock (reef rock) and eventually into a dense solid limestone through consolidation of reef material, binding, cementation and diagenesis (Hubbard et al., 1990; Dudley, 2003). Levels of sedimentation in coral reef environments can vary substantially over spatial and temporal scales, often by several orders of magnitude within kilometres and weeks (Wolanski et al., 2005). Sedimentation is usually highest on inshore reefs and sheltered, wave-protected parts of reef systems, and decreases with distance from shore and with increasing exposure to wave energy (Wolanski et al., 2005).

Due to their geotechnical nature, limestone and coral materials tend to break when dredged and/or transported hydraulically

Table 1
Selected case studies of dredging operations near coral reefs and their impacts.

Country	Location	Year	Activity/purpose	Scale of impact/damage	References
Arabian Gulf	Various countries & locations	1990s–2008	Various mega-reclamations, coastline modifications and associated dredging	Widespread loss and degradation of productive coastal habitats incl. large stretches of coral reef	Sheppard et al. (2010)
Australia	Mud Island, Moreton Bay	1940s–1991	Coral dredging for cement manufacture	Loss of corals, development of shingle ridges that have restricted tidal flushing impacting adjacent mangroves	Allingham and Neil (1995)
Australia	Magnetic Island	1972	Dredging	Reduction in herbivores and reef dwellers	Marszalek (1981)
Australia	Cleveland Bay and Magnetic Island, Queensland	1970s	Capital & maintenance dredging at Ross River mouth and disposal at various dump sites in Cleveland Bay (peak in the early – mid 1970s)	Extensive burial of seagrass and coral habitats and impacts on mangroves (in combination with cyclones)	Pringle (1989)
Australia	Nelly Bay	2000–04	Capital dredging (35,000 m^3) for marina	18 ha Construction area; no detectable impact immediately outside construction area	Chin and Marshall (2003) and Koloi et al. (2005)
Australia	Dampier, DPA & HI	2003–04	Capital dredging for port construction/expansion total dredged volume 4.1 million m^3	one site 80% loss within 1 km from dredging site, no discernable change due to dredging at other sites	Blakeway (2005) and Stoddart and Stoddart (2005)
Australia	Hay Point	2006	Capital dredging for port construction/expansion total dredged volume 9 million m^3	2–5% Loss of coral cover at 2 islands up to 6 km away from dredging site	Smith et al. (2007)
Australia	Dampier, HI	2006–07	Capital dredging for port expansion total dredged volume 3.4 million m^3	<10% Gross coral mortality at impact sites	Hanley (2011)
Australia	Cape Lambert A	2007–08	Capital dredging for port construction/expansion total volume 2.5 million m^3 in <5 months	<3% Net coral mortality at impact sites	Hanley (2011)
Australia	Mermaid Sound, Pluto	2007–10	Capital dredging for port construction/expansion total dredged volume 14 million m^3	<6% Reduction in coral cover (Zone A) due to thermal bleaching; <5% net coral mortality in Zone B; <10% coral bleaching at monitoring sites in Zone C	Hanley (2011)
Bahrain	Fasht Al-Adham (east coast)	1985–92	Dredging and industrial development	Loss of at least 22 hectares of coral reef and degradation of a further 8 ha due to increased turbidity and sedimentation	Zainal et al. (1993)
France	Guadeloupe	1979	Dredging	Unbalanced fish community – disappearance of 20 out of 29 spp.	Galzin (1982)
French Polynesia	Tahura lagoon, Moorea	1981	18 ha dredged	Destruction of corals, reduced species composition, changes in invertebrate fauna favouring gastropods instead of crustaceans, disruption of stability of reef & lagoon ecosystems	Naim (1981)
French Polynesia	Tiahiti (36 sites)	1959–1983	Dredging by hydraulic shore & bucket dredgers total volume 2.5–3.0 × 10^6	Dredge & fill destroyed 43% of fringing reefs in Papette and 75% in FAAA region; hard bottoms colonized by turf algae after dredging; fish populations reduced	Gabrie et al. (1985)
Hong Kong	Ninepin Islands	1991–93	Trailer dredging of up to ~400 million m^3 at 20 borrow areas	Build-up of fine sediment in shallow water; 40% reduction in live coral in 3 months; sign. increase in % *Acropora* colonies damaged	Hodgson (1994)
Indonesia	Turtle Island, Bali	1997	Dredging & reclamation (20 million m^3)	No detectable impacts at 1 km from work area; used an adaptive monitoring & mgt. approach	Driscoll et al. (1997)
Kiribati	Fanning Island	1971	Dredging	Live coral cover reduced from 62% to 31% over time	Roy and Smith (1971)
Malaysia	Bintulu	2005	Dredging at borrow areas (4 million m^3)	No detectable impacts at nearest reef ~2 km from borrow area	Doorn-Groen (2007)
Micronesia	Truk Atoll, Eastern Caroline Islands	1981	Dredging (2 million cubic yards)	Fish abundance and diversity significantly reduced	Amesbury (1981)
Netherlands Antilles	Piscadera Bay, Curacao	1972	Dredging	*Porites astreoides* (plating form) died as result of inability to reject sediment; calcification rates of *Madracis mirabilis* and *Agaricia agaricites* decreased by ~33% over a 4-week period	Bak (1978)
Netherlands Antilles	Bonaire	1980–83	Dredging and large coastal resort development	Significant coral mortality due to sedimentation and excavation for channel & breakwater construction	van 't Hof (1983)
Thailand	Phuket	1981	Tin dredging; 11.6 km^2 dredged with 3 tin dredgers (200,000 yd^3/month)	Reefs adjacent to dredging severely damaged by sedimentation (4% coral cover compared to 26–34% in non-impacted areas)	Chansang et al. (1981)
Thailand	Phuket	1986–87	Dredging of 1.3 million m^3 by hydraulic dredgers (9-months dredging & disposal operation)	30% Reduction in coral cover and a decline in species diversity for up to 1 year; maximum conc. 286 mg/l; rapid recovery in 22 months	Brown et al. (1990)
Singapore	coastline	1970s–90s	Coastal reclamation and dredging along almost the entire shoreline of Singapore	Loss of approx. 60% of Singapore's coral reefs; remaining reefs subjected to sediment impact	Hilton and Manning (1995) and Chou (2006)
Singapore	Southwest Islands	2006	Dredging and reclamation (9 million m^3)	No detectable impacts 300 m outside direct impact area; used adaptive monitoring & management approach	Doorn-Groen (2007)

Table 1 (*continued*)

Country	Location	Year	Activity/purpose	Scale of impact/damage	References
UK	Diego Garcia, Chagos	1980	Dredging	Coral diversity unaffected by dredging	Sheppard, 1980
UK	Castle Harbor, Bermuda	1941–1943	Extensive dredging and filling for construction of Kindley Airfield (US navy base)	Mass coral mortality due to dredging in harbor area major shift in nearby reef community structure towards more tolerant coral species	Dodge and Vaisnys (1977) and Flood et al. (2005)
USA	Johnston Atoll	1966	Dredging (440 ha)	Reduction of living corals by up to 40%; reduction in reef fish abundance & development of blue-green on dead coral	Brock et al. (1965)
USA	Kaneohe Bay, Hawaii	1974	Dredging	Up to 30% of corals died & overgrown with algae	Banner (1974)
USA	Johnston Atoll	1976	Airfield construction activities	40% Reduction in coral cover due to siltation from airfield construction activities	Amerson and Shelton (1976)
USA	Miami Beach, Florida	1977	Large-scale dredging operations	1 cm sediment cover on nearby reef surface in <2 h; partial mortality & paling of affected corals; up to 32% of corals exhibiting signs of stress; small colonies displayed tissue mortality	Marszalek (1981)
USA	Southeast Florida	1995	Dredge & fill (350,000 m³) for beach widening	Burial & loss of 5 ha of nearshore hard-bottom habitat; 30× drop in fish density, 10× drop in fish diversity	Lindeman and Snyder (1999)
USA	Florida	1985–2004	26 Projects involving filling and dredging for beach nourishment and port development	217 Acres of reef impacted by cumulative effects	PBS&J, (2008)
USA	Florida	2005–06	Dredging for Broward County beach nourishment (10.9 km of beach with 1.5×10^6 m³ of sand)	Increased sedimentation during construction, no effects on %cover; minor to moderate coral stress; rapid post-dredging recovery	Fisher et al. (2008)
USA	Key West (Florida)	2006	Key West harbour dredging project	No significant effects on % live coral cover; some paling & bleaching	CSA (2007)

(Schlapak and Herbich, 1978; Maharaj, 2001). From the freshly broken surface, very fine silt and colloidal material can be released into the water, creating milky white "clouds". These fine sediment clouds are difficult to control, as they can remain in suspension for prolonged periods and thus spread over large areas under the action of currents, wind and waves. It is therefore imperative to minimise the need for dredging coral material and to exercise great care and accuracy when dredging in coral reef environments. Some excellent guidelines on best management practices for dredging and port construction near coral reefs were published recently (PBS&J, 2008; PIANC, 2010). In the case of contaminated sediment, dredging may also lead to deleterious effects on water quality and reef-associated biota by the release of contaminants (Brown and Holley, 1982; Lay and Zsolnay, 1989; Esslemont et al., 2004). Dredgers and port engineers possess a wide range of tools to reduce their impact on the environment either by design or by choice of low-impact building methods (Bray, 2008). Various environmental regulatory agency permitting processes are intended to give engineers the information required to maintain any given project's impacts within the legally required, or otherwise agreed-upon, limits. Given the potential for adverse effects of dredging on sensitive marine habitats such as coral reefs, the management and monitoring of those activities that elevate turbidity and sediment-loading is critical. In practice, however, this has proved difficult as the development of water quality threshold values, upon which management responses are based, are subject to a large number of physical and biological parameters that are spatially and temporally specific (Sofonia and Unsworth, 2010).

It should be noted here that many coral reef environments demonstrate substantial natural variability in background turbidity due to resuspension as a result of metocean conditions such as tides, wind, waves, storms, cyclones, tsunamis and river floods, which in some areas can increase the suspended-sediment concentrations to levels similar to those occurring during dredging (Harmelin-Vivien, 1994; Schoellhamer, 2002; Anthony et al., 2004; Larcombe and Carter, 2004; Orpin et al., 2004; Storlazzi et al., 2004; Ogston et al., 2004; Kutser et al., 2007; Jouon et al., 2008).

It is almost impossible to predict levels and patterns of increased turbidity and sedimentation during dredging operations without sophisticated numerical modelling of site-specific hydrodynamic and sediment transport processes (Winterwerp, 2002; Hardy et al., 2004; Aarninkhof and Luijendijk, 2010). Total suspended sediment (TSS) concentrations experienced at a given distance from a dredging operation may vary by up to two orders of magnitude depending on the scale of the operation, the techniques used, background water quality conditions and the nature of the substrate that is dredged (or disposed of). Kettle et al. (2001) recorded suspended-sediment concentrations of >150 mg L^{-1} to be laterally confined to within about 100 m of a dredger in Cleveland Bay (Townsville, Australia). Plumes exceeding 20 mg L^{-1} extended for up to about a kilometre from the actual dredging or placement operation (Kettle et al., 2001). Thomas et al. (2003) reported a general regime of suspended-sediment concentrations >25 mg L^{-1} (90% of the time) for several months during dredging operations over fringing coral reefs at Lihir island (Papua New Guinea) with regular (short-term) peak increases above 1000 and 500 mg L^{-1} (in severe and transitional impact zones) in an area that normally experience background TSS concentrations of <5 mg L^{-1}. In contrast, Stoddart and Anstee (2005) recorded suspended-sediment concentrations above 10 mg L^{-1} for 42% of monitoring days at impacted coral reef sites (within 1 km of dredging locations, occasionally peaking to ~60 mg L^{-1}) during dredging operations in Mermaid Sound (Dampier, Western Australia) against a low background level of ~4 mg L^{-1} at reference sites.

A poor understanding of responses of corals to sediment disturbances can result in inappropriate management of dredging projects that may lead to preventable coral mortality or unnecessarily high costs from down-time and delays in dredging operations. There are many examples of dredging operations near coral reefs where inadequate management has contributed to significant damage to reefs and mortality of corals (Table 1). Conversely, exaggerated (over-conservative) thresholds used for predicting levels of coral mortality from dredging can lead to unrealistically high levels of predicted coral mortality over large areas of presumed impact. A review of ten recent (large) capital dredging projects near coral reefs in the Pilbara region (Western Australia) described how conditions governing environmental controls and monitoring requirements have become increasingly comprehensive, prescriptive and onerous since 2003 (Hanley, 2011). However, in none of these case

studies was there evidence of any breach (non-compliance) of the permitted levels of impacts on corals. In fact, observed mortality of corals in these projects typically was far below predictions and could in many cases be attributed to other factors not related to dredging (e.g. cyclonic events and thermal bleaching). The review warned about the consequences of such routine overestimation of dredging impacts to corals, including the misinformation of the public, unrealistically large offset packages and unnecessarily large monitoring and baseline programs to areas well outside the real range of impacts (Hanley, 2011). These examples from Western Australia, along with the various case studies summarised in Table 1, clearly demonstrate the need for strengthening capacity in predicting and managing impacts of dredging through thorough literature reviews, a critical evaluation of past dredging projects near corals, and targeted experimental research (Lavery and McMahon, 2009).

The main effects of dredging and port construction on corals—besides direct physical removal, damage or burial—include temporarily increased turbidity and enhanced sedimentation. In order to understand how corals are affected by enhanced turbidity and sedimentation, it is important to first gain some basic understanding on how corals function.

3. The impacts of sediment disturbance on corals

With the exception of free-living species, corals—once settled—are sessile organisms (Hoeksema, 1988, 1993; Hubmann et al., 2002; Hoeksema and de Voogd, 2012). As they cannot move away from unfavourable conditions, growth-form and physiological changes regulate their interactions with the environment. Much of the success of reef-building corals relies on symbiotic, unicellular algae called zooxanthellae, which live as symbionts inside the coral tissue (primarily the gastrodermis) and produce the majority of the coral's energy requirements through photosynthesis. Because of this symbiosis, most corals require light to survive (Achituv and Dubinsky, 1990). The major problems arising from turbidity and sedimentation derived from coastal construction and dredging are related to the shading caused by decreases in ambient light and sediment cover on the coral's surface, as well as problems for the feeding apparatus under a sediment blanket and energetic costs associated with mucus production, sediment clearance and impaired feeding. Suspended sediments, especially when fine-grained, decrease the quality and quantity of incident light levels, resulting in a decline in photosynthetic productivity of zooxanthellae (Falkowski et al., 1990; Richmond, 1993). Non-photosynthetic corals are an exception to this but while they may not suffer from light reduction, they can be impacted by high loads of suspended sediment through clogging and smothering. Many corals are primarily light-traps and thus their growth form is not necessarily optimised for sediment-shedding. As a result, certain morphologies are prone to collect more sediment from the water column than the coral is able to clear (Hubbard and Pocock, 1972; Bak and Elgershuizen, 1976; Dodge and Vaisnys, 1977; Rogers, 1983; Stafford-Smith, 1993; Sanders and Baron-Szabo, 2005). Turbidity reduces ambient photosynthetically active radiation (PAR) and leads to a decrease in zooxanthellae productivity which can result in starvation. Sediment settling on coral tissue causes additional shading and smothering, and in this way contributes to a further decrease of the photosynthetic activity by zooxanthellae and can even lead to coral bleaching (Glynn, 1996; Brown, 1997).

High turbidity and sedimentation rates may depress coral growth and survival due to attenuation of light available to symbiotic zooxanthellae and redirection of energy expenditures for clearance of settling sediments. Thus, the potential effects of sediment input not only include direct mortality, but also involve
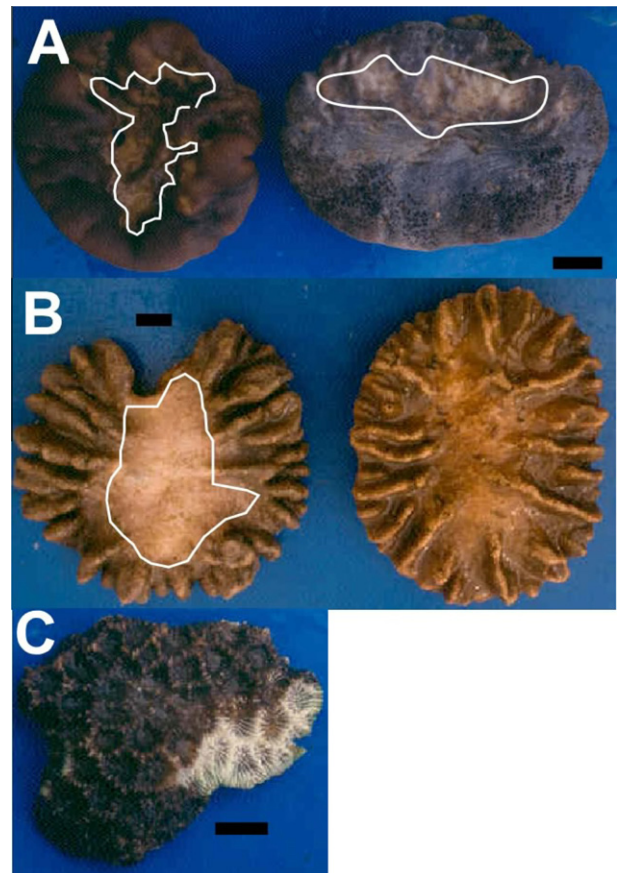

Fig. 1. Sublethal effects of sedimentation on corals. (A) After two weeks of intense sedimentation, large tissue necroses appeared on these *Lobophytum depressum* (left) and *Lobophytum patulum* (right). (B) At the same time *Sinularia dura* colonies were bleached where the sand had rested on them (left experimental animal, right control animal). (C) tissue necrosis on *Favites pentagona* after four weeks of sedimentation.

sublethal effects such as reduced growth, lower calcification rates and reduced productivity, bleaching, increased susceptibility to diseases, physical damage to coral tissue and reef structures (breaking, abrasion), and reduced regeneration from tissue damage (Fig. 1). Sediment disturbance can also affect coral recruitment and have impacts on other (non-coral) reef-dwelling organisms. As pointed out by Johannes (1975), selective mortality of corals results in the migration or death of other fauna, suggesting that the environmental tolerances of the associated reef community are unlikely to exceed those of the component corals. As the stress level caused by enhanced turbidity and sedimentation increases, the response of corals shifts from photo-physiological effects, changes in polyp activity and mucus production at the level of individual coral polyps, to colour changes, bleaching and partial tissue necrosis of coral colonies (Meesters et al., 1992; Stafford-Smith, 1993; Riegl, 1995; Riegl and Branch, 1995; Fabricius, 2005). Ultimately, severe and long-lasting stress from sustained sediment disturbances may result in wide-spread coral mortality, changes in community structure and major decreases in density, diversity and coral cover of entire reef systems (Table 2; adapted from Gilmour et al., 2006).

The risk and severity of impacts from dredging on corals is directly related to the intensity, duration and frequency of exposure to increased turbidity and sedimentation (Newcombe and MacDonald, 1991; McArthur et al., 2002). Very high sediment stress levels over relatively short periods may well result in sublethal and/or lethal effects on corals, while long-lasting chronic exposure

Table 2
Schematic cause-effect pathway for the response of corals and coral communities to sedimentation and turbidity. Level of stress increasing from top to bottom (adapted from Gilmour et al., 2006).

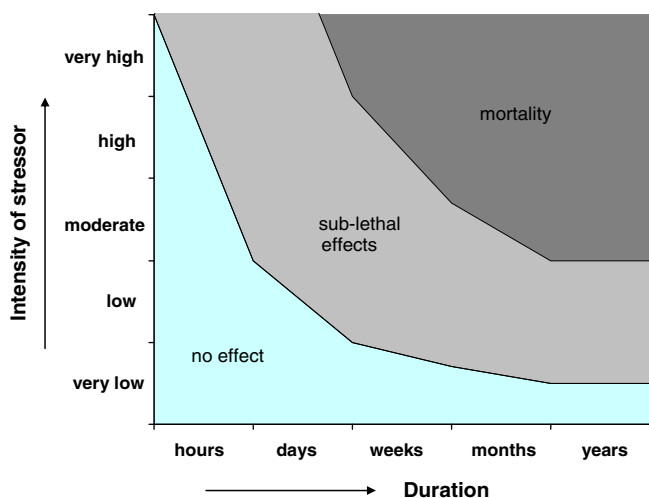|	Sedimentation	Turbidity
Stress		
Photophysiological stress	• Reduced photosynthetic efficiency of zooxanthellae and auto-trophic nutrition to coral	• Reduced photosynthetic efficiency of zooxanthellae and autotrophic nutrition to coral; switch to heterotrophic feeding, ingestion of sediment particles
Changes in polyp activity	• Extrusion of mesenterial filaments following severe stress • Increased ciliary or polyp activity, and tissue expansion in some species, to remove sediment	• Increased ciliary or polyp activity to feed
Mucus production	• Increased mucus production or sheeting to remove sediment	• Evidence of mucus production
Severe stress		
Sediment accumulation	• Accumulation of sediment on tissue of susceptible growth forms due to failure of mechanisms of rejection	
Change in coral colour	• Change in coral colour arising from changes in the density of zooxanthellae and photosynthetic pigments • Paling of coral due to partial bleaching	• Change in coral colour arising from changes in the density of zooxanthellae and photosynthetic pigments • Darkening of coral in response to reduced light due to photoacclimation
Bleaching	• Considerable whitening of corals due to the expulsion of a large proportion of zooxanthellae from the colony	• Not known
Partial mortality	• Injury to coral tissue, loss of polyps and partial mortality of the colony • Decrease in (live) coral cover	• Injury to coral tissue, loss of polyps and partial mortality of the colony • Decrease in (live) coral cover
Mortality	• Mortality of small-sized colonies and partial mortality of large corals • Mortality of susceptible species and size classes. • Decreased density, diversity and coral cover • Changes in community structure • Wide-spread mortality of corals • Major decreases in density, diversity and coral cover • Dramatic changes in community structure, and shifts towards the dominance of non-coral species, such as sponges and algae	• Mortality of susceptible species and size classes • Decreased density, diversity and coral cover • Changes in community structure • Wide-spread mortality of corals • Major decreases in density, diversity and coral cover • Dramatic changes in community structure, and shifts towards the dominance of non-coral species, such as sponges and algae

Fig. 2. Conceptual relationship between the intensity and duration of a stress event and the risk of sublethal and lethal effects on corals. This graph shows the general relationship between the magnitude of an increase in turbidity or sedimentation above background levels (vertical axis), how long it lasts (horizontal axis) and the onset of (sub)lethal effects on corals. Actual thresholds will vary by location based on typical ambient conditions, sediment properties (e.g. grain-size) and the sensitivity of the coral species.

to moderate levels of sediment stress may induce similar effects (Fig. 2). Repetitive stress events could result in deleterious effects much sooner if corals have not been allowed sufficient time to recover between consecutive disturbances (McArthur et al., 2002). Excessive sedimentation from land runoff and dredging events superimposed on other stresses from natural processes and anthropogenic activities can cause substantial impacts on coral health and dramatic declines in live coral cover (Field et al.,

2000). It should be noted, however, that a number of studies have demonstrated the occurrence of coral reefs (often with high live coral cover) in areas of high and fluctuating turbidity and sedimentation, for example from the inner shelf of the Great Barrier Reef (Mapstone et al., 1989; Hopley et al., 1993; Larcombe et al., 1995; Anthony and Larcombe, 2000). Tolerance of corals to increased turbidity and sedimentation may vary seasonally and geographically, similar to what has been demonstrated for thermal thresholds (Weeks et al., 2008).

In this section we provide a brief overview of the main impacts of sediment disturbance on corals by first examining turbidity (light for photosynthesis), then sedimentation (feeding and respiration), then effects on sexual recruitment (larval survival and settlement) and, finally, the impact of associated nutrients and contaminants.

3.1. Turbidity and light for photosynthesis

Turbidity and light availability in the marine environment are measured and expressed in a number of different ways. Common measures for turbidity include concentration of total suspended solids (TSS, in milligrams per litre), suspended-sediment concentration (SSC, in milligrams per litre), nephelometric turbidity units (NTU), Secchi disc readings (in centimetres), and attenuation coefficient (k_d). Conversion factors between these different measures are site-specific, depending on various local factors, including particle-size distribution, contribution of phytoplankton and organic content (Gray et al., 2000; Thackston and Palermo, 2000). Light availability is generally measured directly in micromole photons per square metre per day, or expressed as a relative measure (minimum light requirement) in percentage of surface irradiance (% SI). Photosynthetically active radiation (PAR) is most commonly taken as being between 400 and 700 nm, which corresponds approximately to visible light (Kirk, 1977). At any depth, the

underwater light field is highly variable and exactly how much light reaches any particular habitat will depend on factors such as orientation of the sun, the weather, shading, reflection, and refraction (Weinberg, 1976; Falkowski et al., 1990). The amount of light an organism will be exposed to is also contingent upon its vertical angle and compass direction (Weinberg, 1976; Falkowski et al., 1990; Dunne and Brown, 2001).

Light reduction is probably the most important of all sediment-related effects on corals. Light decreases exponentially with depth due to a process of attenuation (extinction), i.e. the absorption and scatter of light by water molecules, particulate solids, and dissolved matter (Weinberg, 1976; Falkowski et al., 1990). Maximal growth and development of reef corals usually occurs down to 30% to 40% of subsurface irradiance (SI) and rarely is any significant reef formation found below 10% SI (Achituv and Dubinsky, 1990). Photosynthetic carbon fixation by zooxanthellae in *Montastrea annularis* (a species with one of the widest depth distributions) was found to decrease by more than 93% between 0.5 and 50 m depth (Battey and Porter, 1988). Available light was found to be the primary factor responsible for monthly variations in growth of three hermatypic coral species in Curaçao (Bak, 1974). Shading by large *Acropora hyacinthus* table corals (causing light levels to fall exponentially to ∼1% of outside values as a light meter was moved under the table) was found to significantly reduce "understorey" coral density, cover and diversity beneath the table corals compared with adjacent unshaded areas (Stimson, 1985). Shading of a 20 m^2 area of San Cristobal Reef off south-western Puerto Rico for five weeks altered community structure, decreased net reef productivity and caused bleaching and death of several hard coral species (Rogers, 1979).

As a response to lower light levels, most mesophotic reef corals often exhibit flat, plate-like morphologies to maximise light capture and may also utilise different symbionts (Bongaerts et al., 2010, 2011). Such plate-like morphology, however, more easily traps sediment, and although this increased susceptibility to sedimentation is normally not problematic due to the relatively lower rates of sedimentation on the deeper reef, increased sediment levels can result in large-scale mortality among mesophotic corals (Bak et al., 2005; Bongaerts et al., 2010).

Even in clear tropical waters, light intensity is reduced by 60% to 80% in the top 10 m of water (Kinzie, 1973) but attenuation increases in turbid waters (Kirk, 1977). Concordantly, the total energy available for the life processes of autotrophs is also reduced (Thurman, 1994), affecting coral distribution (Roy and Smith, 1971; Jaubert and Vasseur, 1974; Titlyanov and Latypov, 1991) as well as photosynthesis and respiration (Rogers, 1979; Telesnicki and Goldberg, 1995). Decreases in algal productivity causes a drop in the nutrition, growth, reproduction, calcification rate and depth distribution of corals. In some coral species, this drop in productivity can eventually result in the coral starving (Richmond, 1993). In Singapore, chronic levels of sedimentation over the last 30–40 years has resulted in underwater visibility being reduced from 10 m recorded in the early1960s to a contemporary average of 2 m (Chou, 1996). Chuang (1977) found only 10% of surface light reached down to 8 m depth, 5% to 10 m depth and 0.35% to 16 m depth at two sampling stations, whereas Todd et al. (2004a) found <0.6% surface PAR reaching 8.9 m at one of their "best" sampling sites. There is very little coral cover around Singapore beyond 8 m depth. Wave-driven resuspension of bottom sediments in shallow areas and/or tidal currents transporting material off corals may also be important, preventing direct negative effects of sedimentation on reefs in such marginal environments (Chou, 1988; Bak and Meesters, 2000).

Results of field studies on coral distributions have indicated a negative correlation between suspended sediment loads and hard coral abundance (Rice and Hunter, 1992). Coral communities are generally better developed, are more diverse and have greater coral cover and rates of coral growth the lower the sediment load (Rogers, 1990; Fabricius, 2005). Long-term exposure to elevated levels of suspended sediment can cause reduced coral growth and reduced reef development (Rice and Hunter, 1992), although recent studies from nearshore reefs in the Great Barrier Reef would argue against this, where there is evidence of spatially relevant and temporally persistent reef-building having occurred over millennial timescales (Larcombe et al., 1995; Anthony and Larcombe, 2000).

Monitoring data from the west coast of Barbados indicated a 20% reduction in the annual growth rate of *Montastraea annularis* in response to a 28% increase in average long-term background suspended-sediment levels (Hawker and Connell, 1989). Coral cover and diversity are greatly reduced near sources of terrigenous sediment input and runoff (e.g. rivers) and tend to increase with distance from the river mouth (Acevedo et al., 1989; Hoeksema, 1990; van Katwijk et al., 1993; Kleypas, 1996; Woolfe and Larcombe, 1999; Nugues and Roberts, 2003; Fabricius, 2005; Dikou and Van Woesik, 2006a; Cleary et al., 2006, 2008; Golbuu et al., 2008; Hennige et al., 2010; van der Meij et al., 2010). In the geological record, increased turbidity has been implicated as a major factor in the demise of several coral reefs in the western Atlantic (Adey et al., 1977; Lighty et al., 1978; Macintyre, 1988; Achituv and Dubinsky, 1990; Kleypas, 1996). At larger spatial scales, however, increased terrigenous sediment supply due to human impacts on catchments may not necessarily lead to increased turbidity or sedimentation at reefs further offshore and corals can indeed survive well in some turbid environments (Larcombe and Woolfe, 1999; Perry and Larcombe, 2003; Perry, 2005; Perry and Smithers, 2010).

There is some indication that elevated turbidity can reduce thermal bleaching damage to reefs, suggesting a photo-protective effect during thermal anomalies making shallow-water corals in turbid waters less susceptible to bleaching than those in clear waters (Phongsuwan, 1998; Piniak and Storlazzi, 2008) but this requires further study.

3.2. Sedimentation: feeding and respiration

Sedimentation and burial in the marine environment are measured and expressed in a number of different ways. Sedimentation (sometimes also called "siltation" or "deposition") is usually expressed as a rate (in mg cm^{-2} d^{-1}) or in thickness (mm) of the sediment layer (instantaneous, or accumulating over time). Water turbidity and sedimentation correlate only in part because increased turbidity does not necessarily lead to increased sediment deposition (Larcombe and Woolfe, 1999). A range of methods is available for field measurements of sediment accumulation or sediment elevation change in underwater environments, all of which have merits and shortcomings (Thomas and Ridd, 2004). Despite their widespread use in this setting, sediment traps do not provide quantitative information about "net" sedimentation on coral surfaces (Storlazzi et al., 2011). Sediment traps can, however, yield useful information about the relative magnitude of sediment dynamics in different areas, as long as trap deployment standards are used for trap height, trap-mouth diameter, height of trap mouth above the substrate and spacing between traps (Jordan et al., 2010; Storlazzi et al., 2011).

Sedimentation on coral reefs may cause smothering of coral polyps (Fig. 3; Fabricius and Wolanski, 2000), inhibiting photosynthetic production and increasing respiration as well as creating a diffusion barrier. In a study by Abdel-Salam and Porter (1988), daytime photosynthesis in corals exposed to sediments decreased, while at night-time respiration increased. Stafford-Smith (1993) measured a drop in photosynthesis to respiration (P:R) ratios for

Fig. 3. Partial coverage of corals with sediment transported by plume and currents from nearby dredging works (Photo courtesy: Tony Ayling).

smothered corals. Corals will attempt to clean themselves of this sediment by a combination of ciliary action and the production and sloughing off of mucus sheets. This, however, is expensive in energy and can lead to exhaustion of mucus-producing cells (Peters and Pilson, 1985; Riegl and Bloomer, 1995; Riegl and Branch, 1995). At the individual (colony) level, energy diverted to clearing the colony surface of sediment can lead to growth inhibition and a reduction in other metabolic processes (Dodge and Vaisnys, 1977; Rogers, 1983; Edmunds and Davies, 1989). At the population level, increased sedimentation may inhibit sexual population recruitment, cause changes in the relative abundance of species, decrease live coral cover and reduce the abundance and diversity of corals and other reef fauna, including fish (Brock et al., 1965; Amesbury, 1981; Rogers, 1990; Gilmour, 1999; Bray and Clark, 2004). It may also, however, cause increased rates of asexual reproduction in free-living corals that show partial mortality (Gilmour, 2002, 2004).

Furthermore, cover by sediment interferes with the coral's feeding apparatus, by causing polyps to retract and tentacular action to cease. Sufficient sediment overburden may make it completely impossible for corals to expand their polyps and thus can inhibit the coral compensating for its losses in autotrophic food production by heterotrophic activity. While some corals are able to ingest sediment particles in turbid conditions and derive some nutritional value from them (Rosenfeld et al., 1999; Anthony et al., 2007) or even build up higher lipid energy reserves (Anthony, 2006), most corals cease activity when confronted with heavy sediment loads.

Corals can withstand a certain amount of settling sediment, as this occurs naturally (Rogers, 1977, 1990; Perry and Smithers, 2010). Many species have the ability to remove sediment from their tissues, either passively (through their growth form) or actively (by polyp inflation or mucus production, for example). Sediment rejection is a function of morphology, orientation, growth habit and behaviour of the coral and the amount and type of sediment (Bak and Elgershuizen, 1976). Corals growing in areas where they typically experience strong currents or relatively high wave energy generally have no need for effective (active) sediment rejection mechanisms, as the turbulence of the water assists in the passive cleaning of any sediment that may have accumulated on the coral tissue (Riegl et al., 1996; Hubmann et al., 2002; Sorauf and Harries, 2010). Many branching corals appear very effective in passive rejection of sediment because of their colony morphology, but they may suffer from reduced light levels. Massive and plating coral colonies, on the other hand, though usually more tolerant of turbid conditions, are more likely to retain sediment because of their shape and a lack of sediment rejection capabilities and thus tend to have a relatively low tolerance to sedimentation (Brown and Howard, 1985).

Various species of free-living mushroom corals that live on reef flats and slopes can occur on a range of substrata, whereas those that live deeper on the sandy reef bases usually live on sediment (Hoeksema and Moka, 1989; Hoeksema, 1990, 1991b). As juveniles, mushroom corals live attached and only after a detachment process

do they become free-living and mobile (Hoeksema, 1989, 2004; Hoeksema and Yeemin, 2011). Some free-living mushroom coral species show a large detachment scar and their juveniles remain relatively long in the attached anthocaulus phase. A possible reason for postponed detachment is to avoid burial of the juvenile coral, especially if the coral remains vertically oriented so that sediment can more easily be shed than in a horizontal position (Chadwick-Furman and Loya, 1992). The evolutionary development of additional mouths over the upper surface in mushroom corals has resulted in the growth of larger coralla but also in a greater chance of survival during sedimentation—if one mouth is blocked by sediments, others remain intact (Hoeksema, 1991a; Gittenberger et al., 2011). In free-living mushroom corals, budding or fragmentation in combination with regeneration and mobility facilitates continuous growth and may result in large and dense accumulations of specimens on sandy surfaces (Pichon, 1974; Littler et al., 1997; Hoeksema, 2004; Hoeksema and Gittenberger, 2010; Hoeksema and Waheed, 2011).

3.3. Effects on sexual recruitment, larval survival and settlement

Sedimentation and turbidity not only influence the survival of adult corals, but also their reproductive success and probability of recruitment, as well as the survival and settlement of coral larvae (Babcock and Smith, 2000; Birrell et al., 2005). Sedimentation at a level that only partially covers the substrate and that is not directly harmful to adult colonies, and even suspended sediment, can significantly reduce larval recruitment by inhibiting settlement and reducing larval survival in the water column (Gilmour, 1999; Babcock and Smith, 2000; Birrell et al., 2005; Goh and Lee, 2008) although this is not always detectable in field studies (Fisk and Harriott, 1989). 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 (Fabricius, 2005).

Babcock and Davies (1991) evaluated effects on settlement rates of *Acropora millepora* larvae in aquaria under 0.5–325 mg cm^{-2} d^{-1} sedimentation. Higher sedimentation rates reduced the number of larvae settling on upper surfaces, but total numbers of settled larvae were not significantly affected by sedimentary regime. This was, however, likely an artefact since, in the field, accumulation of sediment on upward-facing surfaces would indeed greatly reduce the overall amount of suitable substratum available. Hodgson (1990b) investigated the larval settlement rate of *Pocillopora damicornis* on bare glass and on glass covered with measured amounts and area of fine sediment finding significant reduction due to sediment. Sediment cover of 95% completely prevented settlement. There was no increase in settlement when sediment cover was reduced from 90% to 50% of the glass surface area. In highly turbid conditions (>100 mg L^{-1}, which would not be unusual at sites in close proximity to a dredging operation), significant numbers of settled planulae of *Pocillopora damicornis* underwent reversed metamorphosis ("polyp bail-out"), indicating conditions were not appropriate for continued growth and development (Te, 1992). Chronic exposure

to sedimentation rates of 10–15 mg cm^{-2} d^{-1} caused a 50% decrease in fecundity in *Acropora palifera* in Papua New Guinea (Kojis and Quinn, 1984).

Elevated levels of suspended sediment (50 mg L^{-1}, 100 mg L^{-1}) affected fertilisation, larval survival, and larval settlement in *Acropora digitifera* (Gilmour, 1999). While post-fertilisation embryonic development was not inhibited by suspended sediments, larval survival and larval settlement were significantly reduced. Significant declines in fertilisation success were reported for *Acropora millepora* at suspended-sediment levels $\geqslant 100$ mg L^{-1} compared with lower levels ranging from 0 to 50 mg L^{-1} with approximately 36% fertilisation at the highest tested suspended-sediment levels of 200 mg L^{-1} (Humphrey et al., 2008). Elevated concentrations of suspended sediment (43 mg L^{-1}, 159 mg L^{-1}) also significantly reduced fertilisation success in *Pectinia lactuca* compared with controls (Erftemeijer et al., 2012).

These findings imply that increased levels of suspended sediment and/or sedimentation due to dredging operations—especially when coinciding with the main spawning season of corals—may affect their reproductive success, compromise coral recruitment and thereby compromise the recovery of degraded reefs (Erftemeijer et al., 2012). The same issues are probably relevant in naturally or episodically turbid (higher stress) settings.

3.4. Nutrients and contaminants

The mucus coat that surrounds corals, which is moved off the coral by ciliary action and is replaced repeatedly, acts as their primary defence against precipitated sediment particles. A potentially problematic by-product of this abundant mucus production can be fertilisation of the nearby water potentially causing population explosions of bacteria (Mitchell and Chet, 1975; Coffroth, 1990; Ritchie and Smith, 2004; Brown and Bythell, 2005; Klaus et al., 2007). The metabolism of these bacteria can lead to local anoxic conditions and concomitant death of coral tissue in the immediate vicinity. Furthermore, high nutrient contents of silt can lead to microbial activity, eventually causing the underlying coral tissue to become necrotic (Weber et al., 2006; Hodgson, 1990a). Conversely, some coral species have been observed to exploit nutrient-rich suspended particles as a food source, thereby compensating for the stress caused by sedimentation (Fabricius and Wolanski, 2000).

Numerous kinds of terrestrial pollutants, including those from sewage and agricultural runoff, make their way into nearshore sediments that can be resuspended by dredging operations and subsequently cause eutrophication of coastal waters (Kenchington, 1985; Grigg and Dollar, 1990; San Diego-McGlone et al., 2008; Todd et al., 2010). As corals generally grow in oligotrophic waters, elevated nutrient levels can lead to a range of negative effects on coral health (Hawker and Connell, 1989), reduced fertilisation success (Harrison and Ward, 2001) and settlement rates (Hunte and Wittenberg, 1992). Increased phytoplankton concentrations reduce light penetration to the symbiotic zooxanthellae and increased organic sediment loads can smother corals (Bell, 1992). Eutrophication can also increase the severity of diseases (Bruno et al., 2003) and lead to competitive advantage for macroalgae that respond by rapid growth, smothering corals or blocking light (Lapointe, 1997; Walker and Ormond, 1982), although evidence for different trajectories also exists (McCook, 1999a, 1999b). Sediments that are influenced by outflow from industrial areas can contain relatively high levels of lead, cadmium, copper, tin, nickel and iron (Amin et al., 2009; Todd et al., 2010). In particular, copper is known to inhibit coral recruitment, fertilisation and development (Reichelt-Brushett and Harrison, 2005; Negri and Hoogenboom, 2011).

4. Responses among and within coral species

4.1. Responses to turbidity

Light-enhanced calcification is responsible for most of the skeletal growth of reef-building corals (Goreau, 1959). Low light decreases calcification in zooxanthellate scleractinian corals, being approximately three times lower in darkness than in light (Kawaguti and Sakumoto, 1948; Gattuso et al., 1999). Titlyanov (1991), however, noted that enhanced utilisation of light by zooxanthellae in three stony corals can result in stable levels of primary production in a wide light range (20–90% PAR). Low light levels may also inhibit the development of coral larvae (Rogers, 1990). Similar patterns of photo-acclimation (through photophysiological adaptations) across gradients of increased turbidity have been demonstrated by Hennige et al. (2008, 2010).

Although certainly also related to a variety of other environmental factors, species diversity of corals generally tends to decrease sharply with increasing (chronic) turbidity (Rogers, 1990; Becking et al., 2006; Cleary et al., 2008). Long-term turbidity stress can shift the species composition of reefs through the death of more light demanding corals and the subsequent replacement by usually deeper-living, more shade-tolerant ones at certain depths (Pastorok and Bilyard, 1985). Dikou and van Woesik (2006b) noted in Singapore the occurrence of deeper-water genera such as *Merulina*, *Pachyseris* and *Mycedium* found in relatively shallow (3–4 m) depths was most likely due to high turbidity levels. Also in Singapore, Goh et al. (1994) considered the sediment-impacted light environment to be the main factor controlling coral colony form. Foliose forms tended to dominate the shallow reef with more massive and encrusting forms found deeper.

4.2. Responses to sedimentation

Corals can react either actively or passively to sediments, which in many ways defines their capability to withstand prolonged sedimentation. Passive shedding refers to corals taking advantage primarily of their shape to allow increased runoff of sediment, to maintain parts of the corallum above sediment, or to use water currents to remove accumulated sediment (Stafford-Smith and Ormond, 1992; Stafford-Smith, 1993; Riegl, 1995; Riegl et al., 1995; Sanders and Baron-Szabo, 2005). It has long been known that coral shape correlates well to the environment, and in particular in paleo-ecological studies, corallum shape has frequently been equated to sedimentation conditions (Plusquellec et al., 1999; Sanders and Baron-Szabo, 2005). Colony shape plays an obvious role in aiding sediment runoff and hemispherical to columnar species have been found to be efficient passive shedders (Bak and Elgershuizen, 1976; Dodge and Vaisnys, 1977; Stafford-Smith, 1993; Riegl, 1995). Branching species retain little sediment, and many poritids are indeed very sediment-tolerant; however, some acroporids are inefficient sediment rejecters and do not appear well adapted to sedimentation despite an apparently advantageous growth form (Stafford-Smith, 1993). Thin, stick forms such as *Madracis mirabilis* or *Acropora cervicornis* are ideally suited passive shedders. Both species have little surface available for sediment accumulation and staghorn corals have polyps that are widely separated, further reducing the chance of sediment clogging (Meyer, 1989). Another efficient design for passive sediment rejection is the thin, platy and upright growth habit exhibited by *Agaricia tenuifolia* in shallow water. Only a small area is present at the top of each plate for sediment accumulation. This form, coupled with an erect growth habit, is very effective in letting sediment slide passively from the colony (Meyer, 1989). Gorgonians (Octocorallia), especially sea whips, were found to be among the most tolerant species to

sediment-loading and dredging-induced turbidity in Florida (Marszalek, 1981). Five species of gorgonians in the highly sedimented waters of Singapore showed growth rates ranging from 2.3 to 7.9 cm yr^{-1}, which are comparable to published growth rates from non-sedimented environments (Goh and Chou, 1995).

Riegl (1995), Riegl and Bloomer (1995) and Schleyer and Celliers (2003) found in zooxanthellate soft corals, which are generally inefficient and passive sediment shedders, that ridged morphology maintained sediment-free areas and thus maintained photosynthetic efficiency which allowed these corals to persist in relatively sand-laden environments. In scleractinian corals, calyx size, orientation, and degree of meandrisation have been found to correlate in some species with rejection efficiency (Hubbard and Pocock, 1972; Rogers, 1983; Johnson, 1992; Stafford-Smith, 1993; Philipp and Fabricius, 2003; Sanders and Baron-Szabo, 2005; Rachello-Dolmen and Cleary, 2007; Sorauf and Harries, 2010); however, such relationships appear to be dependent on sediment size (Riegl, 1995). A counter-intuitive mechanism of passive sediment rejection is that of funnel-shaped corals (*Acropora clathrata* and *Turbinaria peltata*) occurring in turbid, but also high-energy environments. Riegl et al. (1996) showed in field and laboratory experiments that funnel-opening angle and depth could control hydrodynamic clearance of sediment via generation of unstable vortices in the funnels under high-current (surge) conditions that efficiently removed sediment from corals.

Active sediment-shedding mechanisms include polyp inflation, tentacular action and polyp movement (Stafford-Smith and Ormond, 1992; Riegl, 1995; Bongaerts et al., 2012). The cue to this activity is likely irritation of surface receptors when ciliary motion alone is not capable of removing sediment. Tentacular motion can be coordinated to collect sediment, largely by the action of cilia on the tentacular surfaces, which is then pushed or made to slide off the polyp. In some species, sediment is moved to the centre of the oral disc and ingested. This may be correlated with the observed feeding for energy gain reported by Anthony (1999a, 2000). Tissue expansion is a regularly observed mechanism that consists either of expansion of the entire polyp with ensuing tentacular action, or of an inflation of the oral disc with retracted polyps. The first would be a reaction under light to moderate sediment load, the latter a reaction under heavier sediment load. The inflation of the polyp with retracted tentacles leads to the formation of a smooth colony surface, from which sediment can slide off easily. This mechanism is thus a combination of active and passive sediment-shedding.

In free-living stony corals, such as mushroom corals, tissue inflation can lead not only to the removal of sediments, but also to the relocation of the entire corallum which is capable of pushing itself over the substratum (Chadwick, 1988; Chadwick-Furman and Loya, 1992; Hoeksema and de Voogd, 2012), a dispersion mechanism leading to high densities of evenly distributed corals (Goreau and Yonge, 1968; Schuhmacher, 1979; Fisk, 1983; Hoeksema, 1988, 2004; Yamashiro and Nishihira, 1995). Furthermore, if a free-living mushroom coral is at risk of dying because of sedimentation, it may survive by budding, a mechanism of asexual reproduction in which an adult coral generates clonal polyps that continue to live after the parent coral's death. This mechanism may result in coral aggregations (Gilmour, 2002, 2004; Hoeksema, 2004), but high densities of free-living corals in sediment-rich habitats may also be the result of sexual reproduction to spread the risk of burial and subsequent mortality (Johnson, 1992).

Important for sediment rejection is the production of mucus sheets (Coffroth, 1990; Rogers, 1990; Stafford-Smith, 1993). Some corals produce copious amounts of mucus as their primary mechanism to remove silt (e.g. *Meandrina meandrites*), whereas other corals produce mucus more sparingly but then use additional clearing mechanisms such as ciliary action (*Montastraea annularis*)

(Dumas and Thomassin, 1977). Mucocytes, the cells producing mucus, are common in all coral tissues, but particularly so on the oral surface (Brown and Bythell, 2005). Together with ciliary action, mucus is used to move accumulated sediment off the coral (Schuhmacher, 1977). Mucus production, however, uses up an important part of a coral's daily photosynthetic production and its frequent replacement can lead to excessive demands on energy and a decrease in the number of mucus cells (Riegl and Bloomer, 1995; Vargas-Angel et al., 2006). Under severe sedimentation and turbidity stress, more than three times a coral's daily energy production can be used up for mucus production (Riegl and Branch, 1995)—mucus that is then sloughed off with the adhering sediment. Continued chronic sedimentation as well as frequent, repeated exposure to intermittent pulses of high sedimentation will lead to exhaustion of the sediment-clearing ability of corals, eventually leading to tissue thinning, loss of cilia and mucosecretory cells, and ultimately death (Fig. 4).

4.3. Within-species variation

It is clear that differences exist among species in their ability to withstand the effects of increased sedimentation. Do these differences also occur within species? As not all growth forms will survive equally under sediment stress, some environment-morphology matching can be expected. Certainly, many corals display
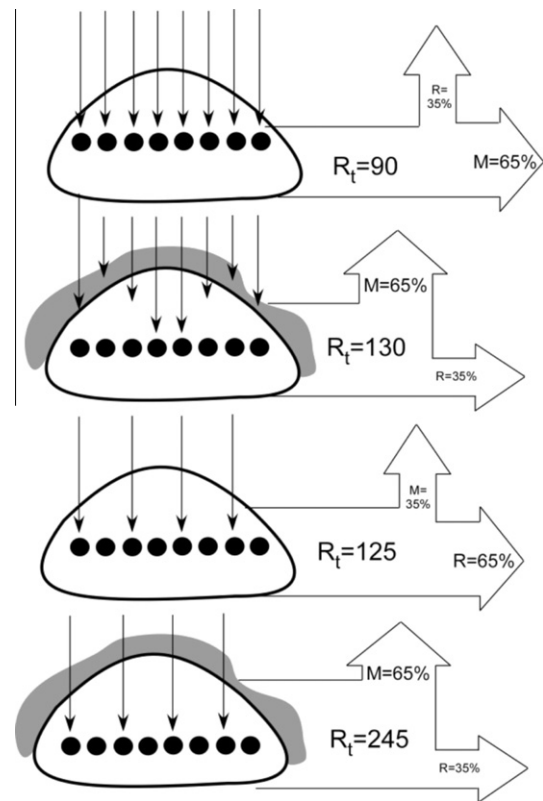

Fig. 4. Why corals starve to death when sedimented. Vertical arrows represent light, the black dots are zooxanthellae, the arrow coming from the coral represents energy use (measured by respirometry). Sediment is shown as grey cover on the coral. Under ~50% light (PAR$_s$) conditions, ~90% of productivity is respired, of which ~35% is due to mucus production and ~65% due to other metabolic functions. Under sedimentation, this is reversed and respiration due to mucus production now dominates. Also, more energy is respired than produced. Under increased turbidity (~25% PAR$_s$), the coral cannot function as autotroph anymore, and when sedimented uses more than two-days energy production in respiration, 65% of this for mucus alone. R$_t$ = total respiration; M = share of respiration due to mucus production; R = share of respiration due to regular metabolic activity. Modified from Riegl and Branch (1995). By permission of Elsevier.

a high degree of intraspecific morphological variation. This can be due to genetic differentiation (polymorphism), environment-induced changes (phenotypic plasticity) or a combination of both (Foster, 1979; Todd et al., 2002a,b; Todd, 2008). Various studies have shown that the ambient light environment (both turbidity and depth-related) can be correlated to intraspecifc colony, corallite, and sub-corallite morphology, but little is known about the within-species differences in relation to settling sediments.

Examples of intraspecific morphological variation that has been related to light include Jaubert (1977) who showed that colonies of *Porites convexa* (as *Synaraea convexa*) were hemispherical with many short branches in high light, flatter with longer branches in medium light, and explanate in the lowest light conditions. Graus and Macintyre (1982) modelled calcification rates and photosynthesis in *Montastraea annularis* and demonstrated that light had the greatest effect on its morphogenesis. Computer models based on light diffusion and light shelter effects accurately matched the dendritic form of *Merulina ampliata* (Nakamori, 1988) via reciprocal transplant experiments, Muko et al. (2000) determined that platy colonies of *Porites sillimaniani* developed branches within eight months when transplanted to high light conditions. Beltran-Torres and Carricart-Ganivet (1993) concluded that light was the principal physical factor influencing corallite diameter and septal number variation in *Montastraea cavernosa*, and Wijsman-Best (1974) suggested light reduction to cause a decrease with depth of both corallites per unit area and number of septa in various faviids. Todd et al. (2004a) concluded that irradiance was the main factor driving small-scale plastic responses in the massive corals *Favia speciosa* and *Diploastrea heliopora* and suggested that this response may enhance light capture by increasing surface area. The corallite shape of *Goniastrea pectinata* also changes in relation to light and Ow and Todd (2010), through modeling light capture, showed this response to be an adaptive response to the immediate light environment.

Some morphologies, both at colony and corallite level, are believed to encourage sediment-shedding (Lasker, 1980; Rogers, 1983, 1990). Marshall and Orr (1931), after smothering various coral taxa with sand, concluded that corals with large polyps were better at removing sediment than those with small polyps. Small polyps equate to less tissue-distension potential and thus to a reduced ability to remove coarse grains. Stafford-Smith and Ormond (1992) found that active-rejection capability was positively correlated with calyx size and Hodgson (1993) concluded that large corallites and extensible polyps were advantageous in his tests on 50 species of coral. Corals that move larger grains tend to have more septa, high relief and numerous septa teeth. The shape of the calyx is also important to sediment-shedding, with V or U floors apparently beneficial for mechanical reasons (Hubbard and Pocock, 1972). Todd et al. (2001) hypothesised that these features in *Favia speciosa* may be advantageous to this species in Singapore's sedimented waters. Further, they found that *Favia speciosa* polyps were significantly larger at their most sediment-impacted study site (Todd et al., 2001). Riegl (1995) also found corallum shape to be important while Dodge (1982) found no clear trend. Gleason (1998) noted green and brown morphs of *Porites astreoides* had different sediment-shedding abilities even though small-scale morphologies were very similar. Even intra-colonial variation can have a great effect on sediment removal; for instance, small differences in colony convexity can lead to areas where sediments accumulate and create anoxic conditions (Stafford-Smith, 1992, 1993).

In the only study to date to specifically examine whether sediment can induce change in coral morphology, Todd et al. (2004b) found a slight increase in rugosity (the height of the wall measured from the outside of the corallite) in fragments exposed to sediment treatment compared with controls (*Favia speciosa* control = 1.36 mm, sediment treatment = 1.53 mm; *Diploastrea heliopora*

control: 1.40 mm, sediment treatment = 1.54 mm). As passive rejection is enhanced by tall polyps with steep surfaces (Lasker, 1980), it is possible that this response would be beneficial to the two species tested. Any attempt to examine plastic responses of corals to chronic sediment is complicated by the reduction in light caused by sediment in the water. For instance, explanate *Porites sillimaniani* form branches under high light (Muko et al., 2000). It is easy to see how the branching form might be advantageous in high sediment conditions, but these are unlikely to develop as they require high light. Also, in *Turbinaria mesenterina*, convoluted forms (good for sediment rejection) became explanate (bad for sediment rejection) in low light and explanate forms became convoluted in high light conditions (Willis, 1985). The same problem also occurs at finer scales. Smaller corallites with fewer septa are likely related to decreased light in *Montastraea cavernosa* and some other faviids (Wijsman-Best, 1974; Beltran-Torres and Carricart-Ganivet, 1993) but the opposite traits are beneficial for sediment removal (Marshall and Orr, 1931; Hubbard and Pocock, 1972; Stafford-Smith and Ormond, 1992; Hodgson, 1993).

5. Tolerance levels and critical thresholds

All coral species are arranged along a gradient of relative tolerance to stress from sediment. Each coral species, therefore, has its own set of threshold values representing the concentrations of sediment which produce sublethal or lethal effects. After a certain maximum concentration, reduction of growth occurs due to smothering, reduced light levels and reduced zooxanthella photosynthesis. Ultimately, when sustained over a longer period, such concentrations can cause mortality.

5.1. Turbidity

There is a clear relationship between substratum cover by live corals and water transparency (K_{PAR}), which determines the compensation depth of corals (Yentsch et al., 2002). Values for the minimum light requirements of corals reported in the literature range from <1% to as much as 60% of surface irradiance (SI) (Table 3). Kleypas et al. (1999) suggested minimum light requirements to allow reef formation (40% SI) to differ from the minimum light requirements to allow survival of individual corals (10% SI). The sensitivity to reduced light is—at least in part—dependent on the growth form of corals, with branching species generally thriving only under at least 60% average SI, while most plocoid and meandroid massive species require only 20% average SI, and several platy corals can survive with as little as 0.15% (Jaap and Hallock, 1990). Typically, the reduced availability of light caused by increased turbidity is experienced more strongly by corals growing in deeper areas of a reef than by corals growing in shallower areas. Turbidity effects on corals depend on the grain size of the suspended sediment, with fine particles contributing most to light reduction while coarser particles may cause scouring and abrasion of coral tissue (PIANC, 2010).

Despite an impressive body of literature (see review by Hubbard, 1986), little quantitative information exists on the specific responses of reef organisms to suspended-sediment loading. There is a highly significant inverse relationship between coral growth rates and suspended-sediment yields (Miller and Cruise, 1995). Practical observations of coral mortality associated with turbidity plumes from dredging projects or increased runoff are inconsistent with laboratory experiments that have documented surprising tolerance by corals to high doses of sediment over short periods of time (Taylor and Saloman, 1978; Rogers, 1983). One of the factors responsible for this discrepancy may be the effect of the duration of exposure (Fig. 2). Tolerance limits of corals for total suspended

Table 3
Some published critical threshold of corals for light availability (% of surface irradiance SI).

Species/type of corals	Location	%SI	References
Plate corals	Florida,USA	0.15	Jaap and Hallock (1990)
Star corals	Curacao	1	Bak (1978)
Scleractinian corals	South China Sea	2–8	Titlyanov and Latypov (1991)
Individual corals	Worldwide	10	Achituv and Dubinsky (1990)
Star and brain corals	Florida, USA	20	Jaap and Hallock, 1990
Coral reefs	Worldwide	35	Achituv and Dubinsky (1990)
Branching corals	Florida, USA	60	Jaap and Hallock (1990)

matter (or suspended-sediment concentration) reported in the literature range from <10 mg L^{-1} in reef areas not subject to stresses from human activities to >100 mg L^{-1} in marginal reefs in turbid nearshore environments (Marshall and Orr, 1931; Roy and Smith, 1971; Mapstone et al., 1989; Hopley et al., 1993; Larcombe et al., 2001; Hoitink, 2003; Sofonia and Anthony, 2008) (Table 4). This wide range demonstrates that different coral species and corals in different geographic regions may respond differently to turbidity increases. Thermal tolerances in corals have also been reported to vary geographically (Weeks et al., 2008). Some corals have been shown to possess the ability to (temporarily) switch between autotrophy and heterotrophy or to make adjustments to their respiratory demands in response to episodic turbidity stress events (Telesnicki and Goldberg, 1995; Anthony and Fabricius, 2000) but these data are limited to a few coral species. Reduced photosynthetic capacity may lead to reduced energy reserves for maintenance and growth. Corals contain large lipid stores under normal (non-stressed conditions), but a recent study indicated that 30–50% depletion of those reserves may occur during stress events within a matter of weeks (Anthony et al., 2007).

In certain locations, coral reefs persist in highly turbid areas (Perry, 2005; Perry and Smithers, 2010). Larcombe et al. (1995) described the characteristics of suspended sediment concentrations of marine waters near inner-shelf fringing coral reefs in northern Australia and related these to the prevailing oceanographic and meteorological conditions. High temporal and spatial variation in near-bed SSCs corresponded to wind-generated swells, which,

Table 4
Some published critical thresholds of corals (reefs) for Total Suspended Sediment (mg L^{-1}).

Description	Location	mg L^{-1}	References
Coral reefs	Great Barrier Reef (GBR), Australia	3.3	Bell (1990)
Coral reefs	Fanning lagoon, Florida, USA	10	Roy and Smith (1971)
Coral reefs	Caribbean	10	Rogers (1990)
Coral reefs	Papua New Guinea	15	Thomas et al. (2003)
Coral reefs	Florida, USA	20	Bogers and Gardner (2004)
Corals	Dominican Republic	20	Van der Klis and Bogers (2004)
Marginal reef environments	Banten Bay, Java, Indonesia	40	Hoitink (2003)
Marginal reef environments	Paluma Shoals, QLD Australia	40	Larcombe et al. (2001)
Nearshore fringing reefs	Magnetic Island, GBR, Australia	75–120	Mapstone et al. (1989)
Nearshore fringing reefs	Cape Tribulation, GBR, Australia	100–260	Hopley et al. (1993)
Seven resistant coral species	Florida, USA	165	Rice and Hunter (1992)

within 1 km of the reefs, produced near-bed SSCs of well over 200 mg L^{-1}. At the fringing coral reefs SSCs ranged from 5 mg L^{-1} to 40 mg L^{-1}. Flushing of these bays by tidal currents was important to prevent the build-up of suspended sediment in the water around the coral reefs. Other extremely turbid reefs were described by Anthony and Larcombe (2000) from Halifax Bay, Australia, where "coastal turbid-zone reefs" occur in water less than 4 m deep, with turbidity sometimes over 100 NTU ($\sim$220 mg L^{-1}) as a result of wave-induced resuspension, and wind-driven longshore currents prevent accumulation of fine-grained sediment. In turbid situations, the key to sustained coral growth appears to be low sediment accumulation, frequently assured by strong tidal flushing, although recent studies from the GBR indicate that reefs in these settings can have quite high accretion rates. While reef growth was found to be possible under such conditions, these reefs hosted relatively moderate species numbers and sometimes had poorly consolidated frameworks (Hopley et al., 2007). Hoitink (2004) found that tidal currents around reefs in Indonesia resuspended sediments to give average Suspended-sediment concentrations between 2 and 10 mg L^{-1}, with maxima up to 50 mg L^{-1}. Riegl (1995) found surge-induced peak suspended-sediment concentrations of up to 389 mg L^{-1} in sandy gullies and 112 mg L^{-1} over coral on South African reefs; this, however, was local sediment stirred up and immediately re-deposited.

While the studies above demonstrate that coral reefs and turbidity/sedimentation can coexist, it also shows the danger of introducing sediment since it is likely to be remobilised repeatedly. All the reef systems discussed in the previous two paragraphs were clearly adapted to sedimentation and turbidity, with mostly low accretion rates demonstrated in South Africa (Ramsay and Mason, 1990; Riegl et al., 1995) and quite high accretion rates on inshore reefs from the Great Barrier Reef (Larcombe et al., 1995), comparable to those in "optimal" environments. Corals that are naturally exposed to high and variable background conditions of turbidity and sedimentation (e.g. due to storms and/or river influence) will show higher tolerances to short increases in turbidity or sedimentation caused by dredging (Nieuwaal, 2001). Corals from shallow-water environments, where they are frequently exposed to elevated temperatures, storms and wave action, are more likely to be tolerant of environmental stresses than corals in deeper waters (Brown and Howard, 1985; Hoeksema, 1991b; Hoeksema and Matthews, 2011).

A synthesis of literature data regarding the sensitivity of different coral species to turbidity is presented in Table 5. These data were reworked and related to a relative sensitivity index according to the response matrix presented in Table 6. Sensitivity classes were then given scores from 1 to 5, with 1 corresponding to "very tolerant" and 5 to "very sensitive". The scores for individual coral species were subsequently related to their dominant growth form and mean calyx diameter. Analysis of these data (90 entries for 46 species) confirmed that there is a significant relationship (Kruskal–Wallis, $P < 0.05$) between the growth form of corals and their sensitivity to turbidity (Fig. 5a). Most soft corals and many massive coral species are relatively sensitive to turbidity while laminar, plating and tabular corals as well as some morphologically variable corals are relatively tolerant. There was no significant relationship between the calyx diameter of corals and their sensitivity to turbidity (Fig. 5b).

5.2. Sedimentation

Most coral species are sensitive to enhanced sedimentation, even in the order of a few centimetres per year (Rogers, 1990). Pastorok and Bilyard (1985) suggested that sedimentation rates of >50 mg cm^{-2} d^{-1} (equivalent to 500 g m^{-2} d^{-1}) may be considered catastrophic for some coral communities, while 10–50 mg cm^{-2} d^{-1}

Table 5

Sensitivity of different coral species for turbidity. Overview of the response of different species of corals to various levels of turbidity tested, as reported in the literature. Nomenclature of coral species was updated according to the most recent taxonomic revisions. Growth forms (as stated or inferred): B = branching; C = columnar (incl. digitate); E = encrusting; F = foliaceous; L = laminar (incl. plate & tabular); M = massive; S = solitary (free-living); So = soft corals & gorgonians. Calyx diameter measured on museum specimen, supplemented with data from Stafford-Smith and Ormond (1992).

Coral species	Turbidity level (tested)	Response	Growth form	Calyx (mm)	References
Acropora cervicornis (Lamarck, 1816)	Severe light reduction (shading) for 5 weeks	Mass bleaching (3 weeks), mortality/algal cover (7 weeks), no recovery (8 months)	B	1.0	Rogers (1979)
Acropora cervicornis (Lamarck, 1816)	50 mg/l (96 h)	No effect	B	1.0	Thompson (1980b)
Acropora cervicornis (Lamarck, 1816)	150 mg/l (96 h)	Polyp retraction, mucus production but no mortality	B	1.0	Thompson (1980b)
Acropora cervicornis (Lamarck, 1816)	476 mg/l (96 h)	Partial mortality after 96 h.	B	1.0	Thompson (1980b)
Acropora cervicornis (Lamarck, 1816)	Total shading (3 weeks)	Bleaching and mortality, no recovery	B	1.0	Quoted in Nieuwaal (2001)
Acropora cervicornis (Lamarck, 1816)	25 mg/l (drilling mud) (24 h)	62% Decrease in calcification rate	B	1.0	Kendall et al. (1983)
Acropora cervicornis (Lamarck, 1816)	100 mg/l (drilling mud) (24 h)	50% Decline in soluble tissue protein	B	1.0	Kendall et al. (1983)
Acropora cervicornis (Lamarck, 1816)	50 and 100 mg/l (kaolin, 24 h)	Reduced calcification rate and free amino acids at 100 mg/l (recovery in 48 h)	B	1.0	Kendall et al. (1985)
Acropora cervicornis (Lamarck, 1816)	1000 mg/l (for 65 h)	Mortality of colonies	B	1.0	Thompson and Bright (1980)
Acropora digitifera (larvae)	50–100 mg/l (lab and feld tests)	Adverse effects on fertilisation, larval survival and settlement			Gilmour (1999)
Acropora millepora (Ehrenberg, 1834)	1–30 mg/l SPM (hours)	Increased feeding capacity at high SPM concentrations	B	1.0	Anthony (1999a)
Acropora millepora (Ehrenberg, 1834)	1–30 mg/l SPM (days)	Increasing contribution of heterotrophy at high SPM conc.	B	1.0	Anthony (2000)
Acropora millepora (Ehrenberg, 1834)	1, 3, 10, 30 and 100 mg/l TSS (16 weeks)	Full colony mortality at 100 mg/l for 12 weeks (50% mortality after 4 weeks)	B	1.0	Negri et al. (2009) and Flores et al. (2011)
Acropora nobilis (Dana, 1846)	10 mg/l (42 days)	Increased survival from high temperature treatment compared to control	L	1.5	Anthony et al. (2007)
Acropora spp.	170 mg/l (hours) of marine snow/SPM	Mucus production in response to flocculation			Fabricius and Wolanski (2000)
Agaricia agaricites (Linnaeus, 1758)	Severe light reduction (shading) for 5 weeks	Partial bleaching after 5 weeks, recovery within weeks	L	5.0	Rogers (1979)
Agaricia agaricites (Linnaeus, 1758)	50 mg/l (96 h)	No effect	L	5.0	Thompson (1980b)
Agaricia agaricites (Linnaeus, 1758)	150 mg/l (96 h)	Polyp retraction, mucus production but no mortality	L	5.0	Thompson (1980b)
Agaricia agaricites (Linnaeus, 1758)	476 mg/l (96 h)	Mortality after 65 h	L	5.0	Thompson (1980b)
Agaricia agaricites (Linnaeus, 1758)	<1% SI (several days)	33% Decrease in calcification rate (for >1 month), but survival	L	5.0	Bak (1978)
Agaricia agaricites (Linnaeus, 1758)	1000 mg/l (for 65 h)	Mortality of colonies	L	5.0	Thompson and Bright (1980)
Cladocora arbuscula (Lesueur, 1812)	49, 101, 165 and 199 mg/l (10–20 days)	No effect on growth rate or survival (10 d), minor bleaching (20 d)	B	4.0	Rice and Hunter (1992)
Colpophyllia natans (Houttuyn, 1772)	Severe light reduction (shading) for 5 weeks	Partial bleaching (5 weeks), limited recovery & some algal growth (15 weeks)	M	25.0	Rogers (1979)
Dichocoenia stokesi Milne Edwards & Haime, 1848	0–2 NTU and 7–9 NTU (weeks)	No effect on P:R ratio	M	11.0	Telesnicki and Goldberg (1995)
Dichocoenia stokesi Milne Edwards & Haime, 1848	14–16 NTU (weeks)	Mucus production, P:R ratio <1 after 6 days exposure	M	11.0	Telesnicki and Goldberg (1995)
Dichocoenia stokesi Milne Edwards & Haime, 1848	28–30 NTU (weeks)	Mucus production, P:R ratio <1 after 3 days exposure	M	11.0	Telesnicki and Goldberg (1995)
Dichocoenia stokesi Milne Edwards & Haime, 1848	50–150–476 mg/l (96 h)	No effect at 50 and 150 mg/l; extreme sublethal stress but survival at 476 mg/l	M	11.0	Thompson (1980b)
Dichocoenia stokesi Milne Edwards & Haime, 1848	1000 mg/l (for 65 h)	No mortality	M	11.0	Thompson and Bright (1980)
Diploria labyrinthiformis (Linnaeus, 1758)	Severe light reduction (shading) for 5 weeks	Substantial bleaching (5 weeks), no recovery & some algal growth (15 weeks)	M	8.0	Rogers (1979)
Eusmilia fastigiata (Pallas, 1766)	severe light reduction (shading) for 5 weeks	No visible effects	M	12.0	Rogers (1979)
Favia favus (Forskål, 1775)	Light reduced to 50% and 25% PAR (surface)	Severely diminished productivity, increased carbon loss and mucus	M	14.0	Riegl and Branch (1995)
Favites pentagona (Esper, 1794)	Light reduced to 50% and 25% PAR (surface)	Severely diminished productivity, increased carbon loss and mucus	M	7.0	Riegl and Branch (1995)
Fungiidae (mushroom corals)		Adapted to highly turbid environments			Dikou and Van Woesik, (2006)
Galaxea fascicularis (Linnaeus, 1767)	>40 NTU (c.40 d), at times up to 175 NTU	Shift from autotrophy to heterotrophy (reversible)	C	8.0	Larcombe et al. (2001)
Goniastrea retiformis (Lamarck, 1816)	Shading (equivalent to 16 mg/l) – 2 months	Increased particle feeding & heterotrophy; survival and tissue gains	M	4.0	Anthony and Fabricius (2000)

Table 5 (continued)

Coral species	Turbidity level (tested)	Response	Growth form	Calyx (mm)	References
Goniastrea retiformis (Lamarck, 1816)	1–30 mg/l SPM (weeks)	Gained tissue & skeletal mass (all treatments); increasing heterotrophy	M	4.0	Anthony and Fabricius (2000)
Goniastrea retiformis (Lamarck, 1816)	1–16 mg/l suspended matter (8 weeks)	Increased growth rate as function of SPM concentration	M	4.0	Anthony (1999b)
Goniastrea retiformis (Lamarck, 1816)	Shading (equiv. 16 mg/l at 4 m) (8 weeks)	Significant reduction in growth rate	M	4.0	Anthony (1999b)
Gorgonia flabellum Linnaeus, 1758	Severe light reduction (shading) for 5 weeks	No visible effects	So		Rogers (1979)
Gorgonians & soft corals		Very tolerant to high turbidity			Fabricius and Dommisse (2000)
Gyrosmilia interrupta (Ehrenberg, 1834)	Light reduced to 50% and 25% PAR (surface)	Severely diminished productivity, increased carbon loss and mucus	M/E	16.0	Riegl and Branch (1995)
Isophyllia sinuosa (Ellis & Solander, 1786)	49, 101, 165 and 199 mg/l (10–20 days)	No effect on growth rate or survival after 10 d, minor bleaching after 20 d	N	15.0	Rice and Hunter (1992)
Leptastrea sp.		Well adapted to turbid waters			Dikou and Van Woesik, (2006)
Lobophytum depressum Tixier-Durivault, 1966	Light reduced to 50% and 25% PAR (surface)	Severely diminished productivity, increased carbon loss and mucus	So		Riegl and Branch (1995)
Lobophytum venustum Tixier-Durivault, 1957	Light reduced to 50% and 25% PAR (surface)	Severely diminished productivity, increased carbon loss and mucus	So		Riegl and Branch (1995)
Madracis auretenra Locke, Weil & Coates, 2007	<1% SI (several days)	33% Decrease in calcification rate (for >1 month), but survival	B	1.0	Bak (1978)
Manicina areolata (Linnaeus, 1758)	49, 101, 165 and 199 mg/l (10–20 days)	No effect on growth rate or survival after 10 d, minor bleaching after 20 d	M	14.0	Rice and Hunter (1992)
Meandrina meandrites (Linnaeus, 1758)	0–2 NTU and 7–9 NTU (weeks)	No effect on P:R ratio	M/E	15.0	Telesnicki and Goldberg (1995)
Meandrina meandrites (Linnaeus, 1758)	14–16 NTU (weeks)	Mucus production, P:R ratio < 1 after 6 days exposure	M/E	15.0	Telesnicki and Goldberg (1995)
Meandrina meandrites (Linnaeus, 1758)	28–30 NTU (weeks)	Mucus production, P:R ratio < 1 after 3 days exposure	M/E	15.0	Telesnicki and Goldberg (1995)
Millepora alcicornis Linnaeus, 1758	Severe light reduction (shading) for 5 weeks	Partial bleaching (5 weeks), algal growth (6 weeks), no recovery of damaged tissue	B	0.5	Rogers (1979)
Montastraea annularis (Ellis & Solander, 1786)	Severe light reduction (shading) for 5 weeks	Substantial bleaching (5 weeks), partial recovery (6–8 weeks), some algae/mucus	M/E	5.0	Rogers (1979)
Montastraea annularis (Ellis & Solander, 1786)	50 mg/l (96 h)	No effect	M/E	5.0	Thompson (1980b)
Montastraea annularis (Ellis & Solander, 1786)	150 mg/l (96 h)	Polyp retraction, mucus production but no mortality	M/E	5.0	Thompson (1980b)
Montastraea annularis (Ellis & Solander, 1786)	476 mg/l (96 h)	Mortality after 65 h	M/E	5.0	Thompson (1980b)
Montastraea annularis (Ellis & Solander, 1786)	100 mg/l (6-weeks)	Major sublethal effects (photosynthesis, respiration, calcification & nutr.uptake)	M/E	5.0	Szmant-Froelich et al. (1981)
Montastraea annularis (Ellis & Solander, 1786)	1–10 mg/l (6 weeks)	Only (some) effect on feeding response	M/E	5.0	Szmant-Froelich et al. (1981)
Montastraea annularis (Ellis & Solander, 1786)	525 mg/l	Decreased net production & tissue Chl, increased respiration & mucus	M/E	5.0	Dallmeyer et al. (1982)
Montastraea annularis (Ellis & Solander, 1786)	1000 mg/l (for 65 h)	Mortality of colonies	M/E	5.0	Thompson and Bright (1980)
Montastraea cavernosa (Linnaeus, 1767)	Severe light reduction (shading) for 5 weeks	No visible effects	M	11.0	Rogers (1979)
Montipora aequituberculata Bernard, 1897		Common on shallow, turbid inshore fringing reefs	F	0.6	Stafford-Smith (1993)
Montipora aequituberculata Bernard, 1897	1, 3, 10, 30 and 100 mg/l TSS (16 weeks)	Full colony mortality at 30 mg/l after 12 weeks (50% mortality after 4 weeks)	F	0.6	Negri et al. (2009) and Flores et al. (2011)
Montipora capitata Dana 1846	Light reduction from 57 to 44% SI (field; hours)	Photophysiological sublethal response; 1.4 times lower rETR, higher F_v/F_m	B	1.0	Piniak and Storlazzi (2008)
Montipora digitata (Dana, 1846)	1–30 mg/l SPM (hours)	Increased feeding capacity at high SPM concentrations	B	1.0	Anthony (1999a)
Montipora digitata (Dana, 1846)	>95% shading (transplanted into caves)	Survival/acclimation, reduced photosynthetic rate	L	1.0	Anthony and Hoegh-Guldberg (2003)
Montipora digitata (Dana, 1846)	70% light reduction (permanent transplantation)	Complete photoacclimation within 3 weeks	L	1.0	Anthony and Hoegh-Guldberg (2003)
Montipora verrucosa (Lamarck, 1816)	8 and 20 mg/l (modelling)	Reduced photosynthesis at 8 mg/l; negative energy balance at 20 mg/l	M/L	1.0	Te (1998)
Montipora sp.		Well adapted to turbid waters			Dikou and Van Woesik, (2006)
Mussa angulosa (Pallas, 1766)	Severe light reduction (shading) for 5 weeks	No visible effects (1 colony showing minor bleaching after 8 weeks)	M	40.0	Rogers (1979)
Pectinia lactuca (Pallas, 1766) (larvae)	6, 43 and 169 mg/l (lab test)	Adverse effects on fertilisation success and embryo development			Erftemeijer et al. (2012)
Pectinia sp.		Well adapted to turbid waters			Dikou and Van Woesik, (2006)
Phyllangia americana Milne Edwards & Haime, 1849	49, 101, 165 and 199 mg/l (10–20 days)	No effect on growth rate or survival after 10 d, minor bleaching after 20 d	E	9.0	Rice and Hunter (1992)

Table 5 (continued)

Coral species	Turbidity level (tested)	Response	Growth form	Calyx (mm)	References
Platygyra daedalea (Ellis & Solander, 1786)	Light reduced to 50% and 25% PAR (surface)	Severely diminished productivity, increased carbon loss and mucus	M	5.0	Riegl and Branch (1995)
Pocillopora damicornis (Linnaeus, 1758)	1–30 mg/l SPM (hours)	Increased feeding capacity at high SPM concentrations	B	1.1	Anthony (1999a)
Pocillopora damicornis (Linnaeus, 1758)	1–30 mg/l SPM (days)	Increasing contribution of heterotrophy at high SPM conc.	B	1.1	Anthony (2000)
Pocillopora damicornis (Linnaeus, 1758) (larvae)	10, 100, 1000 mg/l (modelling)	Reverse metamorphosis (reduced settlement success) at 100 and 1000 mg/l	B	1.1	Te (1998)
Pocillopora damicornis (Linnaeus, 1758)		Characteristic of turbid waters	B	1.1	Dikou and Van Woesik, (2006)
Porites astreoides Lamarck, 1816	50–150–476 mg/l (96 h)	No effect at 50 and 150 mg/l; extreme sublethal stress (but survival) at 476 mg/l	M/E	1.5	Thompson (1980b)
Porites astreoides Lamarck, 1816	<1% SI (several days)	Bleaching and mortality	M/E	1.5	Bak (1978)
Porites astreoides Lamarck, 1816	1000 mg/l (for 65 h)	No mortality	M/E	1.5	Thompson and Bright (1980)
Porites cylindrica Dana, 1846	Shading (equivalent to 16 mg/l) – 2 months	Energy deficiency/C-loss not compensated by particle feeding; sublethal stress	M	1.5	Anthony and Fabricius (2000)
Porites cylindrica Dana, 1846	1–30 mg/l SPM (weeks)	Skeletal growth sustained, tissue biomass decreased at high SPM	M	1.5	Anthony and Fabricius (2000)
Porites cylindrica Dana, 1846	1–30 mg/l SPM (hours)	Increased feeding capacity at high SPM concentrations	M	1.5	Anthony (1999a)
Porites cylindrica Dana, 1846	1–16 mg/l suspended matter (8 weeks)	No effect on growth rates	M	1.5	Anthony (1999b)
Porites cylindrica Dana, 1846	Shading (equiv. 16 mg/l at 4 m) (8 weeks)	Significant reduction in growth rate	M	1.5	Anthony (1999b)
Porites divaricata Lesueur, 1821	50–150–476 mg/l (96 h)	No effect at 50 and 150 mg/l; extreme sublethal stress (but survival) at 476 mg/l	B	1.2	Thompson (1980b)
Porites divaricata Lesueur, 1821	1000 mg/l (for 65 h)	No mortality	B	1.2	Thompson and Bright (1980)
Porites furcata Lamarck, 1816	50–150–476 mg/l (96 h)	No effect at 50 and 150 mg/l; extreme sublethal stress (but survival) at 476 mg/l	B	2.0	Thompson (1980b)
Porites furcata Lamarck, 1816	1000 mg/l (for 65 h)	No mortality	B	2.0	Thompson and Bright (1980)
Porites lobata Dana, 1846		Dominant in turbid waters			Stafford-Smith (1993)
Porites lutea Milne Edwards & Haime, 1851		Dominant in turbid waters	M	1.5	Stafford-Smith (1993)
Porites lutea Milne Edwards & Haime, 1851	Increased turbidity up to 286 mg/l (4 months)	Partial mortality of 25% of colonies, recovery within 22 months	M	1.5	Brown et al. (1990)
Porites porites (Pallas, 1766)	Significant light reduction due to eutrophication	Reduced reproductive success (ova maturation, larval development)	M	2.0	Tomascik and Sander (1987)
Porites sp.	General increase in SPM	Decreasing tissue thickness from nearshore to offshore			Barnes and Lough (1992)
Porites sp.	General increase in SPM	Decreasing skeletal density, linear extension, increasing calcification			Lough and Barnes (1992, 2000)
Porites sp.		Well adapted to turbid waters			Dikou and Van Woesik, (2006)
Sarcophyton glaucum (Quoy & Gaimard, 1833)	Light reduced to 50% and 25% PAR (surface)	Severely diminished productivity, increased carbon loss and mucus	So		Riegl and Branch (1995)
Scolymia cubensis (Milne Edwards & Haime, 1849)	49, 101, 165 and 199 mg/l (10–20 days)	No effect on growth rate or survival after 10 d, minor bleaching after 20 d	S	91.0	Rice and Hunter (1992)
Scolymia cubensis (Milne Edwards & Haime, 1849)	49–199 mg/l (10 days)	Partial polyp death and partial bleaching (in some indivduals)	S	91.0	Rice (1984)
Siderastrea radians (Pallas, 1766)	49–199 mg/l (10 days)	Partial polyp death and partial bleaching (in some indivduals)	M/E'	5.0	Rice (1984)
Siderastrea siderea (Ellis & Solander, 1786)	Severe light reduction (shading) for 5 weeks	Partial bleaching after 5 weeks, partial recovery in 6–8 weeks	M	3.0	Rogers (1979)
Sinularia dura (Pratt, 1903)	Light reduced to 50% and 25% PAR (surface)	Severely diminished productivity, increased carbon loss and mucus	So		Riegl and Branch (1995)
Sinularia leptoclados (Ehrenberg, 1834)	Light reduced to 50% and 25% PAR (surface)	Severely diminished productivity, increased carbon loss and mucus	So		Riegl and Branch (1995)
Solenastrea hyades (Dana, 1846)	49, 101, 165 and 199 mg/l (10–20 days)	No effect on growth rate or survival after 10 d, minor bleaching after 20 d	M	5.0	Rice and Hunter (1992)
Solenastrea hyades (Dana, 1846)	49–199 mg/l (10 days)	Partial polyp death and partial bleaching (in some individuals)	M	5.0	Rice (1984)
Stephanocoenia intersepta (Lamarck, 1816)	49, 101, 165 and 199 mg/l (10–20 days)	No effect on growth rate or survival after 10 d, minor bleaching after 20 d	M	3.0	Rice and Hunter (1992)
Stephanocoenia intersepta (Lamarck, 1816)	49–199 mg/l (10 days)	Partial polyp death and partial bleaching (in some individuals)	M	3.0	Rice (1984)
Turbinaria mesenterina (Lamarck, 1816)		Tolerant to high turbidity	L	1.5	Quoted in Nieuwaal (2001)
Turbinaria reniformis Bernard, 1896		Tolerant to high turbidity	L	2.0	Quoted in Nieuwaal (2001)
Turbinaria spp.		Most tolerant to high turbidity and sedimentation			Stoddart and Stoddart (2005)

Table 6
Response matrix ranking the relative sensitivity of corals according to their type of response to different levels of turbidity (mg L^{-1}). Severe shading, total shading and <1%SI were categorised as >100 mg L^{-1}, NTU values were categorised as follows: 0–2 NTU:<10 mg L^{-1}, 7–9 NTU: 10–20 mg L^{-1}, 14–16 NTU: 20–40 mg L^{-1}, 28–30 NTU: 40–100 mg L^{-1}, >40 NTU: >100 mg L^{-1}.

Response category	Turbidity level (mg L^{-1}) tested				
	<10	10–20	20–40	40–100	>100
No effect	(most spp.)	Intermediate	Tolerant	Very tolerant	Very tolerant
Sublethal effects (minor) (reduced growth/calcification, mucus production etc.)	Sensitive	Sensitive	Intermediate	Tolerant	Very tolerant
Sublethal effects (major) (bleaching, tissue damage)	Very sensitive	Sensitive	Intermediate	Tolerant	Tolerant
Lethal effects (partial mortality)	Very sensitive	Very sensitive	Sensitive	Intermediate	Tolerant
Major lethal effects (mass mortality)	Very sensitive	Very sensitive	Sensitive	Intermediate	(most spp.)

could be classified as moderate to severe. Other studies, however, revealed how many coral species and reefs are capable of surviving sedimentation rates as high as 100 mg cm^{-2} d^{-1} for several days to weeks without any major negative effects, while some (nearshore) reefs naturally experience sedimentation rates well over 200 mg cm^{-2} d^{-1} (Table 7). Nearshore fringing reefs in the Great Barrier Reef region that are characterised by high and variable sedimentation rates, ranging from 2 to 900 mg cm^{-2} d^{-1} (short-term rates) with long-term means of 50–110 mg cm^{-2} d^{-1}, were found to harbour highly diverse coral growth with a mean coral cover of 40–60% (Ayling and Ayling, 1991). A few coral species, such as *Montastraea cavernosa* and *Astrangia poculata*, can tolerate sedimentation rates as high as 600–1380 mg cm^{-2} d^{-1} (Lasker, 1980; Peters and Pilson, 1985). This wide range demonstrates that different coral

Fig. 5. Relationship between the sensitivity of corals to turbidity and [A] their growth form, and [B] their calyx size. Sensitivity (mean score ± SD) was determined by ranking corals according to their type of response to different levels of turbidity (see text and Table 6). Legend (growth forms): B = branching; C = columnar (incl. digitate); E = encrusting; F = foliaceous; L = laminar (incl. plate & tabular); M = massive; S = solitary (free-living); So = soft corals & gorgonians.

species and corals in different geographic regions may respond differently to increased amounts and rates of sedimentation.

Frequent short-term exposure to high sedimentation events or chronic (long-term) exposure to relatively high sedimentation rates results in increased mortality rates in populations of many coral species (Tomascik and Sander, 1985). If moderate levels of increased turbidity and sedimentation on a reef persist for particularly long periods of time (years or decades), the coral reef may undergo changes in diversity, with the most sensitive coral species (gradually) disappearing as can be seen on reefs in the proximity of big cities such as Singapore and Jakarta (Chou, 1988, 1996; Hoeksema and Koh, 2009; van der Meij et al., 2010; Hoeksema et al., 2011). These losses may also affect other species that depend on coral reefs, such as molluscs (van der Meij et al., 2009), especially if these live in close associations with specific coral hosts (Stella et al., 2011; Hoeksema et al., 2012). Such changes in species composition may cause (sometimes catastrophic) shifts in the coral reef ecosystem, resulting in a loss of ecological functions and ecosystem stability (Scheffer et al., 2001).

Stafford-Smith and Ormond (1992) summarised the conventional wisdom regarding sediment particle size and rejection, i.e. that silts and small particles are generally transported off the colony by ciliary currents whereas larger particles are moved by tissue expansion. Fine grain sizes flow off a colony more easily than coarse grains (Lasker, 1980) but nutrient-rich silts in calm waters can still be very stressful (Fabricius, 2005). Stafford-Smith and Ormond (1992) also explained the energetic costs of different sediment inputs, noting that sporadic downward fluxes of sediment are less costly than a continual light rain of particles. This is because short bursts of sediment leave accumulations in only a few colony areas, such as concave or flat surfaces, whereas a continual rain of particles affects a much larger expanse of tissue.

Some of the variation in sensitivity of corals to sedimentation reported in the literature may have been caused by differences in the particle size of sediments applied in the respective experiments, which calls for a more standardised approach in future experiments. Mud- and silt-sized sediments frequently have a more adverse impact than sand because of different physical and chemical properties (Thompson, 1980a,b; Weber et al., 2006; Piniak, 2007). Mud- and silt-sized sediments are more cohesive and colloidally bind nutrients better than sand. Therefore, a more active bacterial community is likely to develop in silt sheets causing damage to the corals. Ciliary action accompanies more or less all sediment-clearing activity, but is sensitive to grain size. Some of the fungiid corals and *Solenastrea hyades* appear to depend on ciliary action alone to rid the colony of fine sediment (Meyer, 1989). Tentacular action is especially effective for removing larger sediment particles. Surprisingly few coral species can use their tentacles to remove sediment, with *Porites porites* and *P. astreoides* being two notable exceptions (Meyer, 1989). Corals using ciliary action or mucus are more sensitive to continuous siltation. Some of these species simply quit their cleaning action after a short period of repeated sedimentation. A continuous rain of sediment
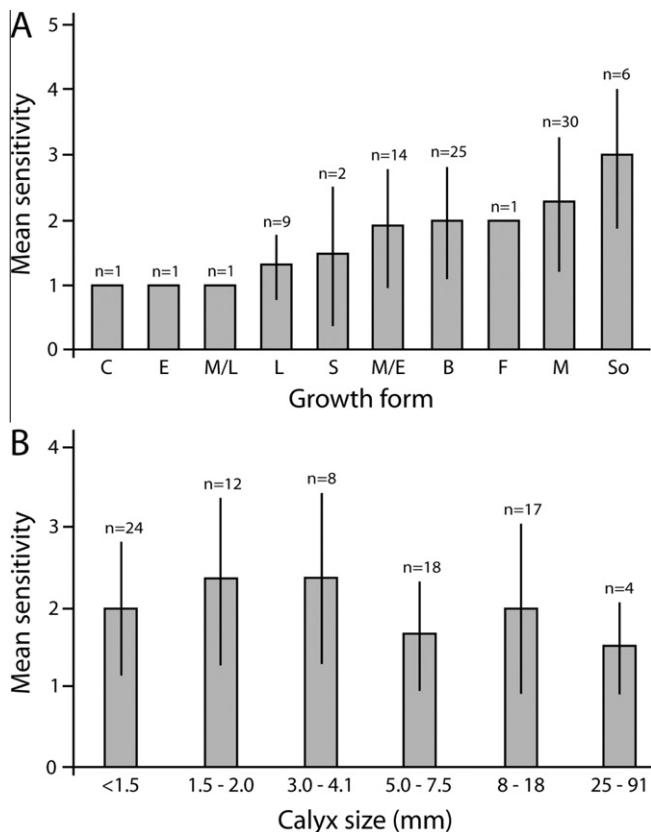
Table 7
Some published critical thresholds of coral reefs for sedimentation (mg cm^{-2} day^{-1}).

Species/type of corals	Location	mg cm^{-2} day^{-1}	References
Coral reefs	Worldwide (moderate to severe)	10	Pastorok and Bilyard (1985)
Coral reefs	Caribbean	10	Rogers (1990)
Coral reefs	Caribbean	37	Pastorok and Bilyard (1985)
Coral reefs	Worldwide (catastrophic)	50	Pastorok and Bilyard (1985)
Coral reefs	Puerto Rico	90	Miller and Cruise (1995)
Coral reefs	Indo-Pacific	228	Pastorok and Bilyard (1985)
Most coral species	Worldwide	300	Bak and Elgershuizen (1976)

Table 8
Some examples of the duration coral species can survive very high sedimentation rates (burial).

Species	Survival characteristics	Reference
Porites sp.	90% Bleaching after 68 h burial, recovery within 4 weeks	Wesseling et al. (1999)
Acropora sp.	100% Mortality after 20 h burial, no recovery	Wesseling et al. (1999)
Galaxea sp.	Sublethal stress after 20–68 h burial, recovery within 3–4 weeks	Wesseling et al. (1999)
Heliopora coerule	Sublethal stress after 20–68 h burial, recovery within 3–4 weeks	Wesseling et al. (1999)
Scolomia cubensis	LT50 after 7 days (complete burial)	Rice and Hunter (1992)
Isophyllia sinuosa	LT50 after 7.2 days (complete burial)	Rice and Hunter (1992)
Manicina areolata	LT50 after 10 days (complete burial)	Rice and Hunter (1992)
Siderastrea radians	LT50 after 13.6 days (complete burial)	Rice and Hunter (1992)
Cladocora arbuscula	LT50 after 15 days (complete burial)	Rice and Hunter (1992)
Solenastrea hyades	LT50 after 15 days (complete burial)	Rice and Hunter (1992)
Stephanocoenia intersepta	LT50 after 16.2 days (complete burial)	Rice and Hunter (1992)

temporarily exhausts both the mucus-secreting and ciliary drive for a period of one or two days. Recovery is possible only if siltation stops during the recovery period (Schuhmacher, 1977; Fortes, 2001).

Extreme sediment loads can lead to burial and eventual mortality (Rogers, 1983; Stafford-Smith, 1992). Wesseling et al. (1999) completely buried corals of the genera *Acropora, Porites, Galaxea* and *Heliopora* and found that, even after 68 h, all corals except *Acropora* eventually recovered. Rice and Hunter (1992) also determined that seven species near Florida were highly resistant to sediment burial. However, a heavy influx of sediment from a dredging operation resulted in complete or partial mortality in explanate colonies of *Porites astreoides* (Bak, 1978). Upland forest logging caused a nearly 100-fold increase in suspended sediment loads of Manlag River, resulting in prolonged sediment deposition at rates of 20 mg cm^{-2} d^{-1} in Bacuit Bay (Philippines), injuring and killing many of the ~50 coral species in the area, reducing species diversity, coral cover and average colony size (Hodgson, 1993; Birkeland, 1997; Hodgson and Dixon, 2000).

Heavy sedimentation is associated with fewer coral species, less live coral, lower coral growth rates, greater abundance of branching forms, reduced coral recruitment, decreased calcification, decreased net productivity of corals, and slower rates of reef accretion (Rogers, 1990). Tolerance of corals to high sediment loads varies considerably among species, with some corals being fairly resistant to low light levels and/or sedimentation effects (Rice and Hunter, 1992).

Field and laboratory experiments in Florida (USA) have shown that some of the most tolerant coral species in the Caribbean can survive complete burial with sediment for periods ranging from 7 to 15 days (Rice and Hunter, 1992) (Table 8). Burial with sediment of several Philippine corals caused sublethal effects (bleaching) and mortality within 20 to 68 h (Wesseling et al., 1999). Polyp inflation is an effective means of actively shedding sediment and corals with large inflation ratios are among the best sediment rejecters. Inflators are not only capable of (re)moving sediment continuously, but they also can endure siltation rates 5–10 times higher than regularly found on coral reefs. Many of these coral species are small forms, living attached or loose in sand bottoms, such as the Caribbean faviid *Manicina areolata* and the Pacific fungiid corals (Schuhmacher, 1977, 1979; Hoeksema, 1993; Johnson, 1992; Hubmann et al., 2002; Uhrin et al., 2005; Sorauf and Harries, 2010; Bongaerts et al., 2012).

A synthesis of literature data regarding sensitivity of different coral species to sedimentation is presented in Table 9. These data were reworked and related to a relative sensitivity index according to the response matrix presented in Table 10. Sensitivity classes

were then given scores from 1 to 5, with 1 corresponding to "very tolerant" and 5 to "very sensitive". The scores for individual coral species were subsequently related to their dominant growth form and mean calyx diameter. Analysis of these data (102 entries for 71 species) confirmed that there is a significant relationship (Kruskal–Wallis, $P < 0.05$) between the growth form of corals and their sensitivity to sedimentation (Fig. 6a). Free-living corals (such as mushroom corals), branching corals and many massive corals (especially with fleshy polyps) are quite tolerant to high rates of sedimentation, while laminar, plating and tabular corals as well as several soft corals are relatively sensitive. There was no significant relationship between the calyx diameter of corals and their sensitivity to sedimentation (Fig. 6b).

This relatively straightforward relationship (Figs. 5 and 6) can of course be complicated and altered by the interaction of several other factors such as active or passive sediment-clearing mechanisms, turbulence and exposure to wave action, colony orientation, morphological variability and adaptation within species, depth distribution, and the cumulative effects of extreme temperatures and salinities. However, despite some variability, complication by other factors and even some potential contradictions, it is clear from the overall findings that corals can indeed be roughly categorised according to their relative sensitivity to turbidity and sedimentation based on their growth form and morphology (Fig. 5 and 6).

6. Mitigating factors and potential for recovery

The sensitivity of corals to, and their ability to recover from, the impacts of dredging and related activities depends on a range of factors, including the ecological state or condition of the reef (e.g. degraded or pristine; dominated by algae, bio-eroders or reef-builders; level of fishing; and temperature anomalies), its resilience (species diversity; presence of keystone species; loss and replacement of keystone species; spatial heterogeneity; presence of refugia and connectivity to nearby unaffected reefs) and the

Table 9
Sensitivity of different coral species for sedimentation. Overview of the response of different species of corals to various sedimentation rates tested, as reported in the literature. Nomenclature of coral species was updated according to the most recent taxonomic revisions. Growth forms (as stated or inferred): B = branching; C = columnar (incl. digitate); E = encrusting; F = foliaceous; L = laminar (incl. plate & tabular); M = massive; S = solitary (free-living); So = soft corals & gorgonians. Calyx diameter taken from Stafford-Smith and Ormond (1992) supplemented with own measurements (BWH – Naturalis).

Coral species	Sedimentation rate (tested)	Response	Growth form	Calyx (mm)	References
Acropora cervicornis (Lamarck, 1816)	200 mg/m^2/d (daily for 45 days)	No effect (not even on growth rate) even after 45 days	B	1.0	Rogers (1979)
Acropora cervicornis (Lamarck, 1816)	200 mg cm^{-2} d^{-1} (daily)	No effect	B	1.0	Rogers (1990)
Acropora cervicornis (Lamarck, 1816)	430 mg cm^{-2} d^{-1} (>1 day)	Physiological stress	B	1.0	Bak and Elgershuizen (1976)
Acropora cervicornis (Lamarck, 1816)	Burial (10–12 cm of reef sand)	Sublethal stress within 12 h; 100% mortality within 72 h	B	1.0	Thompson (1980a)
Acropora formosa (Dana, 1846)	Up to 14.6 mg/m^2/d (fine silt) due to dredging	No effect on growth rate (in situ)	B	1.2	Chansang et al. (1992)
Acropora formosa (Dana, 1846)	200–300 mg cm^{-2} d^{-1} (up to 7 days)	Decreased growth	B	1.2	Simpson (1988)
Acropora millepora (Ehrenberg, 1834) (larvae)	0.5–325 mg cm^{-2} d^{-1} (2 days)	Reduction of larval settlement			Babcock (1991)
Acropora millepora (Ehrenberg, 1834)	83 mg cm^{-2} d^{-1} (up to 16 weeks)	Onset mortality after 4 weeks, full mortality after 12 weeks	B	1.0	Negri et al. (2009) and Flores et al. (2011)
Acropora palifera (Lamarck 1816)	Field site comparison (<1 versus 13.5 mg cm^{-2} d^{-1})	Reduced fecundity at site with higher sedimentation	L	2.0	Kojis and Quinn (1984)
Acropora palmata (Lamarck, 1816)	Up to 600 mg cm^{-2} d^{-1} (natural events)	Poor rejection ability; sediment accumulation	B	2.0	Abdel-Salam and Porter (1988)
Acropora palmata (Lamarck, 1816)	430 mg cm^{-2} d^{-1} (>1 day)	Physiological stress	B	2.0	Bak and Elgershuizen, 1976
Acropora palmata (Lamarck, 1816)	200 mg cm^{-2} d^{-1} (once)	Partial mortality	B	2.0	Rogers (1977)
Acropora palmata (Lamarck, 1816)	200 mg cm^{-2} d^{-1} (field application)	Death of underlying tissue	B	2.0	Rogers (1990)
Acropora palmata (Lamarck, 1816)	Burial (10–12 cm of reef sand)	100% mortality within 72 h	B	2.0	Thompson (1980a)
Acropora sp.	5 mg cm^{-2} d^{-1}	Massive mucus production (within 1 h), sublethal			Fabricius and Wolanski (2000)
Acropora sp.	Burial for 20 h	Mortality of all colonies			Wesseling et al. (1999)
Acropora spp.	39.6 mg cm^{-2} d^{-1} (for 2 weeks)	Partial bleaching (less affected)			Fabricius et al. (2007)
Agaricia agaricites (Linnaeus, 1758)	Heavy sedimentation event (>1 cm)	Reduced growth but survival	L	5.0	Bak (1978)
Agaricia agaricites (Linnaeus, 1758)	430 mg cm^{-2} d^{-1} (sand)	Mortality after 1 day	L	5.0	Bak and Elgershuizen (1976)
Agaricia agaricites (Linnaeus, 1758)	Burial (10–12 cm of reef sand)	60% Tissue loss within 24 h; 100% mortality after 72 h	L	5.0	Thompson (1980a)
Agaricia lamarcki Milne Edwards & Haime, 1851	140 mg/m^2/d (mean) for several weeks	Mass mortality (4 years after steep decline in growth)	L	8.0	van 't Hof (1983)
Agaricia sp.	30 mg/m^2/d (natural)	No effect; dominant species			Loya (1976)
Alveopora spp.		Can survive high sedimentation rates			Stafford-Smith and Ormond (1992)
Astrangia poculata (Ellis & Solander, 1786)	<600 mg cm^{-2} d^{-1}	Survival	S	6.0	Peters and Pilson (1985)
Catalaphyllia jardinei (Saville-Kent, 1893)		Survive high sedimentation rates	M	40.0	Stafford-Smith and Ormond (1992)
Cladocora arbuscula (Lesueur, 1812)	Complete burial	50% Survival after 15 days	B	4.0	Rice and Hunter (1992)
Ctenactis echinata (Pallas, 1766)	Continuously repeated burial (sand)	Tissue mortality and colony death after 24–72 h	S	200.0	Schuhmacher (1977)
Cycloseris costulata (Ortmann, 1889)	Continuously repeated burial (sand)	Survival (endurance with no apparent effect)	S	15.0	Schuhmacher (1977)
Cycloseris costulata (Ortmann, 1889)	40 mm3/cm^2/d	Maximum rate tolerated (field gradient)	S	15.0	Schuhmacher (1977)
Cycloseris distorta (Michelin, 1842)		Efficient sediment rejector (polyp inflation)	S	7.5	Schuhmacher (1977)
Cycloseris spp.		Can actively dig through overlying sediment			Stafford-Smith and Ormond (1992)
Danafungia horrida (Dana, 1846)	Continuously repeated burial (sand)	Tissue mortality and colony death after 24–72 h	S	215.0	Schuhmacher (1977)
Danafungia scruposa (Klunzinger, 1879)	Continuously repeated burial (sand)	Tissue mortality and colony death after 24–72 h	S	380.0	Schuhmacher (1977)
Dichocoenia stokesi Milne Edwards & Haime, 1848	430 mg cm^{-2} d^{-1} (sand + oil)	Mortality after 1 day	M	11.0	Bak and Elgershuizen (1976)
Diploastrea heliopora (Lamarck, 1816)	20 mg cm^{-2} d^{-1} (mixed sand)	Survival (4 months)	M	14.0	Todd et al. (2004a)
Diploria clivosa (Ellis & Solander, 1786)	Repeated application of 200 mg/cm^2	Extensive damage	M	9.0	Rogers (1983)
Diploria labyrinthiformis (Linnaeus, 1758)	High sedimentation rates (dredging)	Survival (no effect)	M	8.0	Dodge and Vaisnys (1977)
Diploria strigosa (Dana, 1846)	Up to 600 mg cm^{-2} d^{-1} (natural events)	High sediment clearing rate	M	8.0	Abdel-Salam and Porter (1988)
Diploria strigosa (Dana, 1846)	200 mg cm^{-2} d^{-1} (daily)	No effect	M	8.0	Rogers (1990)
Diploria strigosa (Dana, 1846)	High sedimentation rates (dredging)	Mass mortality (4 years after steep decline in growth)	M	8.0	Dodge and Vaisnys (1977)

Table 9 (*continued*)

Coral species	Sedimentation rate (tested)	Response	Growth form	Calyx (mm)	References
Diploria strigosa (Dana, 1846)	Burial (10–12 cm of reef sand)	Partial bleaching and sublethal stress within 24 h	M	8.0	Thompson (1980a)
Duncanopsammia axifuga (Milne Edwards & Haime, 1848)		Can survive high sedimentation rates	B	14.0	Stafford-Smith and Ormond (1992)
Echinopora spp.		Active sediment rejector			Stafford-Smith and Ormond (1992)
Echinopora mammiformis (Nemenzo, 1959)		Active sediment rejector	L	5.0	Stafford-Smith and Ormond (1992)
Euphyllia spp.		Can survive high sedimentation rates			Stafford-Smith and Ormond (1992)
Favia favus (Forskal, 1775)	200 mg cm^{-2} d^{-1} (6 weeks)	Minor tissue damage, mucus production, no bleaching	M	14.0	Riegl (1995) and Riegl and Bloomer (1995)
Favia speciosa (Dana, 1846)	20 mg cm^{-2} d^{-1} (mixed sand)	Survival (4 months)	M	12.0	Todd et al. (2004a)
Favia spp.	(0.9–1.3 mg/m^2/day)	Described as relatively 'sensitive' to sedimentation			McClanahan and Obura (1997)
Favia stelligera (Dana, 1846)	200 mg cm^{-2} d^{-1}	Mortality within 1–2 days	M	6.0	Stafford-Smith (1993)
Favites pentagona (Esper, 1794)	200 mg cm^{-2} d^{-1} (6 weeks)	Tissue damage, mucus production	M	7.0	Riegl (1995) and Riegl and Bloomer (1995)
Favites spp.	(between 1.3 and 4 mg cm^{-2} d^{-1}; not quoted)	tolerance to sedimentation described as 'intermediate'			McClanahan and Obura (1997)
Fungia fungites (Linnaeus, 1758)	Continuously repeated burial (sand)	Tissue mortality and colony death after 24–72 h	S	310.0	Schuhmacher (1977)
Fungia fungites (Linnaeus, 1758)	10 mm^3/cm^2/d	Maximum rate tolerated	S	310.0	Schuhmacher (1977)
Galaxea fascicularis (Linnaeus, 1767)	39.6 mg cm^{-2} d^{-1} (for 2 weeks)	Sublethal (sed.accum.), act.removal (polyp), recovery	M	8.0	Fabricius et al. (2007)
Galaxea fascicularis (Linnaeus, 1767)	Burial for 20 h	Tissue bleaching, recovery after 4 weeks	M	8.0	Wesseling et al. (1999)
Galaxea spp.	(4 mg/m^2/day)	Tolerance to sedimentation described as 'intermediate'			McClanahan and Obura (1997)
Gardineroseris planulata (Dana, 1846)	200 mg cm^{-2} d^{-1}	Partial mortality after 6 days	M	7.0	Stafford-Smith (1993)
Goniastrea retiformis (Lamarck, 1816)		Common on reefs affected by sedimentation	M	4.0	Brown and Howard (1985)
Goniopora lobata Milne Edwards & Haime, 1860		Active sediment rejector	c	4.0	Stafford-Smith and Ormond (1992)
Goniopora spp.		Survive high sedimentation rates			Stafford-Smith and Ormond (1992)
Gyrosmilia interrupta (Ehrenberg, 1834)	200 mg cm^{-2} d^{-1} (6 weeks)	Tissue damage, mucus production, no bleaching	M/E	16.0	Riegl (1995) and Riegl and Bloomer (1995)
Heliofungia actiniformis (Quoy & Gaimard, 1833)		Efficient sediment rejector (polyp inflation)	S	210.0	Schuhmacher (1977)
Heliopora coerulea (Pallas, 1766)	Burial for 20 h	Tissue bleaching, recovery after 4 weeks	B	0.8	Wesseling et al. (1999)
Heteropsammia cochlea (Spengler, 1783)		Obligate commensal sipunculid prevents burial	S	7.0	Stafford-Smith and Ormond (1992)
Hydnophora spp.	(4 mg/m^2/day)	Tolerance to sedimentation described as 'intermediate'			McClanahan and Obura (1997)
Isopora palifera (Lamarck, 1816)	10–15 mg cm^{-2} d^{-1}	50% Reduction in fecundity	C	2.0	Kojis and Quinn (1984)
Isophyllia sinuosa (Ellis & Solander, 1786)	Complete burial	50% Survival after 7.2 days	M	15.0	Rice and Hunter (1992)
Leptoria phrygia (Ellis & Solander, 1786)	25 mg cm^{-2} d^{-1}	Minor tissue damage within 3 weeks	M	4.1	Stafford-Smith (1992)
Leptoria phrygia (Ellis & Solander, 1786)	50–100 mg cm^{-2} d^{-1}	Major tissue damage and bleaching after 4 days	M	4.1	Stafford-Smith (1992)
Leptoria phrygia (Ellis & Solander, 1786)	100–200 mg cm^{-2} d^{-1}	Partial mortality and bleaching after 4 days	M	4.1	Stafford-Smith (1992)
Leptoria phrygia (Ellis & Solander, 1786)	>200 mg cm^{-2} d^{-1}	Mortality within 1–2 days	M	4.1	Stafford-Smith (1992, 1993)
Lobophytum depressum Tixier-Durivault, 1966	200 mg cm^{-2} d^{-1} (6 weeks)	Tissue damage, bleaching and partial mortality	So		Riegl (1995) and Riegl and Bloomer (1995)
Lobophytum venustum Tixier-Durivault, 1957	200 mg cm^{-2} d^{-1} (6 weeks)	Minor tissue damage and bleaching	So		Riegl (1995) and Riegl and Bloomer (1995)
Madracis auretenra Locke, Weil & Coates, 2007	Heavy sedimentation event (>1 cm)	Reduced growth but survival	B	1.0	Bak (1978)
Manicina areolata (Linnaeus, 1758)	Complete burial	50% Survival after 10 days	M	23.0	Rice and Hunter (1992)
Meandrina meandrites (Linnaeus, 1758)		Produces copious amounts of mucus to remove silt	M	15.0	Dumas and Thomassin (1977)
Millepora spp.	(4 mg/m^2/day)	Tolerance to sedimentation described as 'intermediate'			McClanahan and Obura (1997)
Montastraea annularis (Ellis & Solander, 1786)		High sediment clearing rate	M/E	5.0	Abdel-Salam and Porter (1988)
Montastraea annularis (Ellis & Solander, 1786)	200 mg cm^{-2} d^{-1} (daily applications)	Tolerant for at least 38 days	L/E	5.0	Rogers (1979)
Montastraea annularis (Ellis & Solander, 1786)	400–800 mg cm^{-2} d^{-1} (single application)	Mortality	M	5.0	Rogers (1979)

Table 9 (*continued*)

Coral species	Sedimentation rate (tested)	Response	Growth form	Calyx (mm)	References
Montastraea annularis (Ellis & Solander, 1786)	19 mg cm^{-2} d^{-1} (permanent)	Reduced growth rate	M/E	5.0	Torres (1998)
Montastraea annularis (Ellis & Solander, 1786)	200 mg cm^{-2} d^{-1} (daily)	No effect	M/E	5.0	Rogers (1990)
Montastraea annularis (Ellis & Solander, 1786)	400 mg cm^{-2} d^{-1}	Temporary bleaching	M/E	5.0	Rogers (1990)
Montastraea annularis (Ellis & Solander, 1786)	800 mg cm^{-2} d^{-1}	Death of underlying tissue	M/E	5.0	Rogers (1990)
Montastraea annularis (Ellis & Solander, 1786)	800 mg cm^{-2} d^{-1} (single application)	Mortality	M/E	5.0	Rogers (1977)
Montastraea annularis (Ellis & Solander, 1786)	430 mg cm^{-2} d^{-1} (sand + oil)	Mortality after 1 day	L/M	5.0	Bak and Elgershuizen (1976)
Montastraea annularis (Ellis & Solander, 1786)	10 mg cm^{-2} d^{-1} (natural)	Reduced %cover	M	5.0	Torres and Morelock (2002)
Montastraea annularis (Ellis & Solander, 1786)	19 mg cm^{-2} d^{-1} (resuspended carbonate mud)	Reduced growth rate	M	5.0	Dodge et al. (1974)
Montastraea annularis (Ellis & Solander, 1786)	Burial (10–12 cm of reef sand)	40% Tissue loss within 24 h; 90% tissue loss within 72 h	M	5.0	Thompson (1980a)
Montastraea annularis (Ellis & Solander, 1786)		Produces little mucus; removes silt by by ciliary action	M	5.0	Dumas and Thomassin (1977)
Montastraea cavernosa (Linnaeus, 1767)	<1390 mg cm^{-2} d^{-1}	Survival	M	11.0	Lasker (1980)
Montastraea cavernosa (Linnaeus, 1767)	150 mg/m^2/d (natural)	Survival/dominance	M	11.0	Loya (1976)
Montastraea cavernosa (Linnaeus, 1767)	Burial (10–12 cm of reef sand)	30% Tissue loss after 72 h; remaining tissue in decay	M	11.0	Thompson (1980a)
Montipora aequituberculata Bernard, 1897	200 mg cm^{-2} d^{-1}	Bleaching after 6 days (but no mortality)	L	0.6	Stafford-Smith (1993)
Montipora aequituberculata Bernard, 1897	25 mg cm^{-2} d^{-1} (up to 16 weeks)	Onset mortality after 4 weeks, full mortality after 12 weeks	F	0.6	Negri et al. (2009) and Flores et al. (2011)
Montipora capitata Dana, 1846	Burial (2.2–2.8 g/cm^2 for 45 h)	sublethal effects after 30 h, little recovery after 90 h	B	2.0	Piniak (2007)
Montipora foliosa (Pallas, 1766)		Active sediment rejector	L	0.7	Stafford-Smith and Ormond (1992)
Montipora peltiformis Bernard, 1897	33–160 mg/cm^2 (silt) exposure for 36 h	Reduced photosynthesis within 12–60 h	F	1.0	Weber et al. (2006)
Montipora peltiformis Bernard, 1897	79–234 mg/cm2 (up to 36 h)	Signifcant decline in photosynthesis (quantum yield)	M/L	1.0	Philipp and Fabricius (2003)
Montipora spp.	(0.9–1.3 mg/m^2/day)	Described as 'sensitive' to sedimentation			McClanahan and Obura (1997)
Montipora verrucosa (Lamarck, 1816)	30 mg cm^{-2} d^{-1} (daily applications)	Survived (10 days of application)	M	1.5	Hodgson (1990a)
Mycetophyllia aliciae Wells, 1973	430 mg cm^{-2} d^{-1} (sand + oil)	Mortality after 1 day	L	14.0	Bak and Elgershuizen (1976)
Oxypora glabra Nemenzo, 1959	30 mg cm^{-2} d^{-1} (daily applications)	Total mortality within 10 days	L/E	5.0	Hodgson (1990a)
Pectinia lactuca (Pallas, 1766)		Active sediment rejector	L	18.0	Stafford-Smith and Ormond (1992)
Pectinia paeonia (Dana, 1846)		Active sediment rejector	L	15.0	Stafford-Smith and Ormond (1992)
Pectinia sp.		Active sediment rejector			Stafford-Smith and Ormond (1992)
Platygyra daedalea (Ellis & Solander, 1786)	200 mg cm^{-2} d^{-1} (6 weeks)	Minor tissue damage, mucus production, no bleaching	M	5.0	Riegl (1995) and Riegl and Bloomer (1995)
Platygyra sinensis (Milne Edwards & Haime, 1849)	Complete burial	Bleaching and tissue damage after 48 h	M	4.0	Wong (2001)
Platygyra spp.	(4 mg/m^2/day)	Tolerance to sedimentation described as 'intermediate'			McClanahan and Obura (1997)
Pleuractis granulosa (Klunzinger, 1879)	Continuously repeated burial (sand)	Survival (high endurance with no apparent effect)	S	185.0	Schuhmacher (1977)
Pleuractis granulosa (Klunzinger, 1879)	15 mm^3/cm^2/d	Maximum rate tolerated	S	185.0	Schuhmacher (1977)
Pleuractis moluccensis (Van der Horst, 1919)		Adapted to withstand considerable sedimentation rates	S	19.0	Schuhmacher (1977)
Pocillopora damicornis (Linnaeus, 1758)	50–95% sediment cover	Complete inhibition of larval settlement	B	1.0	Hodgson (1990b)
Pocillopora damicornis (Linnaeus, 1758)	67 and 186 mg cm^{-2} d^{-1} (fine silt; 83 days)	50–100% Mortality of transplanted fragments (esp. small)	B	1.0	Sakai et al. (1989)
Pocillopora damicornis (Linnaeus, 1758)	11–490 mg cm^{-2} d^{-1}ay (11 months)	Reduced growth rate of transplanted fragments	B	1.0	Piniak and Brown (2008)
Pocillopora meandrina Dana, 1846	30 mg cm^{-2} d^{-1} (daily applications)	Mortality within 10 days	B	1.0	Hodgson (1990a)
Pocillopora sp.	Increased sedimentation (dredging)	Considerable mortality			Hudson et al. (1982)

Table 9 (*continued*)

Coral species	Sedimentation rate (tested)	Response	Growth form	Calyx (mm)	References
Pocillopora spp.	(0.9–1.3 mg/m^2/day)	Described as 'sensitive' to sedimentation			McClanahan and Obura (1997)
Porites astreoides Lamarck, 1816	Heavy sedimentation event (>1 cm)	Mortality (inability to reject sediment)	L	1.5	Bak (1978)
Porites astreoides Lamarck, 1816		Abundant in heavily sedimented areas	M	1.5	Cortes and Risk (1985)
Porites astreoides Lamarck, 1816	430 mg cm^{-2} d^{-1} (sand)	Mortality after 1 day	M/E	1.5	Bak and Elgershuizen (1976)
Porites astreoides Lamarck, 1816	10 mg cm^{-2} d^{-1} (natural)	No effect	M/E	1.5	Torres and Morelock (2002)
Porites astreoides Lamarck, 1816	Burial (10–12 cm of reef sand)	Bleaching within 24 h; 70% tissue loss after 72 h	M/E	1.5	Thompson (1980a)
Porites lobata Dana, 1846	30 mg cm^{-2} d^{-1} (daily applications)	Mortality within 10 days	M	1.5	Hodgson (1990a)
Porites lobata Dana, 1846	Burial (1.5–1.6 g/cm^2 for 45 h)	Sublethal effects after 30 h, little recovery after 90 h	M	1.5	Piniak (2007)
Porites lobata Dana, 1846	200 mg cm^{-2} d^{-1}	Bleaching after 6 days (but no mortality)	M	1.5	Stafford-Smith (1993)
Porites lobata Dana, 1846	Complete burial (48 h)	Bleaching; complete recovery after sediment removal	M	1.5	Yeung (2000)
Porites lutea Milne Edwards & Haime, 1851	200 mg cm^{-2} d^{-1}	Bleaching after 6 days (but no mortality)	M	1.5	Stafford-Smith (1993)
Porites lutea Milne Edwards & Haime, 1851		Common on reefs affected by sedimentation	M	1.5	Brown and Howard (1985)
Porites lutea Milne Edwards & Haime, 1851	Increased sedimentation (dredging)	Survival	M	1.5	Hudson et al. (1982)
Porites lutea Milne Edwards & Haime, 1851	Up to 14.6 mg/m^2/d (fine silt) due to dredging	No effect on growth rate (in situ)	M	1.5	Chansang et al. (1992)
Porites porites (Pallas, 1766)		Uses tentacles to remove larger sediment particles	M	2.0	Meyer (1989)
Porites porites (Pallas, 1766) *forma* furcata	Burial (10–12 cm of reef sand)	90% bleaching within 24 h; 70% tissue loss after 72 h	B	2.0	Thompson (1980a)
Porites rus (Forskal, 1775)	39.6 mg cm^{-2} d^{-1} (for 2 weeks)	Massive mortality (anoxia)	M	0.5	Fabricius et al. (2007)
Porites sp.		Persists in areas of heavy sedimentation			Fabricius (2005)
Porites sp.	Burial for 6 h	No effect			Wesseling et al. (1999)
Porites sp.	Burial for 20 h	Discoloration & bleaching after 3 weeks			Wesseling et al. (1999)
Porites sp.	39.6 mg cm^{-2} d^{-1} (for 2 weeks)	Mucus production, survival (most tolerant)			Fabricius et al. (2007)
Porites spp.	(between 1.3 and 4 mg cm^{-2} d^{-1}; not quoted)	Tolerance to sedimentation described as 'intermediate'			McClanahan and Obura (1997)
Sarcophyton glaucum (Quoy & Gaimard, 1833)	200 mg cm^{-2} d^{-1}	Tissue damage and partial mortality within 6 weeks	So		Riegl (1995)
Scolymia cubensis (Milne Edwards & Haime, 1849)	Complete burial	50% Survival after 7 days	S	75.0	Rice and Hunter (1992)
Scolymia cubensis (Milne Edwards & Haime, 1849)	3 g of 3 grain-sizes: 62 μm, 250 μm, 2 mm (24 h)	Sediment-shedding efficiency related to calical angle	S	75.0	Logan (1988)
Siderastrea radians (Pallas, 1766)	Complete burial	50% Survival after 13.6 days	M/E	5.0	Rice and Hunter (1992)
Siderastrea radians (Pallas, 1766)	Total burial	Survival for more than 73 h	M/E	5.0	Mayer (1918)
Siderastrea radians (Pallas, 1766)	Burial (chronic)	Reduced growth and some mortality	M/E	5.0	Lirman et al. (2003)
Siderastrea siderea (Ellis & Solander, 1786)	10 mg cm^{-2} d^{-1} (natural)	No effect	M	3.0	Torres and Morelock (2002)
Siderastrea siderea (Ellis & Solander, 1786)	0.3–64 mg cm^{-2} d^{-1}	Partial mortality	M	3.0	Nugues and Roberts (2003)
Siderastrea siderea (Ellis & Solander, 1786)	Burial (10–12 cm of reef sand)	50% Bleaching and sublethal stress within 24 h	M	3.0	Thompson (1980a)
Sinularia dura (Pratt, 1903)	200 mg cm^{-2} d^{-1} (6 weeks)	Minor tissue damage and bleaching	So		Riegl (1995) and Riegl and Bloomer (1995)
Sinularia leptoclados (Ehrenberg, 1834)	200 mg cm^{-2} d^{-1} (6 weeks)	Minor tissue damage and bleaching	So		Riegl (1995), Riegl and Bloomer (1995)
Solenastrea hyades (Dana, 1846)	Complete burial	50% Survival after >15 days	M	5.0	Rice and Hunter (1992)
Stephanocoenia iniersepta (Lamarck, 1816)	Complete burial	50% Survival after 16.2 days	M	3.0	Rice and Hunter (1992)
Trachyphyllia geoffroyi (Audouin, 1826)		Actively dig through overlying sediment	S	45.0	Stafford-Smith and Ormond (1992)
Turbinaria mesenterina	110 mg/cm^2 (5 weeks)	No significant sublethal physiological effects	L	1.5	Sofonia and Anthony (2008)
Turbinaria (several spp.)		Active sediment rejector			Stafford-Smith and Ormond (1992)

typical ambient conditions experienced by the reef (McClanahan et al., 2002; Marshall and Schuttenberg, 2006). Reefs with effective management that minimises anthropogenic stresses are likely to have higher resilience than reefs that are already experiencing multiple stressors (West and Salm, 2003). Cumulative effects from or on related (adjacent) ecosystems such as mangroves and sea-grass meadows (including effects from maintenance dredging cycles) may also have indirect consequences for the coral reef

Table 10
Response matrix ranking the relative sensitivity of corals according to their type of response to different rates of sedimentation.

| Response category	Sedimentation rate (mg cm^{-2} d^{-1}) tested:				
	<10	10–50	50–200	>200	Complete burial
No effect	(most spp.)	Intermediate	Tolerant	Very tolerant	Very tolerant
Sublethal effects (minor)	Sensitive	Intermediate	Tolerant	Very tolerant	Very tolerant
Sublethal effects (major) (bleaching, tissue damage)	Sensitive	Sensitive	Intermediate	Tolerant	Tolerant
Lethal effects (partial mortality)	Very sensitive	Sensitive	Intermediate	Tolerant	Tolerant
Major lethal effects (mass mortality)	Very sensitive	Very sensitive	Sensitive	(most spp.)	(most spp.)
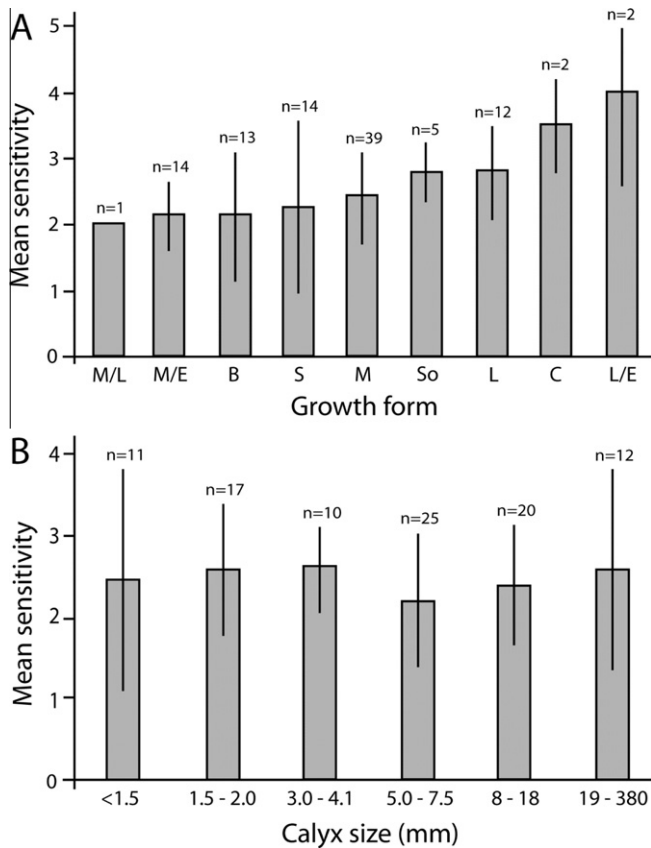
Fig. 6. Relationship between the sensitivity of corals to sedimentation and [A] their growth form, and [B] their calyx size. Sensitivity (mean score ± SD) was determined by ranking corals according to their type of response to different rates of sedimentation (see text and Table 10). Legend (growth forms): B = branching; C = columnar (incl. digitate); E = encrusting; L = laminar (incl. plate & tabular); M = massive; S = solitary (free-living); So = soft corals & gorgonians.

ecosystem. This is particularly so for ecological processes, functions and reef species that have important inter-linkages with mangrove and seagrass systems (Hemminga et al., 1994; Adams et al., 2006; Pollux et al., 2007). The timing of the dredging and construction activities may also affect the severity of impact, depending on the degree of seasonality and day–night cycles characterising the particular reef. Impacts during, or shortly prior to and after spawning events are of particular concern, since not only adult organisms may be negatively affected, but recruitment for the entire season may be jeopardised.

While sedimentation certainly is a major stressor that can lead to significant coral mortality, strong, isolated sediment pulses need not necessarily kill a reef. Many reefs, and certainly corals in most settings, can indeed survive repeated, even severe, sediment input (Browne et al., 2010). One of the most important factors mitigating against permanent damage is strong water motion, either by surge or by currents, that serves to re-suspend and remove the sediment

from the corals (Stafford-Smith and Ormond, 1992; Riegl, 1995; Riegl et al., 1996; Schleyer and Celliers, 2003). As long as the coral's surface is free from sediment, regeneration is relatively easily achieved, even if damage occurred. A continuous cover of sediment on corals may lead to beginning tissue necrosis within 24 h in sensitive coral species, while in tolerant species there may still be no signs of necrosis after 14 days (Table 8). This process is particularly readily observed in soft corals. Once the sediment has been removed, however, even if tissue necroses have occurred, regeneration can take place in the space of only a few weeks (Meesters et al., 1992). Strong currents can aide passive sediment-clearing. Purely oscillating currents or surge, while temporarily cleaning colonies, may not help overall since sediments will build up around the corals and eventually smother them.

Provided that environmental conditions return to the pre-impact situation and that these conditions are not hampering recovery, time-scales for natural recovery of coral reefs are in the order of a few years to several decades, depending on the degree of damage, types of species affected, and possibilities for recruitment (Pearson, 1981; Moberg and Rönnbäck, 2003). Recovery of corals from sublethal stress can be rapid (weeks to months), while recovery from partial mortality takes several years. Reef recovery from mass mortality is generally slow and may take many years to decades, while in some cases recovery has not occurred at all. Few examples of recovery of coral reefs after severe sediment damage have been documented. Increased sedimentation is sometimes accompanied by other stresses, prolonging or inhibiting recovery, making it difficult to generalise or make predictions about recovery (Rogers, 1990). Of 65 examples for which sufficient data exist to make a judgment, coral cover recovered in 69% of cases after acute, short-term disturbances, but only in 27% of cases after chronic, long-term disturbance (Connell, 1997).

Wesseling et al. (1999) noted that the recovery time of corals following experimental short-term burial varied among coral species, ranging from several weeks to months, and also depended on the duration of the sedimentation event. In larger massive corals, sediment burial may cause bleaching and damaged patches, which—if larger than about 2 cm in diameter—do not recover, but will be colonised by algae or sponges preventing recovery of the coral (Hodgson, 1994). Brown et al. (1990) reported a 30% reduction in living coral cover 1 year after the start of dredging operations at Phuket (Thailand). After the dredging event had ceased, the reef recovered rapidly with coral cover values and diversity indices restored to former levels around 22 months after dredging began. The domination of this reef by massive coral species, which are physiologically adapted to intertidal living and which display partial rather than total colony mortality, may have contributed to its apparent resilience (Brown et al., 2002). Maragos (1972) estimated that 80% of the coral communities in the lagoon of Kaneohe Bay (Hawaii) died because of a combination of dredging, increased sedimentation and sewage discharge. Six years after discharge of sewage into Kaneohe Bay ceased, a dramatic recovery of corals and a decrease in the growth of smothering algae was reported (Maragos et al., 1985).

Coastal coral reefs adjacent to population centers often do not recover from disturbances, in contrast to remote reefs in relatively pristine environments, because chronic human influences have degraded water and substratum quality, thereby inhibiting recovery (McCook, 1999a; Wolanski et al., 2004). In the Seychelles, where corals had to recover from an intense bleaching event, *Acropora* species—usually the first to rapidly colonise new empty spaces—recovered substantially more slowly due to recruitment limitation, because these species were virtually eliminated throughout almost the entire Indian Ocean (Goreau, 1998). As a result, these species will not be able to re-establish themselves for many years or even decades. Poor water quality and excessive algal growth in some areas hampered recovery even when coral larvae were available (Goreau, 1998).

7. Management of dredging operations near coral reefs

For an overview of best practices for the management of dredging operations near coral reefs, reference is made to the recent PIANC report No. 108 (PIANC, 2010). Setting realistic and ecologically meaningful thresholds for model interrogation, as permit conditions to dredging contractors and for use as triggers in a reactive monitoring and management program, can be a challenge in coral reef environments. One of the problems encountered when trying to determine realistic thresholds for dredging near coral reefs includes a lack of knowledge, since only 10% of coral species has ever been studied with respect to their response to sediment disturbance. There is still a rather poor understanding of the relationship between sediment stress and the response of most corals. While meaningful sets of thresholds or criteria would ideally have to incorporate the intensity, duration and frequency of turbidity (or sedimentation) events generated by the dredging activities, actual values are difficult to determine with confidence and at present remain little more than estimates.

In some cases, uncertainties in model predictions of dredging plumes and a conservative approach by regulators applying the precautionary principle may have led to overestimation of impacts of dredging operations on corals while field monitoring suggested less coral mortality than predicted (Hanley, 2011). In other cases, the opposite situation may have led to unnecessary and avoidable damage on coral reefs. To prevent coral mortality, there is clearly a need for reliable sublethal coral health indicators as early warning for stress but the science for this is still in its infancy (Jameson et al., 1998; Vargas-Angel et al., 2006; Cooper and Fabricius, 2007; Cooper et al., 2009). Such bio-indicators, some of which can show remarkable temporal dynamics in response to variations in water quality (Cooper et al., 2008), require on-site validation before use in monitoring programs (Fichez et al., 2005).

Recently, some significant advances have been made in establishing reactive (feedback) monitoring programs that have proven a meaningful tool for minimising coral mortality during large-scale dredging operations in Singapore and Australia (Koskela et al., 2002; Doorn-Groen, 2007; Sofonia and Unsworth, 2010). The design of such monitoring programs should guarantee sufficient statistical power to detect a required effect size, which can be as much a challenge as the availability of suitable reference sites. Seasonal restrictions during mass coral spawning are sometimes placed on dredging programs, but the effectiveness of such mitigating measures on long-term coral reef resilience is not well understood. Given the wide variation in sensitivity among coral species, meaningful criteria to limit the extent and turbidity of dredging plumes and their effects on corals will always require site-specific evaluations. We emphasise the importance of taking into account the species assemblage present at any given site and understanding the dynamics of local ambient background conditions, including spatial and temporal variability of turbidity and sedimentation, before setting thresholds in any dredging operation near coral reefs. A combination of reactive (feedback) monitoring of water quality and coral health during dredging activities and spill-budget modelling of dredging plumes to guide decisions on when to modify (or even stop) dredging appears to be the most promising approach to effectively minimise negative impacts on corals and coral reefs.

Acknowledgments

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