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Coral reefs of the turbid inner-shelf of the Great Barrier Reef, Australia: An environmental and geomorphic perspective on their occurrence, composition and growth

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ABSTRACT

Investigations of the geomorphic and sedimentary context in which turbid zone reefs exist, both in the modern and fossil reef record, can inform key ecological debates regarding species tolerances and adaptability to elevated turbidity and sedimentation. Furthermore, these investigations can address critical geological and palaeoecological questions surrounding longer-term coral-sediment interactions and reef growth histories. Here we review current knowledge about turbid zone reefs from the inner-shelf regions of the Great Barrier Reef (GBR) in Australia to consider these issues and to evaluate reef growth in the period prior to and post European settlement. We also consider the future prospects of these reefs under reported changing water quality regimes. Turbid zone reefs on the GBR are relatively well known compared to those in other reef regions. They occur within 20 km of the mainland coast where reef development may be influenced by continual or episodic terrigenous sediment inputs, fluctuating salinities (24–36 ppt), and reduced water quality through increased nutrient and pollutant delivery from urban and agricultural runoff. Individually, and in synergy, these environmental conditions are widely viewed as unfavourable for sustained and vigorous coral reef growth, and thus these reefs are widely perceived as marginal compared to clear water reef systems. However, recent research has revealed that this view is misleading, and that in fact many turbid zone reefs in this region are resilient, exhibit relatively high live coral cover (>30%) and have distinctive community assemblages dominated by fast growing (*Acropora*, *Montipora*) and/or sediment tolerant species (*Turbinaria*, *Goniopora*, *Galaxea*, *Porites*). Palaeoecological reconstructions based on the analysis of reef cores show that community assemblages are relatively stable at millennial timescales, and that many reefs are actively accreting (average 2–7 mm/year) where accommodation space is available, despite recent anthropogenic pressures. These turbid zone reefs challenge traditional views on the environmental conditions required for active reef growth, but given their proximity to land and associated stresses, current knowledge on these less well understood reefs should be synthesised to aid coastal management directives. Terrigenous sediments are a dominant influence on turbid zone reef occurrence, composition and growth, and, therefore, the assessment of their future prospects will require a detailed understanding of the sedimentary regimes under which they occur and of their differential response modes.

Contents

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1. Introduction

Coral reefs that develop in turbid water settings, where suspended sediment loads are frequently above those normally associated with vigorous reef growth, are described as turbid zone reefs (Roy and Smith, 1971; Partain and Hopley, 1989; Perry, 2003; Perry and Smithers, 2006). Turbid zone reefs are typically situated in nearshore coastal settings where they may be directly or indirectly exposed to terrigenoclastic sediments through sediment deposition and accumulation, or by sediment resuspension and elevated turbidity. High levels of sedimentation can reportedly increase coral mortality by smothering and burial (Loya, 1976), reduce larval settlement, and increase the prevalence of tissue infections (Bruno et al., 2003; Nugues and Callum, 2003; Fabricius, 2005), whilst high levels of turbidity (>10 mg/L) will reduce light availability for photosynthesis and energy production (Rogers, 1990; Wolanski and De'ath, 2005). Nutrient (e.g. nitrogen and phosphate) concentrations may also be elevated near the coast due to increased land and river runoff. Elevated nutrients threaten reefs by causing macro-algal proliferation (Fabricius, 2005), increasing the abundance of bioeroding filter feeders (Hallock, 1988), and raising the frequency and severity of coral disease (Bruno et al., 2003). Consequently, where clear-water environmental conditions are used as a benchmark, environmental conditions inshore are widely considered sub-optimal for 'healthy' coral reef growth. As such, it is commonly claimed that turbid zone reefs are stressed and/or degraded (Neil et al., 2002; McCulloch et al., 2003; Woolridge et al., 2006; Hughes et al., 2011). However, many turbid zone coral reefs actually have high live coral cover (>30%) and diversity (>100 species; Veron, 1995; DeVantier et al., 2006), contain temporally stable community assemblages over decadal to centennial timescales (Riegl et al., 1995; McClanahan and Oburu, 1997; Ayling and Ayling, 1999a; Perry et al., 2008, 2009), have actively and rapidly accreted (Smithers and Larcombe, 2003; Perry and Smithers, 2006; Palmer et al., 2010; Perry et al., 2012), and are able to recover quickly from periodic setbacks such as flood events and cyclones to which they are regularly exposed (Ayling and Ayling, 2005; Browne et al., 2010).

Over the past decade research on turbid zone reefs has intensified to include ecological, palaeoecological and geological studies, due to growing concerns over their exposure to both local threats such as increased sediment, nutrient and pollutant delivery (Cooper and Fabricius, 2007; De'ath and Fabricius, 2010), and global threats such as rising sea surface temperatures (coral bleaching) and ocean acidification (Table 1; Hughes et al., 2003). Ecological studies suggest that turbid zone reefs are more vulnerable to reef degradation than their clear-water mid- and outer-shelf reef counterparts (Cooper and Fabricius, 2007; Fabricius et al., 2007; Fabricius et al., 2008). However, evidence from reef cores from Holocene turbid zone reefs (Perry, 2003; Smithers and Larcombe, 2003; Perry et al., 2008), indicate that many turbid zone reefs initiated and continued to grow where terrigenous sediment inputs were high, similar to contemporary conditions, suggesting a degree of resilience to sedimentation and turbidity. Furthermore, radiometrically-dated reef cores indicate the regional demise of turbid zone reefs on the inner GBR several thousand years ago but also record a second phase of inner-shelf reef establishment and growth following a hiatus of several hundred years: a recovery that extends to the present despite the modern day sedimentary regimes and anthropogenic threats (Perry and Smithers, 2011). These palaeoecological and geological studies provide a context for understanding current community dynamics and indicate that turbid zone reefs may be far more robust than generally considered.

There is also mounting evidence that turbid zone reefs are characterised by coral species and community assemblages that are tolerant to typically unfavourable environmental conditions. The first comprehensive assessment of a turbid zone reef was performed at Low Isles Reef, northern GBR, in 1928 by the Great Barrier Reef Committee and the Royal Society of London (Hopley et al., 2007). Low Isles has been further monitored over the intervening years (Stephenson et al., 1958; Fletcher, 2000; Frank and Jell, 2006; Frank, 2008) and has provided some of the first evidence to suggest that many coral reef communities can tolerate sediment loads and turbidity regimes well above those which negatively affect clear-water reefs. However, despite recent advances in our understanding of these 'marginal reefs', knowledge of coral community persistence, of the influence of high sedimentation and turbidity on both coral community assemblages and reef growth, and on the mode (carbonate accretion versus terrigenous sediment accumulation) and the rate of reef growth remains poor. Furthermore, it is unclear how resilient turbid zone reefs are given increasing human pressures and associated stressors.

Here we review geological, palaeoecological and ecological data from the GBR to assess the key environmental controls on turbid zone reef occurrence, coral community composition and reef growth over a range of timescales. The influence of fine-grained terrigenous sediments on the rate and mode of reef growth is investigated, and we provide a synthesis of current knowledge on coral composition and distribution on turbid zone reefs. Given the increased frequency and severity of threats, such as reduced water quality, disturbance events and projected environmental changes, to inshore turbid zone reefs, we discuss some of the conflicting arguments about the vulnerability of turbid zone reefs from the perspective of management and conservation initiatives. Data from the GBR augmented with data from the Caribbean, Asia and Africa, are used to address these issues. Since the 1980's studies on turbid zone reefs of the GBR have become more numerous and diversified to include small-scale assessments of coral growth rates to broad scale assessments of disturbance events, and today over 20 inshore turbid reefs are regularly monitored by the Australian Institute of Marine Science (AIMS) (Fig. 1; Table 2). In addition, over 80 reef cores have been collected to provide the most extensive data available on turbid zone reef growth and development. These data highlight important links between reef ecology and geology,

Table 1
Summary of natural and anthropogenic pressures potentially experienced by turbid zone reefs and the potential consequences of these pressures.

		Consequences	References
Natural environmental pressures			
Fine-grained sediment load	Sedimentation	Smothers and bury corals	Loya, 1976
		Reduces surface area for larval settlement	Nugues and Callum, 2003; Fabricius, 2005; Fabricius et al., 2005,
		Increases coral juvenile mortality	Wittenberg and Hunte, 1992
		Increases disease prevalence	Bruno et al., 2003
		Reduces energy for other metabolic functions e.g. reproduction, immunity and coral growth	Tomascik and Sanders, 1987; Rogers, 1990; Davies, 1991
	Turbidity	Lowers light availability for energy production	Rogers, 1990; Wolanski et al., 2005
Freshwater	Low salinity	Causes freshwater bleaching	DeVantier et al., 1997
Water temperature	Higher during summer months	Causes bleaching	Glynn, 1993; Berkelmans et al., 2004
Physical damage	Storms, cyclones etc.	Leads to coral breakage and loss of coral cover and diversity	Fabricius et al., 2007; Fabricius et al., 2008
		Shifts community assemblage composition	Done and Potts, 1992
		Re-distributes carbonates	Fabricius et al., 2007
		Reduces structural complexity	Done, 1992
Anthropogenic environmental pressures			
Nutrients	Nitrates, phosphates etc.	Decreases water clarity due to algal blooms	Fabricius, 2005
		Increases macro-algal cover and may lead to an algal-phase shift	De'ath and Fabricius, 2010
		Increases bioeroders and other heterotrophic organisms e.g. sponges which compete with corals for space	Hallock, 1988; Hutchings et al., 2005
		Increases phytoplankton availability which has been linked to *Acanthaster planci* outbreaks	Fabricius et al., 2010
		Stresses corals and potentially reduces reproduction and coral growth rates	Tomascik and Sanders, 1987
Pollutants	Agrochemicals, pesticides etc.	Reduces the success rate for coral larval development	Markey et al., 2007
Physical damage	Boating activities e.g. boat groundings and anchor damage	Damages corals and may lead to coral death	Wachenfeld et al., 1998
Harvesting	Fishing, lobster pots etc.	Effects trophic cascades and may lead to decline in reef health	Jackson et al., 2001
Coastal development	Sedimentation	See sedimentation effects	
Dredging	Turbidity	See turbidity effects	
	Release of pollutants	See pollutant effects	
Invasive species	Ship fouling	Decreases the coral community abundance and diversity	Bauman et al., 2010
Future climate change scenarios			
	Higher rainfall	Increases the delivery of terrestrial sediments, nutrients, pollutants and freshwater to inshore regions	Goldberg and Wilkinson, 2004;
	Higher mean SST	Increases sea surface temperature fluctuations inshore which may lead to increased levels of coral bleaching	Fabricius et al., 2007; Hoegh-Guldberg, 1999; Hughes et al., 2003
	Ocean acidification	Reduces ocean pH will lead to carbonate dissolution, weakening of carbonate organisms and increase the fragility of coral reef ecosystems	

and are used to address controversial issues regarding the influence of anthropogenic activities on their long-term reef development.

2. Distribution of turbid zone reefs on the inner GBR

Turbid zone reefs on the GBR occur in shallow (<20 m), inshore lagoon waters within 20 km of the coast, where environmental conditions are often considered marginal for reef growth. The substrate within the inshore zone includes a thick (5–10 m) wedge of terrigenous mixed sand and mud referred to as the inshore sediment prism (ISP) derived from long-term fluvial inputs deposited on the shelf during the last sea-level lowstand together with those reworked shorewards during the post-glacial transgression (Larcombe and Carter, 1998; Hopley et al., 2007). The inshore zone is one of three shelf parallel sedimentary zones on the GBR shelf and is distinct from the mid-shelf (22–40 m) and outer sedimentary zones (40–80 m) which are starved of terrigenous sediments (Fig. 2; Belperio, 1988; Larcombe and Carter, 2004). Numerous coral reefs dominate the outer zone but in the mid-shelf zone they are generally restricted to fringing reefs surrounding high islands (Maxwell and Swinchatt, 1970; Larcombe and Carter, 2004). The distribution and morphological development of coral reefs within the inner-shelf sedimentary zone is well known and understood, and has been reviewed in detail by Smithers et al. (2006) and Hopley et al. (2007). Based on bathymetric charts and available remotely sensed imagery it is estimated that there are approximately 900 inshore reefs (Hopley et al., 2007) including both fringing reefs, and nearshore reefs and shoals, representing approximately a third of the reefs on the GBR. Kennedy and Woodroffe (2002) provide a review of global fringing reef morphology and growth, and have found that many fringing reefs initiated as nearshore reefs and then became shore-attached either through shorewards progradation of the leeward reef edge (e.g. King Reef, central GBR; Hopley et al., 2007) or coastal progradation towards the reef (e.g. Yule Point, far north GBR; Bird, 1971).

2.1. Fringing reefs

Mainland fringing reefs are common north of Cairns and along the Whitsunday coastline where the local geology forms steep headlands and embayments to which fringing reefs are attached. Headlands provide stable and firm rocky substrates long considered optimal for

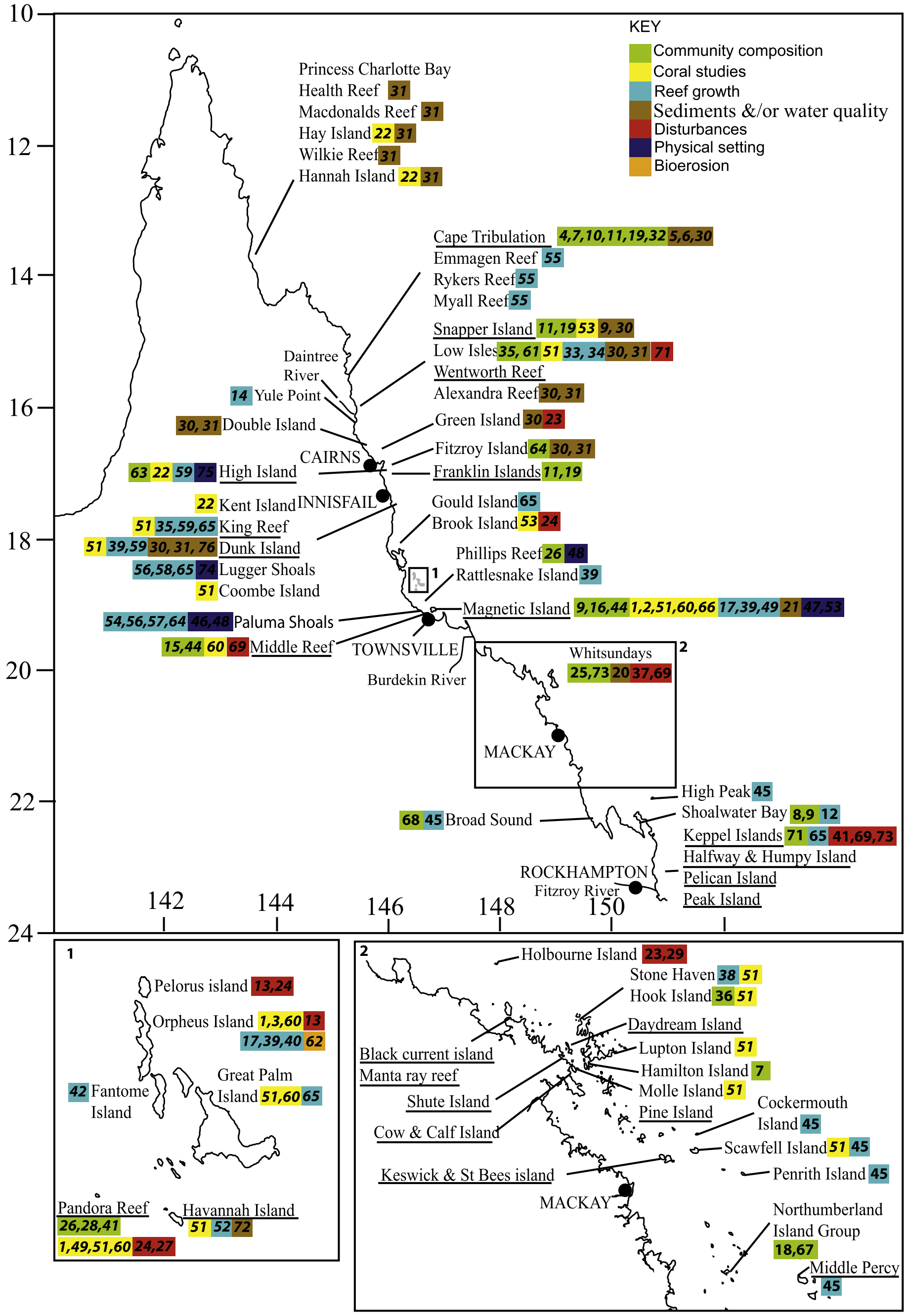

Fig. 1. Surveys conducted on fringing and nearshore turbid reefs on the inner GBR shelf. Coloured boxes denote the type of survey and numbers refer to source in Table 2. Long-term monitoring sites of the Australian Institute of Marine Sciences (AIMS) are underlined.

reef initiation and growth (Veron, 1995). However, on the GBR many fringing reefs have developed within the embayments where suitable substrates were available, either at the bay head or at the base of beaches (e.g. King Reef, (Fig. 3a); Hopley et al., 2007). Large rivers discharging freshwater and terrestrial sediments may locally and even regionally impede the development of fringing reefs, accounting for the absence of fringing reefs a considerable distance north of the Fitzroy and Burdekin Rivers (Fig. 1). By comparison the Whitsundays coastline is less affected by river discharge, improving fringing reef initiation and survival. The negative influence of sediments, in particular high turbidity, on coral growth and carbonate production has limited reef growth around Broad Sound to the south of the Whitsundays, although in this region high turbidity is produced through sediment resuspension by strong tidal flows associated with a high tidal range (>10 m) (Kleypas, 1996; Van Woesik and Done, 1997). Inshore fringing reefs are also found on continental islands within and north of the Whitsundays (e.g. Five Beach Bay, Magnetic Island (Fig. 3b); Hopley et al., 2007).

2.2. Nearshore reefs and shoals

Nearshore reefs and shoals occur close to the coast and are more evenly distributed along the GBR than fringing reefs (Hopley et al., 2007). Although they are poorly represented in the literature, nearshore shoals represent an important reef type; many have high coral cover (>30%), are morphologically complex with a well-developed back reef, reef flat and reef slope (e.g. Paluma Shoals, Halifax Bay; Palmer et al., 2010). Nearshore reefs and shoals can be found in turbid waters within

Table 2
Reference list for Fig. 1 which illustrates the location and type of study carried out on inshore turbid reefs on the GBR.

Number	Reference	Number	Reference	Number	Reference
1	Anthony, 2000	28	Done et al., 2007	55	Partain and Hopley, 1989
2	Anthony, 2006	29	Endean et al., 1989	56	Perry and Smithers, 2006
3	Anthony and Fabricius, 2000	30	Fabricius et al., 2003	57	Perry et al., 2008
4	Ayling and Ayling, 1985	31	Fabricius et al., 2005	58	Perry et al., 2009
5	Ayling and Ayling, 1986	32	Fisk and Harriott, 1986	59	Perry and Smithers, 2010
6	Ayling and Ayling, 1991	33	Frank, 2008	60	Risk and Sammarco, 1991
7	Ayling and Ayling, 1995	34	Frank and Jell, 2006	61	GBRE, 1928-1929
8	Ayling and Ayling, 1996	35	Graham, 1993	62	Sammarco and Risk, 1990
9	Ayling and Ayling, 1998	36	Harriott and Fisk, 1990	63	Smith et al., 2005
10	Ayling and Ayling, 1999a	37	Hedley, 1925	64	Smithers and Larcombe, 2003
11	Ayling and Ayling, 2005	38	Hopley et al., 1978	65	Smithers et al., 2006
12	Ayling et al., 1998	39	Hopley et al., 1983	66	Sofonia and Anthony, 2008
13	Baird and Marshall, 2002	40	Hopley and Barnes, 1985	67	Van Woesik, 1992
14	Bird, 1971	41	Johnson et al., 1985	68	Van Woesik and Done, 1997
15	Browne et al., 2010	42	Johnson and Risk, 1987	69	Van Woesik et al., 1995
16	Bull, 1982	43	Jones et al., 2008	70	Van Woesik et al., 1999
17	Chappell et al., 1983	44	Stafford-Smith et al., 1994	71	Wachenfeld, 1995
18	Cheal et al., 2001	45	Kleypas, 1996	72	Weber et al., 2006
19	Chin and Ayling, 2000	46	Larcombe and Woolfe, 1999a	73	Weeks et al., 2008
20	Cooper et al., 2007	47	Larcombe et al., 1995	74	Whinney, 2007
21	Cooper et al., 2008a	48	Larcombe et al., 2001	75	Wolanski et al., 2005
22	Cooper et al., 2008b	49	Lewis, 2005	76	Wolanski et al., 2008
23	DeVantier, 1995	50	Lough and Barnes, 1992		
24	DeVantier et al., 1997	51	Lough and Barnes, 1997		
25	DeVantier et al., 1998	52	McCulloch et al., 2003		
26	Done, 1982	53	Orpin et al., 2004		
27	Done and Potts, 1992	54	Palmer et al., 2010		

open sedimentary coastal settings (e.g. Paluma Shoals; Fig. 3c), semi-protected coastal settings (e.g. Middle Reef, Cleveland Bay (Fig. 3d); Browne et al., 2010) and occasionally within highly turbid muddy coastal embayments (e.g. Broad Sound; Kleypas, 1996). Less is known about nearshore reefs than fringing reefs despite their relatively common occurrence, as turbid waters hinder field research, and only a few detailed reef accretion and morphological descriptions are available (Smithers and Larcombe, 2003; Smithers et al., 2006; Perry et al., 2009; Palmer et al., 2010; Perry et al., 2012). It was only recently that submerged turbid reefs were discovered in the Gulf of Carpentaria, northern Australia, using multibeam swath sonar (Harris et al., 2004), which suggests that they may be more common than generally considered. For example, six nearshore reefs and shoals have been identified in Halifax Bay, north of Townsville (Fig. 2), a wave exposed bay with relatively high wave activity (>1 m wave height) and wind-driven resuspension of deposited sediments (Larcombe et al., 2001).

3. Environmental controls on turbid zone distribution and development

Turbid zone reefs occur within a number of geomorphic settings ranging from wave protected and sheltered muddy embayments to open coastal and high island settings, and have initiated over substrate types which vary from mobile alluvial and subtidal sands and gravels, to hard rocky substrates (Fig. 4). Varied reef morphology from site to site reflects differences in environmental controls including: substrate type and pre-existing topography, water depth and sea level history, sedimentation and turbidity regimes which in turn are influenced by the hydrodynamic setting, fluctuations in water quality linked to both natural (e.g. storm runoff or resuspension) and anthropogenic influences, and disturbance events such as cyclones and associated flood events (Table 3). Substrate type will influence reef initiation and, as such, reef location. For example, the availability of suitable substrate within Halifax Bay, usually Pleistocene fluvial cobbles and pebbles, is regarded as the primary control on reef location (Larcombe et al., 2001), however, high sediment resuspension rates and low sediment accumulation is also an important factor. In addition, the physical setting inshore, namely shallow water depths and often mobile sedimentary substrate, amplifies the effects of these environmental controls which, in combination, strongly influence the community composition and growth histories of turbid zone reefs. This section discusses the nature of these interacting influences using available data from the GBR.

3.1. Substrate availability

An underlying control on reef development is the probability of reef initiation, which is controlled largely by substrate availability (Kennedy and Woodroffe, 2002), as well as light availability (Larcombe and Woolfe, 1999a) and recruitment potential. Reef initiation is widely perceived to be limited to hard substrates, but cores through many turbid reefs on the inner GBR suggest initiation is possible over a diverse range of substrates, including unconsolidated sands, Pleistocene clays and 'coffee rock' (rock-like formations of indurated sands derived from deposited Pleistocene riverine sediments; Hopley et al., 1983; Smithers et al., 2006; Roche et al., 2011). For a few turbid zone reefs, reef initiation and subsequent reef growth has been largely controlled by the position of the ISP: in regions where wave energy was low near-shore, sediments accumulated and the ISP became shore attached preventing reef initiation near the coast. However, where the coast was exposed to SE winds, wave resuspension limited deposition and maintained a corridor of low sedimentation between the ISP and the shoreline where reefs could initiate if suitable substrates were available. As sea level has changed over the Holocene the ISP has migrated across the shelf influencing the position of this inshore corridor of reef initiation potential (Larcombe and Woolfe, 1999a).

3.2. Sedimentary and hydrodynamic regimes

The sedimentary regime is a dominant control on community assemblages and turbid zone reef growth (Woolfe and Larcombe, 1999). Key aspects of the sedimentary regime relevant to turbid zone reef growth and survival include: the source and rate of fine-grained sediment supply; coastal sediment transport; sediment deposition; and resuspension regimes. Sources of sediments to the inshore GBR include runoff from terrestrial catchments, and the resuspension and redistribution of shallow seabed sediments. The latter are composed

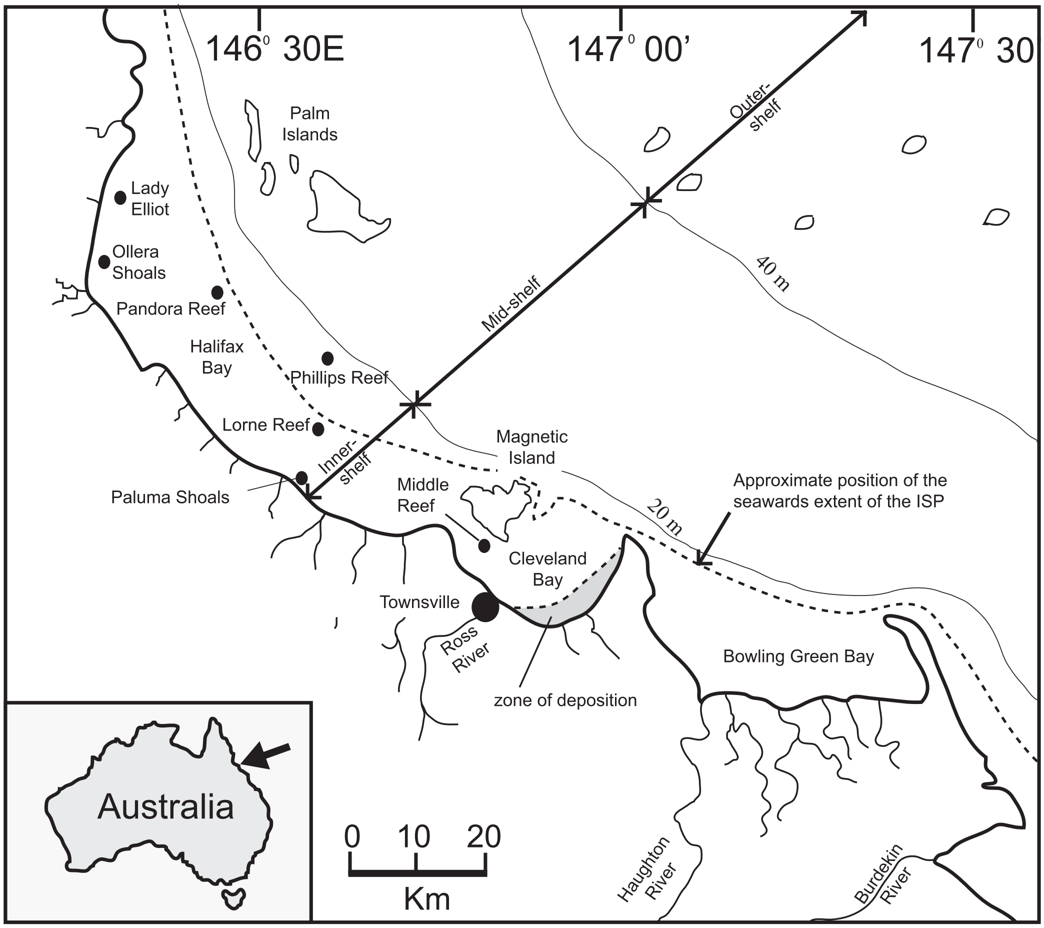

Fig. 2. Boundaries for the three sedimentary zones (inner, mid- and outer-shelf) on the central GBR, and the location of six nearshore reefs in Halifax Bay and one in Cleveland Bay, and the inner-shelf sedimentary prism (ISP).

of terrigenous sediments delivered to the coast by rivers, that have accumulated in coastal waters since sea level stabilised around 6000 years ago (Larcombe and Woolfe, 1999b), as well as fine sediments worked landwards during the postglacial transgression.

Sediment resuspension and turbidity is largely controlled by the hydrodynamic regime (waves, currents, tides); turbidity rapidly rises (>100 mg/L) during high wave energy events such as storms. However, turbid reefs located close (<10 km) to large rivers that supply large quantities of sediments to coastal regions (e.g. Lugger Shoals, 10 km north of the Tully River which delivers ~130,000 tonnes of sediment annually; Furnas, 2003) often experience extreme levels of prolonged turbidity (<3 days, Larcombe et al., 2001; Whinney, 2007). For example, suspended sediment concentrations in coastal waters near the Tully River increased from <0.05 to 0.2 kg m^{-3} (measured at approximately 500 mg/L at Lugger Shoals; Whinney, 2007) near the surface during a 10 day flood event in 2007 with a further increase to 0.5 kg m^{-3} (measured as <1500 mg/L at Lugger Shoals; Whinney, 2007) during strong winds (Wolanski et al., 2008). It is often during such events, that benthic communities on turbid zone reefs are threatened by sediments, and their survival will depend on: the duration and intensity of the event; the rate at which sediments accumulate on the reef (which typically increases with depth (Wolanski et al., 2005), and within sheltered reef habitats); and the natural background turbidity regime (see Section 3.3).

The relationship between sedimentation, turbidity and turbid zone reef distribution on the GBR has been discussed by several authors (Done, 1982; Larcombe and Woolfe, 1999b; Orpin et al., 1999; Woolfe and Larcombe, 1999), and it has been argued that the balance between sediment deposition and resuspension rather than the rate of sediment supply is actually most critical to turbid zone reef distribution and survival. The balance between sediment deposition and resuspension is controlled by the hydrodynamic regime: sediment deposition is typically high in relatively low energy hydrodynamic settings where currents are reduced (<5 cm/s) and wave energy is limited (<0.5 m wave height), whereas low levels of net sediment deposition occur in hydrodynamic settings where currents are stronger (>10 cm/s) and wave energy is higher (>1 m wave height). High rates of sedimentation (>10 mg/cm^2/day; Rogers, 1990) may smother and bury corals, and debilitate corals more than high turbidity (>10 mg/L; Rogers, 1990) particularly given that many coral species common on turbid reefs have adapted to low light levels produced by high turbidity (see Section 5.1; Woolfe et al., 1998; Anthony, 2000; Anthony, 2006). Turbid zone locations with high sediment resuspension and turbidity but low sedimentation are, therefore, more benign environments for turbid zone reef growth than high sedimentation (net depositional) settings. For example, numerous nearshore and fringing reefs are located in Halifax Bay, immediately north of Cleveland Bay (Fig. 2), which lies to the left of the ISP where waves resuspend sediments and currents transport sediments alongshore. Although these conditions facilitate an active sediment transport regime, deposition on reefs is generally low (Browne et al., 2012). In contrast, the north-east (NE) facing shoreline at the southern fringe of Cleveland Bay is a zone of net deposition (Fig. 2; Lou and Ridd, 1997; Lambrechts et al., 2010), as it is protected from the stronger SE wind-driven waves, the major sediment transport process on the GBR inner shelf (Larcombe et al., 1995; Larcombe et al., 2001; Whinney, 2007), and also from the primary longshore currents which regionally transport sediments northward. As predicted by the Larcombe and Woolfe (1999a) model of reef growth in

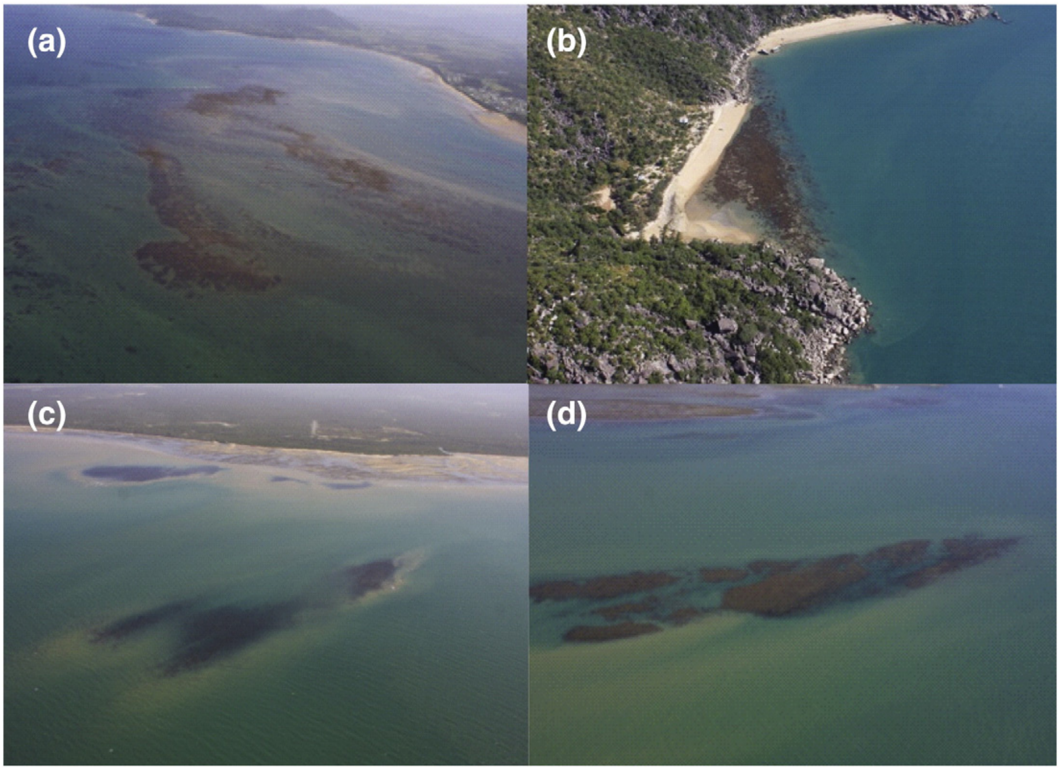

Fig. 3. Arial photographs of turbid zone reefs within different geomorphic settings: (a) Wide beach base fringing reef, King Reef; (b) Headland attached fringing reef, Magnetic Island; (c) Nearshore shoal, Paluma Shoals; (d) Nearshore patch reef, Middle Reef.

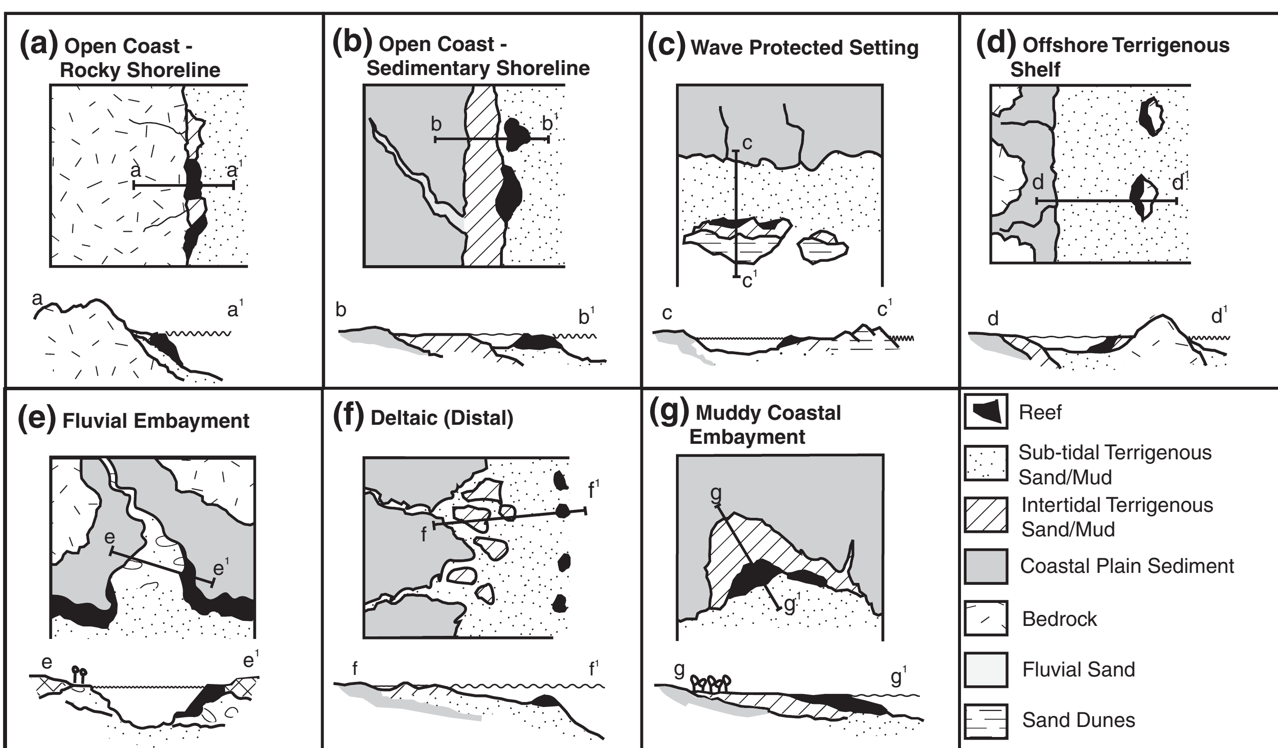

Fig. 4. Conceptual model of turbid zone reef growth in different marine settings (a) open coast, rocky shoreline (e.g. Great Palm Island, central GBR; Hopley et al., 2007), (b) open coast, sedimentary shoreline (e.g. Paluma Shoals, central GBR; Smithers and Larcombe, 2003), (c) wave protected setting e.g. the leeward side of submerged rocky outcrops in deeper water (<20 m) (e.g. Sodwana Bay, South Africa; Schleyer and Celliers, 2003), (d) offshore terrigenous shelf (e.g. Inhaca Island, southern Mozambique; Perry, 2005), (e) fluvial embayment (e.g. Discovery Bay, Jamaica; Mallela et al., 2004), (d) distal to river delta (e.g. Bay of Baten, Indonesia; Hoitink and Hoekstra, 2003), and (g) muddy coastal embayment (e.g. Phuket, South Thailand; Tudhope and Scoffin, 1994).

Table 3
Key differences in environmental setting, reef development and community assemblages between clear-water offshore reefs and inshore turbid zone reefs on the GBR.

Environmental controls	Clear-water offshore reefs			Inshore turbid reefs		
	Typical conditions	Description	References	Typical conditions	Description	References
Oceanography	Oceanic conditions characterised by exposure to swell	High energy environments dominated by robust *Acropora* communities and high coralline algae cover	Done, 1986	Locally wind driven waves	Lack of coralline algae and robust *Acropora* communities reflect lack of oceanic swell	Done, 1986; Giesters, 1977
	Well mixed and flushed environments	Increased mixing due to up-wellings and large-scale turbulence generated by the flow around the reefs	Wang et al., 2007	Low level of mixing and flushing rates	Large differences in seasonal water temperatures due to higher water residency times and increased distance from up-wellings	Wolanski, 1994
Fine-grained sediment load	Low levels of sedimentation and turbidity	Sedimentation rate <10 mg/cm^2/day and a turbidity <10 mg/L is considered to be 'normal' on reefs not subjected to human pressures	Rogers, 1990	High levels of sedimentation and turbidity	Sedimentation rate >10 mg/cm^2/day and turbidity levels from <10 mg/L to >50 mg/L	Todd et al., 2001; Riegl et al., 1995; Edinger et al., 2000; Sofonia and Anthony, 2008
Freshwater	Stable salinity	~36 ppt	Lirman et al., 2003	Extreme fluctuations	24–36 ppt Low salinities can lead to freshwater bleaching events	Walker, 1981
Nutrient inputs	Low	Low chlorophyll *a* concentrations ($<$0.3ug/l)	De'ath and Fabricius, 2010	Potentially high	High nutrient inputs can lead to a shift to algal dominance; increase bioerosion; increase prevalence of coral disease	Fabricius, 2005; Hallock, 1988
Physical disturbance events	Variable	Physical disturbance events (e.g. cyclones) cause damage to greater depths on offshore reefs	Fabricius et al., 2008	Variable	Potentially less resistant to physical damage due to fragile coral skeletons or less stable substrate type	Fabricius et al., 2008; Fabricius et al., 2007; Massel and Done, 1993
Reef development						
Reef initiation	Holocene	10,000–5000 yBP	Hopley et al., 2007	Holocene	6000–1000 yBP	Smithers et al., 2006; Hopley et al., 2007
Substrate availability	Hard substrate	Reefal foundations e.g. Pleistocene and Miocene reefs	Hopley et al., 2007	Mixed	Most inshore reefs on the GBR have grown on sediment deposits within shallow coastal embayments	Smithers et al., 2006
Average rate of reef growth	Variable	2–7 mm/year	Hopley et al., 2007;	Variable	2–7 mm/year	Partain and Hopley, 1989; Palmer et al., 2010; Kennedy and Woodroffe, 2002

Mode of growth	Carbonate	Internal structure dominated by shingle, rubble, in situ corals and coarse sand	Hopley et al., 2007	Mixed	Reefal foundations, terrigenous sand and mud, in situ corals and rubble	Hopley et al., 1983; Smithers et al., 2006; Perry and Smithers, 2010
Surrounding bathymetry	Deep water (<50 m)	Coral reefs need sufficient light for photosynthesis, therefore restricted to ~50 m in clear water	Yentsch et al., 2002	Shallow water (<15 m)	Reef growth restricted by shallow, turbid waters	Perry and Smithers, 2010; Hopley et al., 2007;
					High level of wind driven resuspension of sediments	Larcombe et al., 1995; Lou and Ridd, 1996;
Sea level					Inshore reefs have been strongly affected by sea-level change which has influenced both substrate availability and reef morphology.	Kennedy and Woodroffe, 2002
Composition	Variable to high coral diversity	~300 species High diversity provides resilience to change following a disturbance event	Veron, 1995; Ninio and Meekan, 2002	Variable to low coral diversity	100–150 species Many inshore reefs have diverse coral communities, but many are also dominated by physiologically robust corals which may be more tolerant to change	Veron, 1995; DeVantier et al., 2006
	High coralline algae (CCA) cover	~35% CCA cover on the GBR	Fabricius and De'ath, 2001	Low CCA cover	<1% cover on the GBR	Fabricius and De'ath, 2001
Community age structure	Mixed	Community assemblages contain both young and old corals due to successful recruitment of coral larvae and low mortality rates	Done, 1982; Sweatman et al., 2008	Mixed to older	Many inshore reefs characterised by large, older coral colonies which are capable of tolerating high sediment loads	Done, 1982; Sweatman et al., 2008
	High recruitment and survival rates	More suitable substrate availability would allow for more successful recruitment	Fabricius et al., 2008	Low recruitment and survival rates	Less suitable substrate availability due to high sediment cover and high level of algal competition. High sediment loads can affect the survival of coral juveniles.	Fabricius et al., 2003

terrigenous-sedimentary settings, the southern shoreline of Cleveland Bay has high sedimentation and limited coral reef development.

3.3. Flood plumes

Flood plumes pose a greater threat to inshore turbid reefs than wind-driven resuspension events, according to some researchers (Wolanski et al., 2008), due to the rise in sediment yields from coastal catchments since European settlement (McCulloch et al., 2003; Devlin and Schaffelke, 2009) and changes to the nature of sediments delivered. Coral reefs in Cleveland Bay are considered to be threatened by an increasing number of high turbidity events due to sediment accumulation within the southern regions at an estimated 60,400 tonnes per year from river discharge (Lambrechts et al., 2010). However, the sediment layer inshore is more than four metres thick and has provided an abundant supply of material for resuspension by wind-driven waves prior to any recent increases in sediment delivery which are estimated to add <1.5 mm of sediment to the substrate each year (Larcombe and Woolfe, 1999a, 1999b). Contemporary suspended sediment concentrations (SSC) in the bay are probably similar to levels over the past 6000 years despite a heavily modified catchment and busy shipping port (Larcombe et al., 1995). Furthermore, there is no direct evidence that suggests that coral reefs in the bay are being degraded from present day flood events, and there are even reports of increased coral cover over the last 10 years and rapid coral growth rates on nearby turbid zone reefs (Sweatman et al., 2007; Browne et al., 2010; Browne, 2012; Perry et al., 2012). These findings highlight the importance of understanding both the hydrodynamic and sedimentary settings (the natural turbidity regime) within the longer-term geological context when making broad assessments of reef health and growth trajectories.

Spatial variations in the natural background turbidity regime on the inshore GBR will result in spatially variable coral thresholds to reduced light levels and, as such, the influence of flood events on the reef communities, and thus on their growth and development will vary. In the case of Lugger Shoals (situated on the central inner GBR; Fig. 1) floods and plumes are generally not considered to have a major impact on the turbidity levels given that during the wet season the average turbidity over the reef is high (185 mg/L, Whinney, 2007) as a function of wave driven sediment resuspension. Corals at Lugger Shoals will thus have acclimatised to naturally high turbidity regimes and, therefore, have a higher threshold to low light levels, even during prolonged and severe disturbance events such as the 10 day flood event in 2007. This is borne out by core records that provide evidence that Lugger Shoals has been influenced by high terrigenous sediment inputs since reef initiation (~800 cal yBP; Perry et al., 2009). In contrast, a 5 day flood event in March 1996 (>1300 mm rain in the Daintree region) which resulted in a flood plume that inundated the southern edge of Snapper Island (a turbid reef situated north of Cairns but also within close proximity to a large river system; Fig. 1), caused hard coral cover to fall from 85% in 1995 to 10% in 1997 (Ayling and Ayling, 1998). This flood event, together with a flood event in 2004 (which caused a 10% fall in hard coral cover), were major disturbance events which have greatly influenced the coral community on the southern edges of Snapper Island (Schaffelke et al., 2007). Typical turbidity levels at Snapper Island are <2 mg/L (Thompson et al., 2011), values which are considerably lower than at Lugger Shoals (>50 mg/L recorded for 49% of the time; Whinney, 2007) and, as such, corals at Snapper Island are likely to have lower thresholds to high turbidity, even for short periods of time. These two examples illustrate the importance of natural turbidity regimes and variable thresholds to sediments, which should play an integral part in the management and conservation of inshore reefs. Vulnerability assessments to disturbance events, such as floods, should be based on a decision matrix which takes into account variable threshold levels, the timing of the event, as well as the duration, severity and frequency of the event.

The nature of sediments discharged into coastal waters during flood events as well as the hydrodynamic regime will influence the rate of sediment delivery, deposition and resuspension. Fine terrigenous sediments travel several 100's km while coarser sediments settle out of the water column within 10 km of the river mouth as salinities approach 10 ppt (Devlin and Brodie, 2005; Wolanski et al., 2008). Flood plumes increase turbidity and limit light availability for reef benthos, but unlike resuspension events which increase suspended sediment concentrations from the sea floor, fine sediments are commonly stratified and confined to the surface waters where mixing by waves is limited. The fate of these fine-grained sediments is largely unknown. However, they may be transported great distances along the inner-shelf and may eventually be deposited on mid-shelf reefs up to 60 km offshore (Lewis et al., 2006; Brodie et al., 2008). This is cause for concern given that fine sediments are often associated with biologically active concentrations of herbicides and pesticides (Bainbridge et al., 2009) and/or nutrients. When nutrients combine with suspended sediments 'marine snow' may form which, once deposited, can negatively influence benthic marine organisms to a greater degree than fine sediment deposition alone (Fabricius and Wolanski, 2000). However, deposited fine sediments are also more easily resuspended to greater depths than coarser sediments which may reduce sediment accumulation rates, particularly at deeper sites beyond the normal wave base (Wolanski et al., 2005).

3.4. Water quality

Evidence directly linking changes in community coral composition to deteriorating water quality, in particular to increased sediment delivery, is tenuous as the naturally turbid conditions driven by wind resuspension (Larcombe et al., 1995) and the natural disturbance regime (see Section 6) confound identification of anthropogenically-driven sedimentation and turbidity events. The use of cores from massive corals may resolve some of these issues by determining when stress events occurred in a coral's life history and evaluating if these events correlate with anthropogenic activities. For example, increased grazing pressure on the Burdekin catchment in the mid 19th century has been linked to increased sediment delivery associated with catchment soil erosion to inshore regions based on trace elements in massive corals (Lewis et al., 2007; Jupiter et al., 2008). However, it should be acknowledged that stress events on a coral colony do not always correlate to stress events that occur on a reef scale. Reef cores as opposed to coral cores have provided evidence that firstly, several turbid reefs have continued to vertically accrete rapidly post-European settlement, and secondly, that recent shifts in community assemblages and declines in reef-building capacity cannot necessarily be attributed to anthropogenic forcing (Perry et al., 2009; Palmer et al., 2010; Perry and Smithers, 2010; Perry and Smithers, 2011). Reef development will go through natural cycles of growth and quiescent phases, independent of anthropogenic activities (Perry et al., 2008; Perry and Smithers, 2010, 2011), and, therefore, a change in reef growth may simply reflect a reef entering a slow growth or 'turn-off' phase, as opposed to reef degradation caused by reduced water quality.

Low species richness inshore is often considered an indicator of excessive nutrient concentrations and sediment loads (Fabricius et al., 2005; DeVantier et al., 2006; Golbuu et al., 2008). However, low species richness may also reflect naturally high sediment loads which have persisted for millennia on the inner-shelf GBR prior to modern day changes in water quality. Furthermore, true species richness may be underestimated on inshore reefs due to high turbidity and limited visibility during field assessments, which hinder surveys and species identification. However, species richness can be high (>50 species) inshore despite both naturally high turbidity and anthropogenic pressures (e.g. >80 coral species at Middle Reef situated within 3 km of a busy international port and heavily modified urban catchment, Fig. 2; Browne et al., 2010). High species richness inshore, particularly where water quality is poor suggests that either hydrodynamic (e.g. wind driven flushing) conditions are preventing the buildup of nutrients and contaminants, or inshore reef species may be tolerant of poor water quality. Given the growing number of studies that have demonstrated high and temporally stable species richness inshore (Larcombe et al., 2001; DeVantier et al., 2006; Browne et al., 2010; Thompson et al., 2011), a better indicator of water quality, given no other limiting factors, may involve the assessment of species composition and community structure (Cooper and Fabricius, 2007). For example, the abundance of corals more sensitive to sediments and nutrients such as *Pocillopora* (Hashimoto et al., 2004), could provide a more appropriate measure of water quality.

4. Reef growth within the GBR turbid zone

A range of environmental (see Section 3) and ecological controls (see Section 5) influence reef growth and development. This section discusses the importance of ecological influences and their interactions for reef growth by examining the balance between carbonate production by reef organisms and removal by biological and physical mechanisms. We present examples of differences in turbid zone reef growth compared to clear-water reefs on the GBR and examine conceptual reef growth models. Fig. 5 provides a summary of factors that contribute to turbid zone reef growth and development.

4.1. Reef growth

Recent examinations of reef cores have identified two discrete episodes of reef initiation and growth on the inner-shelf of the GBR: the first occurred approximately 8000–5000 yBP during the Holocene transgression-early highstand, and the second since approximately 2000 yBP (Smithers et al., 2006; Perry and Smithers, 2011). The timing of the first of these two distinct reef initiation events, described as a reef 'turn-on' event, has been broadly linked to changes in water depth as the sea flooded the continental shelf during the postglacial transgression, and the second event is interpreted to be related to sea-level stabilisation near its present level through the late Holocene (Perry and Smithers, 2010, 2011). Turbid zone reefs that have vertically aggraded since sea level stabilised (~6500 yBP ago; Carter and Johnson, 1986) have done so by rapidly accumulating both carbonate and terrigenous sedimentary material (Woolfe and Larcombe, 1999; Perry et al., 2008, 2009). In contrast, clear-water reefs on the outer-shelf are largely reliant on the accumulation of carbonate material produced by calcifying organisms (e.g. corals). Mid-shelf reefs may have some passive accumulation of terrigenous sediments but could largely be dominated by active reef growth and, therefore, represent a transitional stage between the inner-shelf turbid reefs and outer clear-water reefs. The accumulation of both carbonate and terrigenous material on turbid zone reefs has lead to rapid rates of vertical reef aggradation (average values from inshore turbid reefs range from 2 to 7 mm/year, determined by radiometric dating of a number of reef cores) which in some cases has exceeded rates measured on mid- and off-shelf clear-water reefs (average 2–7 mm/year; Table 3). The accumulation of terrigenous and carbonate sediments provides a distinctive reef accretion signature, which can be used to identify reefs that in the past grew in high terrigenous load sedimentary settings (Perry and Smithers, 2006; Perry and Hepburn, 2008; Perry and Smithers, 2009).

Reefs that develop under terrigenous sedimentary influences are subjected to spatial and temporal variations in sedimentation and turbidity which will result in marked differences in the rate and mode of growth between reefs. Fringing reefs proximal to major rivers may initiate on alluvial fan gravel deposits, and rapid reef growth is due to the accumulation of both alluvial and reef sediments (e.g. Cape Tribulation situated close to the Daintree River vertically accreted at a rate of 3.5–5.1 mm/year following reef initiation in 7800 yBP; Partain and Hopley, 1989). Fringing reefs distal to major rivers, such as those on high-islands, may initiate on siliclastic sediments. For example, the low elevation fringing reefs on the protected leeward side of Dunk Island on the central GBR, initiated on unconsolidated inter-tidal siliclastic sediments which had been actively reworked prior to reef establishment approximately 1600 yBP (Perry and Smithers, 2010). The reef reached sea-level rapidly (by 1300 yBP on the landward margin) due to rapid reef accretion and limited accommodation space

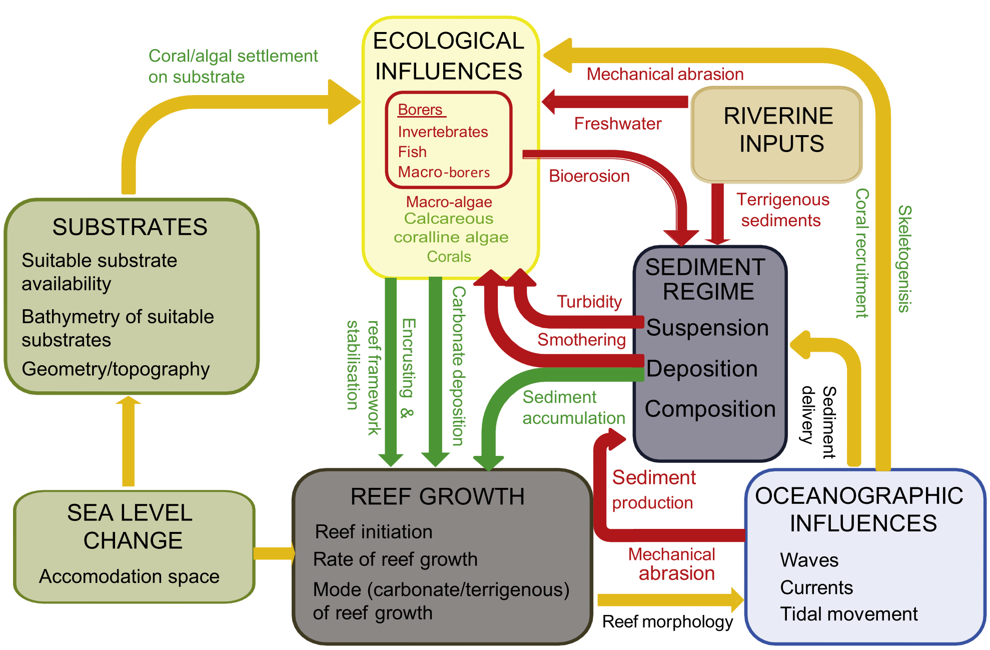

Fig. 5. Inshore turbid reef initiation, growth and development are influenced by a number of complex processes incorporating geophysical, oceanographic and ecological influences as well as the sedimentary regime. This model illustrates the main links between the key influences on inshore turbid reef growth and development. Green arrows represent positive processes for reef growth, red arrows represent negative processes, and yellow arrows indicate both negative and positive processes.

(<3 m), and has since formed a well-developed reef flat, characteristic of a reef approaching reef senility (Hopley, 1982; Smithers and Larcombe, 2003; Perry and Smithers, 2011). In contrast, Paluma Shoals, also situated in a shallow-water setting (<4 m LAT), distal to a large river but within an exposed coastal setting, initiated over Pleistocene clays approximately 1200 yBP, and is still actively accreting albeit more slowly over the last 50 years due to limited accommodation space (Smithers and Larcombe, 2003; Perry and Smithers, 2011). The reef is in its late mature stage and has grown at a rate of 1.1–1.8 mm/year under net fine-grained terrigenous sedimentation and high turbidity conditions (Smithers and Larcombe, 2003; Palmer et al., 2010). These examples highlight variations in the timing of reef initiation, substrates available for reef initiation, and the rate and mode of reef growth.

4.2. Reef growth models

To further current understanding of how turbid reefs have grown within these settings, two conceptual models have been developed: a terrigenous reef growth model presented by Woolfe and Larcombe (1999) and a growth model based on key reef processes developed by Kleypas et al. (2001) which has a broader application but can be applied to turbid zone reef growth. The terrigenous reef growth model depicts the balance between the accumulation of terrigenous sediments on a reef, together with carbonate production and removal to schematically demonstrate how reefs can persist where turbidity is high (Fig. 6a; Woolfe and Larcombe, 1999). It recognises that reef growth is not just based on the balance between carbonate production and destruction, but also depends on additional constructive and/or depositional processes, such as terrigenous sediment deposition, and destructive processes such as sediment removal. The model provides a useful tool for predicting long-term reef growth patterns if environmental variables, particularly the sedimentary regime, should change. The second conceptual model by Kleypas et al. (2001) focuses on how much of the carbonate produced on a reef remains within that system and how much is broken down and lost, and classifies reefs as either production-dominated, bioerosion-dominated, sediment-import-dominated or sediment-export-dominated (Fig. 6b). Although these models were published more than a decade ago they are conceptual reflecting the paucity of detailed data available on rates of carbonate production and removal, sediment import and export rates, and how terrigenous sediments influence the rate of carbonate production, deposition, and removal.

5. Intrinsic controls on reef growth and development

The rate of carbonate production and accumulation, which influences the rate and mode of reef growth and development, is partly controlled by the coral community, the primary carbonate producers, and the intrinsic controls that influence community assemblages and their distribution. Modern coral community assemblages observed on turbid reefs on the GBR have adapted to their sedimentary setting, and are therefore distinctive from their clear-water counterparts (Table 3). These adaptations vary both among species and between coral families, with some corals more adapted to high sedimentation rates, whereas others are more suited to high turbidity and low light environments. As such, spatially variable sedimentary regimes result in heterogeneously distributed community assemblages which are also reflected in the Holocene reef cores (Smithers and Larcombe, 2003; Palmer et al., 2010; Roche et al., 2011). However, throughout reef growth and development, the dominant coral species, typically *Acropora*, *Turbinaria*, and *Montipora*, are temporally stable given their presence throughout the reef cores, that is until sea level is reached where the influence of exposure during low tide results in a different assemblage of corals (e.g. *Goniastrea*, *Galaxea*) which are more tolerant to the additional stress effects of exposure.

5.1. Coral assemblages and adaptations

Many coral species in turbid zone settings have developed either morphological and/or physiological adaptations that enable them to cope with high sediment loads that negatively affect corals and coral reefs normally exposed to low sediment influx (Stafford-Smith and Ormond, 1992: Table 4). For example, *Turbinaria mesenterina* is highly abundant on inshore turbid reefs on the GBR and is well adapted to elevated sedimentation rates and turbidity levels (Sofonia and Anthony, 2008). *Turbinaria* is very plastic morphologically (Riegl et al., 1996), and under high sedimentation regimes, develops a characteristic funnel shape which concentrates sediment at the base of the funnel and away

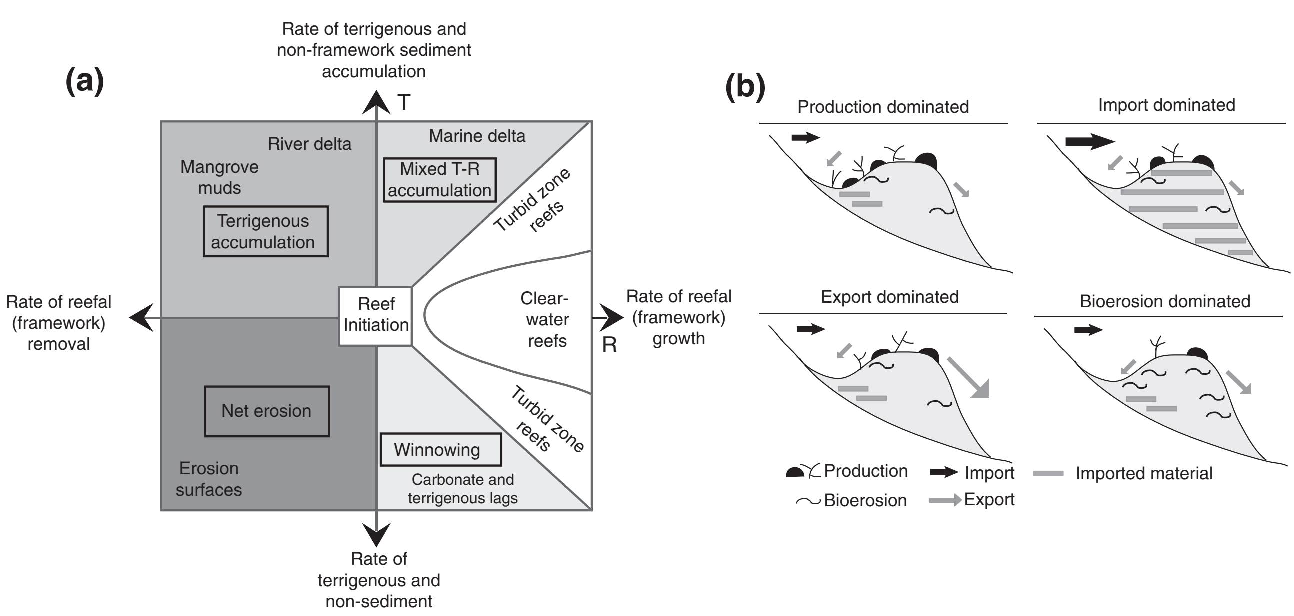

Fig. 6. Conceptual reef growth models adapted from (a) Woolfe and Larcombe, 1999 which recognises the importance of terrigenous accumulation as well as removal, where R represents the accumulation reefal (carbonate) framework and T represents the accumulation of terrigenous, non-framework sediment, and (b) Kleypas et al., 2001 which classifies reefs as either production-dominated, sediment-import-dominated, sediment-export-dominated or bioerosion-dominated.

Table 4
The spatial distribution of coral species on turbid reefs of the GBR. Details on morphological and/or physiological adaptations which have enabled these corals to tolerate high sediment loads are provided.

Reef habitat	Physical conditions	Coral community	Characteristics	Morphological/physiological adaptations to sediments	References
Windward shallow (1–3 m LAT)	High wave energy, variable turbidity, low sedimentation	*Acropora* (robust)	Branching with small polyps (<2 mm)	Fast coral growth rates and rapid regeneration from small coral tissue fragments following breakage during physical disturbances	Diaz-Pulido et al., 2009
		Montipora (plate)	Foliose with small polyps (<2 mm)	High tolerance to sedimentation, despite low sediment rejection rates, partly due to morphology	Bull, 1982; Done, 1982
Windward deep (>3 m LAT)	Lower wave energy down the reef slope results in higher rates of sedimentation, but currents may periodically resuspend sediments and increase turbidity	*Goniopora*	Massive with medium sized polyps (>5 mm)	Quickly removes sediments on its surface by actively modifying the boundary layer through the projection of its polyps above the colony surface	Stafford-Smith, 1993
		Pachyseris	Plate with small polyps (<3 mm)	Very active mesenterial feeders of small particles which allows *Pachyseris* species to tolerate sediments despite a lack of tentacles	Stafford-Smith and Ormond, 1992
		Turbinaria	Foliose with small polyps (<2 mm)	Plastic morphology and typically develops a funnel shape to channel sediments to the base of colony therefore reducing surface area covered in sediments	Sofonia and Anthony, 2008
Leeward shallow (1–3 m LAT)	Low wave and current energy which results in high rates of sedimentation. Fine sediments are typically deposited towards the back of the reef which are more easily resuspended than coarse sediments and may result in large fluctuations in turbidity	*Porites*	Massive with small polyps (<5 mm)	High tolerance to sedimentation due to mucus secretion which traps sediments. The smooth surface of the coral colony allows for the sediments to be sloughed off relatively easily.	Ports et al., 1985
		Galaxea	Sub-massive with medium sized polyps (~7 mm)	Rapidly removes sediments through ciliary mechanisms	Stafford-Smith, 1993
Leeward deep (>3 m LAT)	High rates of sedimentation and limited sediment resuspension due to low wave and current energy	*Goniopora*	See above		
Reef flat (<1 m LAT)	Corals exposed to high wave energy and may be exposed to air during low tides. Low sedimentation rates, but turbidity may increase on the rising tide due to sediment resuspension	*Goniastrea*	Massive with medium sized polyps (>5 mm)	Adapted to high turbidity and low light through heterotrophic feeding off particulates	Anthony, 2000
		Symphyllia	Massive with large polyps (20–25 mm)	Rejects sediments through tissue expansion which prevents sediment build up within the calices	Stafford-Smith, 1993
		Montipora (branching)	Digitate with small polyps (<2 mm)	This coral species can torelate extreme conditions on the reef flat, including high sediment loads, due to its asexual reproductive strategy	Sofonia, 2006; Harpeni and David, 2011
		Platygyra	Massive with medium sized polyps (>5 mm)	Rejects sediments from its surface through tissue expansion	Stafford-Smith and Ormond, 1992

from actively calcifying areas of the colony. Other species such as *Porites* spp. are tolerant to sedimentation rates of <10 mg/cm^2/day, a rate previously believed to impede coral growth (Rogers, 1990). To survive under these conditions *Porites* secretes a mucus coating which traps sediments but is easily sloughed off by waves and currents (Gleason, 1998). Other species common on turbid reefs, such as *Goniastrea* have adapted to high turbidity and low light through heterotrophic feeding off particulates in the water column at a rate that is up to four times greater than their conspecies on less turbid (<1 mg/L) mid-shelf reefs (Anthony, 2000). These spatially variable differences in adaptations to environmental conditions between individuals or geographic communities of the same coral species indicates that certain corals have an intrinsic ability to adapt to conditions previously considered detrimental to coral growth. These robust and resilient corals appear to dominate

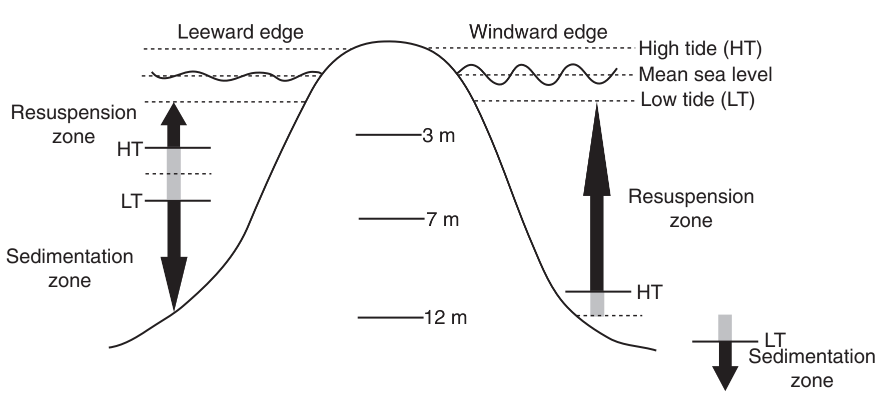

Fig. 7. Variations in the depth of the resuspension and sedimentation zones between the windward and leeward edge, and with the tidal cycle. Adapted from Wolanski et al., 2005.

turbid reef community assemblages throughout reef development on the GBR (Perry et al., 2008; Roche et al., 2011).

5.2. Coral assemblage distribution and reef growth

The balance between sedimentation and turbidity, which fluctuates both spatially and temporally depending on exposure to wave energy and the tidal cycle, will influence community distribution and reef growth. For example at High Island, a turbid zone reef located 5 km offshore from the north Queensland coast, the depth of the sediment resuspension zone extended to 12 m on the windward reef slope and just 5 m on the lower energy leeward reef slope (Fig. 7). Below these depths, limited sediment resuspension and flushing resulted in sediment accumulation and a decline in coral cover from >20% in the resuspension zones to <5% in the depositional zones. Limited resuspension and flushing of sediments also occur within protected internal basins or lagoons that form on some inshore turbid reefs (e.g. Middle Reef; Fig. 8). These inner-reef habitats are composed of corals such as *Porites* and *Goniopora*, both of which are tolerant to high sedimentation and turbidity (Done, 1982; Smithers et al., 2006). In contrast, exposed areas, such as the reef crest, tend to be dominated by fast-growing branching and plate corals, such as *Acropora* and *Montipora*,

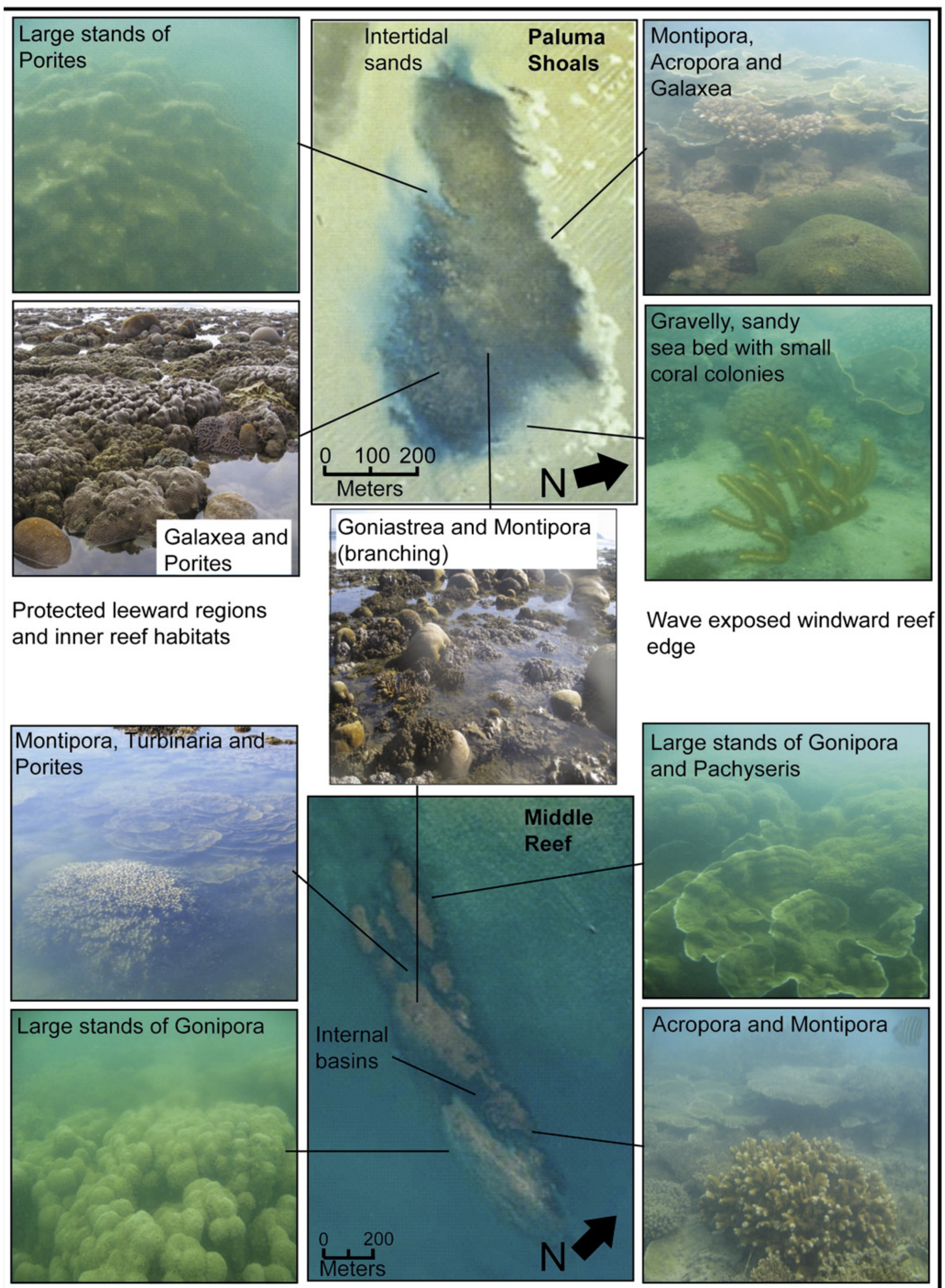

Fig. 8. Spatial distribution of community assemblages typically observed on turbid zone reefs on the inner-shelf GBR, based on Paluma Shoals (a nearshore shoal) and Middle Reef (a nearshore patch reef). Corals resilient to high wave energy (e.g. *Acropora* and *Montipora*) are commonly found on the reef crest whereas corals tolerant to high sedimentation and turbidity (e.g. *Goniopora* and *Pachyseris*) are found at depth on the windward and leeward reef slopes. Inner protected slopes are characterised by corals tolerant to high sedimentation (e.g. *Turbinaria* and *Porites*). Reef flats are often dominated by *Goniastrea* and branching *Montipora*, and large stands of *Galaxea* and *Porites* are found towards the leeward edge where sediments accumulate.

which are tolerant of higher wave energy conditions (Done et al., 2007; Browne et al., 2010). In general sedimentation rates are typically low on the reef flat (<1 g/m^2/day; Browne et al., 2012), which is exposed on the low spring tides and is typically dominated by corals including *Goniastrea aspera* and *Montipora digitata*. Sedimentation rates may increase towards the leeward edge as hydrodynamic exposure falls resulting in a shift in community assemblages to those often dominated by large stands of *Galaxea* (Smithers and Larcombe, 2003). These coral community assemblages result in spatially variable rates of carbonate productivity and, therefore, lead to differences in reef growth and morphological development.

5.3. Shifting community assemblages

Assessments of coral cover and diversity based on short-term studies have concluded that over recent decades many inshore turbid reefs have experienced a community shift from diverse assemblages to those dominated by specialist coral species (DeVantier et al., 1997; Done et al., 2007). These shifts are interpreted as evidence of reef degradation, potentially driven by extrinsic anthropogenic pressures. However, evidence from reef cores suggests that community shifts are intrinsically driven. A total of 17 reef cores from Paluma Shoals, 15 from King Reef and 6 from Lugger Shoals, provide some of the most detailed data on species composition and growth for turbid zone reefs (Smithers and Larcombe, 2003; Perry et al., 2008, 2009; Palmer et al., 2010; Roche et al., 2011). These studies demonstrate that as a reef vertically aggrades within a nearshore sedimentary setting, the dominant coral species (*Acropora*, *Goniopora*, *Turbinaria*, *Galaxea*, *Montipora*) change as the available accommodation space is filled and the reef approaches sea level. The influence of intrinsic and extrinsic factors on coral community assemblages has been conceptually modeled by Perry et al. (2008), which also illustrates the contrasting response of hypothetical coral species on turbid and clear-water reefs (Fig. 9). The model suggests that higher heterotrophic feeding capabilities may buffer coral species on turbid reefs to certain extrinsic factors such as rising SST, but on approaching sea level a shift in coral assemblages occurs to more specialised coral species that can withstand environmental conditions such as higher wave activity and exposure. These shifts are independent of the time at which the reef reaches sea level, confirming that these shifts are intrinsically driven, and not necessarily due to present day stresses. In contrast, on clear-water reefs, coral species are less adapted to shift between feeding strategies, and, as such, extrinsic factors may stress corals and drive mortality events, encouraging new species colonisation.

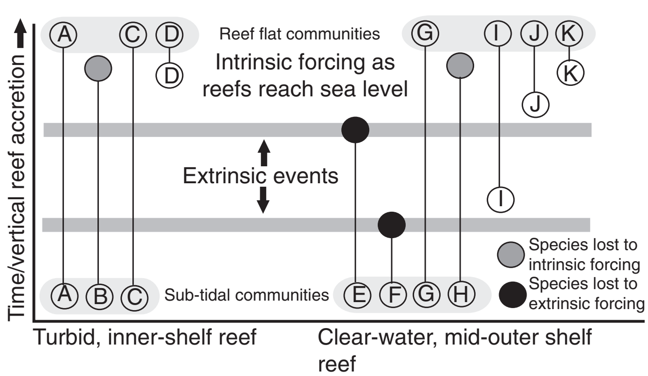

Fig. 9. Conceptual model of changing coral communities to intrinsic and extrinsic forcing factors adapted from Perry et al. (2008). The model illustrates the different responses of hypothetical coral communities between turbid and clear-water reefs, and demonstrates the importance of intrinsic forcing factors as reefs reach sea level. Coral communities on the turbid inner-shelf are more stable than clear-water mid to outer reefs due to their heterotrophic feeding capabilities which buffer them against extrinsic forcing factors. However, as the reef approaches sea level the environmental tolerances of some species (B) are exceeded whereas new species (E), adapted to wave and/or air exposure, may colonise the reef flat. In contrast, as the clear-water reefs vertically aggrade there is a switch in community composition from F, G, H, I to H, I, J, K, L due to extrinsic forcing which encourages new species colonisation.

Extrinsic factors that drive community shifts may also be due to natural shifts in the sedimentary regime as opposed to anthropogenically driven shifts. For example, low coral cover and species diversity on the reef at Cahuita, Costa Rica, initially attributed to high sediment influx associated with deforestation (Cortes and Risk, 1985), was later linked to natural coastal processes rather than human activity (Hands et al., 1993). Previous research had not considered the trend of the net shoreline recession coupled with a slow long-term rise in sea level that created an inherently dynamic shoreline and increased sediment delivery. An example of more recent reef community changes in response to natural processes was described at Low Isles turbid reefs, north of Cairns (Frank and Jell, 2006; Frank, 2008). A fall in hard coral cover and an increase in soft corals and macro-algal cover led to the assumption that the shift was triggered by agricultural activities in local catchments (Bell and Elmetri, 1995). However, geomorphic assessments indicated that changes in the community were due to natural processes associated with the expansion of the mangroves over the reef top (Frank and Jell, 2006). Lower sedimentation and turbidity rates on the reef flat in 1991–1992 than in 1928–1929 despite an increase in the amount of land clearing on the mainland around Cairns since the late 1920s (Johnston, 1996) further suggests that human activities were not the key drivers of community changes at Low Isles.

6. Modern day disturbances on turbid zone reef growth

On the GBR, natural disturbances such as bleaching events, floods and cyclones are relatively common occurrences. Since the 1980s, four major and widespread bleaching events (1983, 1987, 1998, 2002) have occurred resulting in coral cover losses of >50% on some reefs (e.g. Fitzroy Island in 1998; Fig. 8); during the 1990s five major flood plume events (1994, 1995, 1996, 1997, 1998) were recorded from the Burdekin River (Schaffelke et al., 2007), the largest river discharging into the GBR lagoon; and cyclones typically visit a region approximately every 10 years (Bureau of Meteorology). Turbid zone reefs are more frequently exposed to disturbance events than offshore clear-water reefs as they are located close to shore and river mouths (<20 km) and situated within shallow waters (<20 m) which typically experience greater fluctuations in SST. Reef recovery will depend on the nature and severity of the event as well as the level of resistance and resilience of the reef (Nystrom et al., 2000).

Several long-term studies suggest that turbid zone reefs are potentially resilient not only to sedimentation and fluctuating turbidity, but also to disturbance events. Many turbid reefs have both high coral cover and diversity, characteristics considered important for reef resistance and resilience (Nystrom et al., 2008), and as such, many reefs have recovered rapidly (<5 years) following disturbance events (Sweatman et al., 2007; Browne et al., 2010). For example, in 1986 the inshore turbid reefs off Cape Tribulation were visited by Cyclone Manu, a weak cyclonic event (<100 km.hr^{-1} winds), and in the following year a bleaching event occurred; together this reduced coral cover by 33% (Ayling and Ayling, 1999b). A survey two years later showed a very rapid recovery to pre-disturbance levels in coral cover (50%; Ayling and Ayling, 1999a). Given adequate recovery periods (>5 years) between disturbance events, these events may even promote diversity and reef health (Bonin et al., 2011). However, if the frequency and severity of disturbance events increase, reef recovery periods will be shortened, and reefs may experience high coral mortality rates, reduced species diversity (Hughes, 1989) and increased macro-algal cover (Ostrander et al., 2000).

The mechanisms that enable turbid zone reefs to recover from a disturbance event may differ from clear-water reefs, and are potentially dependent on the timing of the disturbance event. Coral larvae recruitment rates are a key mechanism of reef recovery on clear-water reefs, yet on turbid reefs recruitment rates are generally low

(Fabricius, 2005). Instead, the regrowth of surviving coral colonies, particularly fast-growing species such as *Acropora* and *Montipora*, is potentially critical for reef recovery (Fisk and Harriott, 1986; Ayling and Ayling, 2005). Coral growth and reef recovery will occur more rapidly if recovery occurs during a period of non-stressful environmental conditions. For example, the regeneration and regrowth of remnant *Acropora* coral tissue was observed at Keppel Islands after both the 2006 and 2008 bleaching events, and outcompeted macro-algal growth. Coral growth coincided with a seasonal die back of algae which together resulted in rapid coral community recovery (Diaz-Pulido et al., 2009). Fast-growing corals such as *Acropora*, which have a fragile branching structure, are more vulnerable to physical disturbance events (Madin, 2004), but their ability to grow rapidly suggests that these corals are important to the long-term survival of inshore turbid reefs (Osborne et al., 2011).

Despite rapid coral growth and reef recovery, other measures are required for an appropriate assessment of reef resilience to disturbance events and vulnerability to reef degradation. Long-term data that follow reef health trajectories provide a more comprehensive assessment of reef resilience and recovery regimes. However, reef health trajectories based largely on assessments of coral cover without an assessment of why coral cover declined and the demographic processes involved (Hughes et al., 2011) will only provide speculative answers to critical questions such as those regarding the mechanisms of reef resilience. While many researchers consider that declining coral cover on the GBR indicates regional reef degradation (Bellwood et al., 2004; Bruno and Selig, 2007), Sweatman et al. (2011) have recently argued that the GBR is less degraded from its natural, resilient state with coral cover having fallen from 28% in 1986 to 22% in 2004 due to localised rather than regional declines in coral cover. However, Hughes et al. (2011) argue that the GBR, in particular inshore turbid zone reefs, are losing reef resilience due to multiple disturbance events and incomplete recoveries, and calls for better monitoring of recruitment, growth and disease. Fabricius (2005) provides a review on the effects of terrestrial runoff on the ecology of corals (including recruitment, growth and disease) and coral reefs, and lists some of the more comprehensively documented field assessments available for the GBR as well as in Asia and the Caribbean. Of those conducted on the GBR, the effects of increased nutrients and turbidity are largely focused on changes in hard coral and algal cover, the abundance of bioeroders and biodiversity. In contrast, there has been limited research on the effects of sediments on coral recruitment rates on the GBR: notable papers include Fabricius et al. (2003) which concluded that both sediment composition and sediment deposition affect the survival rate of coral juveniles, Birrell et al. (2005) where sediment deposits were found to reduce coral settlement, and Humphrey et al. (2008) who found that the combined effects of sediments, nutrients and salinity resulted in reduced fertilisation rates for *Acropora millepora*. Spatial variations in coral growth (linear extension, density, calcification rates) within inshore GBR are also limited, with most studies conducted on massive corals such as *Porites* (Hendy et al., 2003; Cooper et al., 2008a; De'ath et al., 2009). These studies suggest that coral growth has fallen over the last ~50 years, a trend attributed to declines in water quality inshore. However, a recent study by Browne (2012) on an inshore turbid reef on the central Queensland coast found that growth rates of *Acropora*, *Montipora* and *Turbinaria*, all fast growing corals which typically dominate inshore reefs, were comparable to rates measured on mid-shelf and off-shelf reefs at similar water depths. In recent years there has, however, been an increase in coral disease research on the GBR, which has provided evidence that seasonal rainfall promotes coral disease by increasing pathogen virulence (Haapkyla et al., 2011), and seasonal fluctuations in light and temperature were positively correlated with black band disease on inshore turbid reefs (Sato et al., 2009). In summary, data on these recruitment, growth and disease are rare for inshore turbid reefs given the difficulty in conducting such observations within highly turbid settings, but will be required to assess inshore reef resilience, in particular to global threats such as bleaching which are increasing in frequency and intensity.

7. Projected environmental change

Inshore turbid zone reefs on the GBR are considered by some researchers to be more vulnerable than offshore clear-water reefs to global threats, particularly to bleaching events given greater fluctuations in SST inshore (Berkelmans et al., 2004; Weeks et al., 2008). A study by Berkelmans and Oliver (1999), based on 654 reefs across the GBR, found that in 1998 when SST were between 1 °C and 2 °C greater than normal for that period, 87% of inshore turbid zone reefs bleached to some extent, compared to only 28% of offshore reefs. However, bleaching inshore tends to occur at higher temperatures than on offshore reefs (Berkelmans et al., 2004), partly due to a higher thermal tolerance of corals provided by its algae symbionts (Berkelmans and Van Oppen, 2006). Bleaching may also occur at higher temperatures in turbid regions due to increased UVA and UVB penetration when waters are calm and turbidity has fallen. Turbid waters may, therefore, provide a degree of protection against bleaching for corals adapted to cope with high turbidity through heterotrophic feeding. However, there are still several unknowns regarding coral tolerance thresholds in warmer, turbid waters. For example, it is unknown whether the switch to more temperature tolerant algal symbionts following bleaching events (Jones et al., 2008) is permanent and the extent to which it may affect other coral functions such as growth and carbonate accretion. Indeed a higher thermal tolerance may come at the expense of a greater reef building capacity (Bradshaw and Hardwick, 1989).

Ocean acidification is another major threat to coral reefs. Ocean pH is predicted to decrease by 0.3 to 0.4 by 2100 (IPCC, 2007) which may result in increased carbonate dissolution rates, weakened coral skeletons and lower calcification rates (Kleypas et al., 1999; Hoegh-Guldberg et al., 2007; Anthony et al., 2011). At this stage, there is no evidence to suggest that the direct effects of ocean acidification will be greater on turbid zone reefs than on offshore clear-water reefs. However, if calcification rates decrease globally and coral skeletons weaken in response to ocean acidification, the living veneer of reefs in shallow waters, where the entire reef structure is exposed to wave activity, may be more susceptible to breakages and reef framework destruction. As such, inshore turbid reefs are potentially more vulnerable to the effects of global warming, both rising SST and ocean acidification, but their increased vulnerability is largely the result of their setting within shallow, warmer coastal waters, as opposed to a perceived lower resilience due to naturally high sedimentation and turbidity.

8. Conclusion

Geological and palaeoecological data together with modern ecological data from the GBR have provided insights into the key environmental controls that influence turbid zone reef initiation and growth. Reef initiation and growth, and therefore distribution, on the inner-shelf is largely controlled by the sedimentary regime and its driving hydrodynamic forces; specifically the balance between sedimentation and sediment resuspension. Regions of active sediment resuspension and high turbidity, but low sediment deposition, are more favourable for reef growth than settings where deposition rates are high, although regions of persistent and extreme turbidity will limit light penetration and reef growth. The availability of hard substrates was previously considered the primary control on coral reef initiation and distribution. However, turbid zone reefs have initiated on a range of substrates including mobile sediments, and, as such, have grown within a number of geomorphic settings. Spatial and temporal variations in the sedimentary and hydrodynamic regimes between settings have lead to variable rates and modes of reef growth, and, therefore, morphological development.

Turbid zone reefs are supported by distinctive community assemblages capable of withstanding high sedimentation (>50 kg/m^2/year) and turbidity (>50 mg/L) that far exceed levels generally considered detrimental to coral growth and reef development. These assemblages differ from mid- and outer-shelf reefs, and are composed of coral species (*Porites*, *Goniopora*, *Montipora*, *Galaxea*, *Turbinaria*) which have adapted to inshore sedimentary, hydrodynamic and water quality regimes. Extensive research on coral tolerances and adaptations to increased sediment loads has provided knowledge on the mechanisms by which corals can cope with sedimentation and turbidity. Differences in coral adaptations between families and species have lead to spatial variations in their distribution, with more sediment tolerant corals in protected reef regions with high sedimentation rates, and corals adapted to high turbidity in regions of high sediment resuspension. Evidence from reef cores has indicated that these coral assemblages are temporally stable over centennial timescales. These data highlight the importance of understanding ecological adaptations and interactions with environmental controls as these influence reef morphology and growth.

Turbid zone reefs have displayed a remarkable capacity to recover quickly following natural disturbance events potentially due to an inherent resilience to their marginal environmental conditions. However, an increase in the frequency and severity of disturbance events will lead to shorter intervals between disturbances and limited reef recovery. A multidisciplinary management approach is needed to address growing concerns on turbid zone reef vulnerability to increasing human pressures. This approach could involve the use of a coral threshold matrix for the effects of turbidity and sedimentation, although more research is still required to adequately assess both the spatial variability in these thresholds as well as between and within species variability. Palaeoecological and geological studies provide a temporal assessment on rates of reef growth and a context for current community change, and ecological studies provide data on coral-sedimentary interactions, which may in part explain how reefs have rapidly accreted in turbid zone settings. However, given the importance of terrigenous sediments to turbid zone reef occurrence, composition and growth, a critical step in the assessment of their future prospects will be to develop an improved understanding of the sedimentary regime through the comprehensive assessment of sedimentation rates, resuspension and sediment flux on inshore turbid zone reefs. Furthermore, more research on coral disease, recruitment and growth, measures of reef resilience, need to be conducted to improve current understanding on the effects of sediments on these ecological processes, as well as the possible synergistic effects of sediments, ocean acidification and rising sea water temperatures.

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