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Climate change impedes scleractinian corals as primary reef ecosystem engineers

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Abstract. Coral reefs are among the most diverse and productive ecosystems on our planet. Scleractinian corals function as the primary reef ecosystem engineers, constructing the framework that serves as a habitat for all other coral reef-associated organisms. However, the coral's engineering role is particularly susceptible to global climate change. Ocean warming can cause extensive mass coral bleaching, which triggers dysfunction of major engineering processes. Sub-lethal bleaching results in the reduction of both primary productivity and coral calcification. This may lead to changes in the release of organic and inorganic products, thereby altering critical biogeochemical and recycling processes in reef ecosystems. Thermal stress-induced bleaching and subsequent coral mortality, along with ocean acidification, further lead to long-term shifts in benthic community structure, changes in topographic reef complexity, and the modification of reef functioning. Such shifts may cause negative feedback loops and further modification of coral-derived inorganic and organic products. This review emphasises the critical role of scleractinian corals as reef ecosystem engineers and highlights the control of corals over key reef ecosystem goods and services, including high biodiversity, coastal protection, fishing, and tourism. Thus, climate change by impeding coral ecosystem engineers will impair the ecosystem functioning of entire reefs.

Additional keywords: bleaching, ecosystem goods and services, ocean warming and acidification.

Scleractinian corals as reef ecosystem engineers

Ecosystem engineers are organisms that modulate the availability of resources to other species by causing physical state changes in biotic or abiotic materials (Jones *et al.* 1994, 1997). Scleractinian corals act as key reef ecosystem engineers in two main ways: first, they are autogenic engineers, because through their calcification and ensuing reef accretion, they change the physical, chemical, and biological environment and thereby **provide habitats** for associated reef organisms. The generation of complex, hard, and stable substrates by scleractinian corals underpins the high biodiversity characteristic of tropical coral-reef ecosystems (Bellwood and Hughes 2001).

Second, corals also act as allogenic ecosystem engineers because they **intensively generate and transform inorganic and organic materials**. Coral-derived inorganic calcareous skeletons are transformed into calcareous reef sands by reef-associated bio-eroding organisms (such as molluscs, echinoderms, and sponges) and by other biological, physical, and

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chemical erosion processes (Glynn 1997; Hallock 1997), so that corals, through the production of inorganic materials, control adjacent sediments. These highly permeable biogenic sediments with generally large grain sizes allow intense advective coupling between the water column and the seafloor (Huettel *et al.* 2003; Rasheed *et al.* 2003; Wild *et al.* 2005*a*). Calcareous reef sands support abundant associated heterotrophic microbes (Wild *et al.* 2006). Coral-generated calcareous sediments thereby act as biocatalytic filter systems that facilitate rapid processing and recycling of organic matter (Wild *et al.* 2004*a*, 2005*a*, 2005*b*, 2008). Corals also continuously release large amounts of dissolved and particulate organic materials, which may function as energy carriers and particle traps (Wild *et al.* 2004*a*; Huettel *et al.* 2006; Naumann *et al.* 2009). This release of organic material promotes the formation of mucus–particle aggregations in the water column that increase the sedimentation and recycling rates by which essential elements are retained (Wild *et al.* 2004*b*, 2005*b*; Huettel *et al.* 2006). Consequently, a wide range of biogeochemical processes, important in coral reef functioning, are directly controlled by scleractinian corals acting as the principal ecosystem engineers.

This review sets out to expand our understanding of the impacts of global climate change on coral reef ecosystems owing to the direct impediment of the reef's primary ecosystem engineer – the scleractinian corals. Rather than focusing on the plight of corals *per se*, we chose to explore how the impacts of ocean warming and acidification may affect the corals' ability to act as engineers within this complex ecosystem. We discuss the impact of climate change on scleractinian corals at the organism level and how this translates into responses at the reef ecosystem level.

The impact of global climate change on the coral engineer

As stenothermic and calcifying organisms, corals are particularly sensitive to both ocean acidification and warming. There are several indications that carbon pollution-induced increases in ocean acidity and temperature are impacting the metabolism and growth of reef-building corals (Langdon and Atkinson 2005; De'ath *et al.* 2009; Tanzil *et al.* 2009; Manzello 2010).

Ocean acidification and coral calcification

Increasing acidity of oceanic waters represents a direct threat to reef-building scleractinian corals, with various implications for their role as ecosystem engineers. Ocean acidification is the consequence of global oceanic uptake of increasing anthropogenic atmospheric CO_2 (e.g. Kleypas *et al.* 1999). Such uptake increases CO_2 partial pressure (pCO_2) in the water column, decreases seawater pH, increases concentrations of total dissolved CO_2 ($[CO_2]$ and $[HCO_3]$), and reduces concentrations of $[CO_3^{2-}]$ in seawater (Caldeira and Wickett 2003; Feely *et al.* 2004). Physiological processes (e.g. calcification) in corals may respond to these changes in ocean chemistry (Langdon and Atkinson 2005).

The reduction in $[CO_3^{2-}]$, at constant seawater calcium concentration $[Ca^{2+}]$, consequently results in the decrease of the saturation state of aragonite (Ω_{arag}), the polymorph of $CaCO_3$ produced by coral calcification. Presently, tropical surface waters, with the exception of the eastern Pacific Ocean, are about 4-fold supersaturated with respect to aragonite (Hoegh-Guldberg *et al.* 2007). However, Ω_{arag} is expected to significantly decrease to levels of 2.5–3.0 by the year 2100 (Feely *et al.* 2009). Scleractinian corals generally require seawater that is super-saturated in aragonite for efficient aragonite accretion. In acidified seawater, lowered external Ω_{arag} impedes the essential increase of Ω_{arag} within the internal calcifying fluid, and causes a corresponding decrease in calcification rate (reviewed in Cohen and Holcomb 2009). This decrease in skeletal growth performance, caused by ocean acidification, directly translates to a decline in the engineering capacity of scleractinian corals to construct essential reef habitats.

Various studies have documented the negative effect of ocean acidification and the consequential reduction in seawater Ω_{arag} on coral calcification in both the laboratory (e.g. Anthony *et al.* 2008; Jokiel *et al.* 2008) and the field (Bak *et al.* 2009; De'ath *et al.* 2009; Tanzil *et al.* 2009). However, a very recent study (Jury *et al.*, in press) presents significant differences in calcification rates at equal $[CO_3^{2-}]$ and further suggests $[HCO_3^-]$ as a potentially more important driver for coral calcification, thereby questioning the reliability of Ω_{arag} or $[CO_3^{2-}]$ as sole predictors of the effect of ocean acidification on coral calcification. Another recent study argues that deleterious effects caused by elevated $[CO_2]$, as a result of ocean acidification, may be ameliorated by inorganic nutrient enrichment (Holcomb *et al.* 2010). These authors conclude that naturally elevated inorganic nutrient levels may thus support increased primary and secondary production, consequently facilitating coral calcification in environmenst with naturally high concentrations of CO_2. However, species-specific differences in sensitivity to ocean acidification and thermal stress may occur (Manzello 2010). This could have tremendous effects on the structure of communities in future coral reefs (Loya *et al.* 2001).

Ocean acidification can also affect coral reproduction by reducing sperm motility (Morita *et al.* 2009) or settlement and post-settlement development of planula larvae and coral recruits (Albright *et al.* 2008; Cohen *et al.* 2009). At experimentally reduced aragonite saturation states (Ω_{arag}), the early skeleton of coral recruits showed progressive changes in aragonite crystal morphology and a decline in crystal growth rate (Cohen *et al.* 2009). This implies that ocean acidification may significantly affect recruitment rates and the competitive capacity of coral populations, and may consequently lead to a shift in coral community structure. In addition, a recent study showed that spawning female corals of the temperate species *Astrangia poculata* are more susceptible to the negative effects of ocean acidification than spawning male corals (Holcomb *et al.*, in press). This gender discrimination may be a result of the energetically expensive egg production process, leaving only limited resources to compensate for the effects of acidification on calcification. On a longer time-scale, this lack of energy and growth may reduce recruitment success for gonochoric-spawning coral species.

Finally, and possibly most alarmingly, ocean acidification has been identified as a potential trigger for coral bleaching (Anthony *et al.* 2008). According to this study, branching and massive coral species experience an increase in bleaching with decreasing seawater pH (8.4–7.6) at low (25–26°C) and high

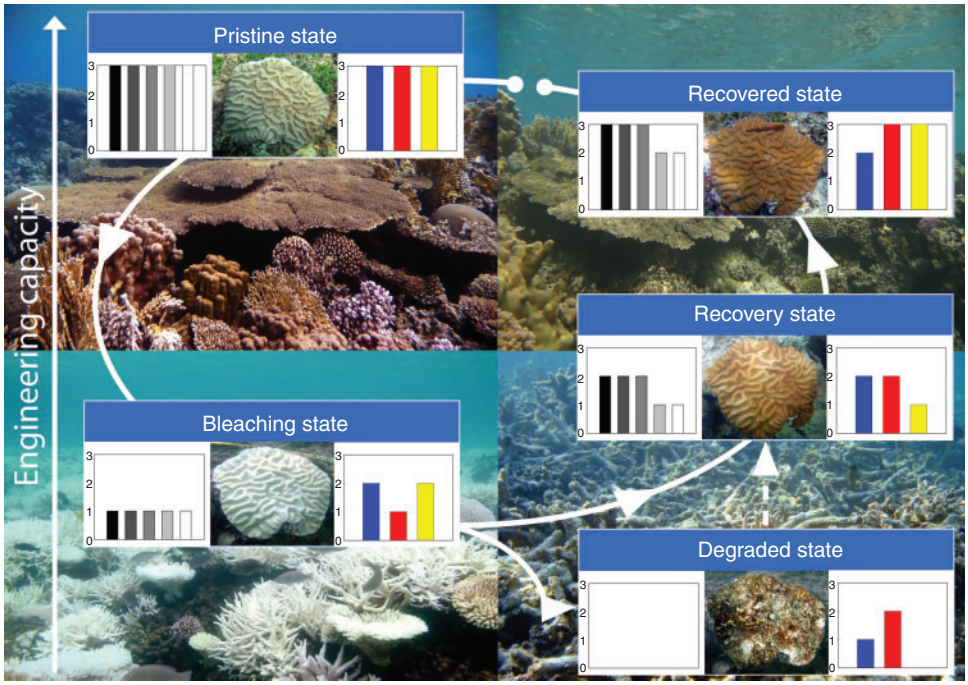

Fig. 1. Relative potential of key physiological functions and resulting ecosystem engineering capacity of corals under pre-, during and post-bleaching conditions (foreground, organism level; background, ecosystem level). Left columns: physiological functions (black to white, coral–dinoflagellate symbiosis stability, primary productivity, calcification, reproductive output, immune defence). Right columns: coral-generated reef ecosystem engineering (blue, facilitation of associated biodiversity via habitat differentiation; red, generation of biocatalytical filter systems via inorganic sediment production; yellow, impact on particle trapping and conservation of essential elements via organic matter release). Scale: 0–3, none, low, medium, high. Coral photographs are modified from Manzello *et al.* (2007) whereas reef photographs are copyright of M. S. Naumann, except that of bleached reef (copyright: R. Berkelmans; www.reefbase.org).

(28–29°C) seasonal temperatures. These findings suggest that ocean acidification may be another primary bleaching-trigger, causing similar and/or other deleterious consequences for scleractinian corals as reef ecosystem engineers.

Ocean warming and coral bleaching

Reef-building corals form a primary habitat for zooxanthellae (endosymbiotic dinoflagellates) of the genus *Symbiodinium*, which are crucial to the physiological integrity and ecological function of reef-building corals within tropical-reef systems. Coral–zooxanthellae interactions reflect a close evolutionary relationship between host and symbiont, with temporal and spatial variability allowing the coexistence of diverse symbionts within the coral host (Rowan *et al.* 1997). In the eastern Pacific Ocean, *Pocillopora verrucosa* colonies inhabiting shallow-water habitats contained different clades of zooxanthellae than *Pavona gigantea* colonies living in deeper water and more shaded habitats (Iglesias-Prieto *et al.* 2004). Similarly, *Symbiodinium* spp., within *Acropora tenuis* appear to be distributed according to light exposure, with two different types of *Symbiodinium* spp. found in sunny and shady parts of the colony, respectively (Van Oppen *et al.* 2001). Such tight interaction leads to the conclusion that the two organisms cannot be considered separately (Iglesias-Prieto *et al.* 2004).

One of the most dramatic impacts of ocean warming on coral reefs is mass coral bleaching, which is the breakdown of the symbiosis between corals and zooxanthellae. Bleaching is associated with a pronounced loss of colour from affected corals caused by the expulsion of the photopigment-rich zooxanthellae (Fig. 1). Mass coral bleaching is strongly associated with anomalously high sea-surface temperatures (Glynn 1993), but it can also be triggered by a range of other environmental stress factors (e.g. altered salinity, light, sedimentation, and toxins). Since the early 1980s, mass coral bleaching events have increased in extent and frequency in response to steadily warming ocean-water temperatures (Hoegh-Guldberg 1999).

Coral bleaching is a reversible process (Fig. 1) if the stressful conditions are relatively mild and short-term, with zooxanthellae populations inside the host tissues returning to pre-bleaching levels after 2–6 months depending on the coral species (Hoegh-Guldberg and Smith 1989; Brown 1997; Hoegh-Guldberg and Jones 1999). Bleached corals, however, are physiologically compromised because of the reduction in the abundance of zooxanthellae and/or their pigments. Under normal conditions, zooxanthellae translocate up to 95% of their photosynthetically fixed carbon to the coral host (Muscatine *et al.* 1984). They also cover 30% of the host's nitrogen requirements for growth, reproduction and maintenance (Bythell 1988) from dissolved nutrient uptake (Bythell 1990). During bleaching, the photosynthetic ability of reef-building corals is greatly reduced

(Porter *et al.* 1989; Suzuki and Kawahata 2003; Rodrigues and Grottoli 2006), leading to the depletion of energy stores, which results in 'food shortage' and starvation (Porter *et al.* 1989; Fitt *et al.* 1993).

As calcification strongly depends on the photosynthetic efficiency of the zooxanthellae within the tissues of corals (Gattuso *et al.* 1999; Allemand *et al.* 2004; Colombo-Pallotta *et al.* 2010), bleached and/or thermally stressed corals have lower growth rates (Jokiel and Coles 1977; Leder *et al.* 1991) and tissue regeneration capacities (Meesters and Bak 1993). In *Montastraea faveolata*, one of the major reef-builders of the Caribbean, bleaching reduced photosynthetic efficiency by 4.6-fold and capacity by up to 4.8-fold (Rodríguez-Román *et al.* 2006). These changes in photosynthetic activity translate directly into a decline in calcification. Calcification rates of bleached *M. annularis* colonies were only 37% of the mean annual calcification observed before bleaching (Leder *et al.* 1991). Laboratory experiments revealed that calcification rates in *Montastraea faveolata*, immediately after bleaching, can be as low as 22% of unbleached control corals (F. Colombo-Pallotta, pers. comm.).

The physiological consequences of bleaching and the time required to return to normal conditions is species-specific. Many branching corals of the genus *Acropora* die within 10 to 14 days after bleaching, whereas some massive species may show greater resistance and recover after several months (Rodrigues and Grottoli 2006; Rodrigues *et al.* 2008). Early life stages of corals seem to be particularly vulnerable to climate change stressors (Edmunds 2007), thus affecting the demographics of coral reefs. Bleaching may impact the reproductive output and planula larvae development of corals (Baird and Marshall 2002) for up to several years (Ward *et al.* 2002). The observed reduction in reproductive output of scleractinian corals that survived bleaching indicates that recovery to former levels is slow (Baird and Marshall 2002), suggesting that sub-lethal bleaching leads to long-term effects on corals and associated ecosystem functioning. Re-establishment of reef corals after major disturbance events with mass coral mortality usually takes years to decades (e.g. Loya 1976, 2004; Done 1992; Loch *et al.* 2004).

The effect of light

For corals under thermal stress, ambient light conditions can significantly affect the onset and severity of bleaching events. Low or reduced irradiance during times of high water temperature reduces photoinhibition and suppresses coral bleaching (Iglesias-Prieto *et al.* 1992; Mumby *et al.* 2001; Brown *et al.* 2002; Takahashi *et al.* 2004). By contrast, reductions in cloudiness exacerbate thermal stress. Nonetheless, the response of clouds to climate change remains one of the largest sources of uncertainty in modelling climate at regional and local scales. Some studies show that warming oceans could reduce upper-level cloudiness, particularly in the tropics, because the higher temperatures increase turnover efficiency (Mumby *et al.* 2001; Lau and Wu 2003; Lau *et al.* 2005). A cause for concern is the modelled simulations of doubled atmospheric CO_2 that predict reductions in total cloudiness, leading to greater absorption of shortwave and long-wave radiation by the oceans (Sud *et al.* 2008).

Coral immunity and diseases

Several studies have correlated climate change, in general (Harvell *et al.* 2001), or temperature anomalies, in particular (Willis *et al.* 2004; Miller *et al.* 2006; Bruno *et al.* 2007; Muller *et al.* 2008), to the increased prevalence of coral disease, and disease incidence has been shown to increase following coral bleaching (Brandt and McManus 2009). Invertebrate immunity can be reduced under starvation conditions (Feder *et al.* 1997; Moret and Schmid-Hempel 2000; Seppälä *et al.* 2008) similar to those induced during coral bleaching. Compromised coral immunity during and following a bleaching event (Fig. 1) (Mydlarz *et al.* 2009; Reed *et al.* 2010) will therefore limit the activation and efficacy of a response to invading organisms or physical injury (Meszaros and Bigger 1999; Rinkevich 1999; Stedman 2000), leading to an increase in disease prevalence following coral bleaching (Harvell *et al.* 2001; Miller *et al.* 2006).

There is also growing consensus that microbes interact strongly with corals, forming an integral part of a symbiosis that includes coral, zooxanthellae, and associated microflora. This has been referred to as the 'holobiont' to connote a biological 'unit' that operates as one, within both ecological and evolutionary time frames (Rohwer *et al.* 2002). The concept of the coral holobiont emerged following several research advances using culture-based and culture-independent molecular techniques. Coral-associated bacterial communities show greater similarity between distantly-separated colonies of the same host species than between adjacent colonies of different host species (Rohwer *et al.* 2002), implying that bacterial communities are host-coral specific. Healthy and diseased corals show distinct differences in microbial community composition (Cooney *et al.* 2002; Frias-Lopez *et al.* 2002, 2004; Ritchie 2006), including the apparently healthy tissues remote from the disease lesion of infected corals (Pantos *et al.* 2003; Pantos and Bythell 2006). This indicates that in a changing climate, there will be pronounced changes in community composition and diversity of microbes associated with corals.

Such microbial associates may perform several different functions, including that of N-fixation (Williams *et al.* 1987; Shashar *et al.* 1994; Lesser *et al.* 2004), and as an antibiotic agent in the case of bacteria associated with coral mucus (Ritchie 2006). The experimental evidence on selective properties of antibacterial substances in the mucus of the coral *Acropora palmata* (Ritchie 2006) indicates a probiotic role of bacteria in corals (Knowlton and Rohwer 2003; Pantos *et al.* 2003; Reshef *et al.* 2006; Rypien *et al.* 2010), whereby the normal microbial flora inhibits the colonisation and growth of potential pathogens via competition and release of antimicrobial compounds (Ritchie 2006; Rypien *et al.* 2010).

Reef ecosystem-level responses

Habitat provisioning by corals and effects on associated organisms

Climate change has the capacity to change reef landscapes and benthic communities. Coral-generated production of framework structures will substantially decrease with climate change-induced bleaching and subsequent reduction of coral

calcification. Such declines will influence associated organisms and significantly alter the reef's biogeochemical functioning (Fig. 1).

On a larger scale, impeding coral ecosystem engineers may cause phase shifts from scleractinian corals to other invertebrates such as gorgonians, soft corals, ascidians and sponges (Bak *et al.* 1996; Maliao *et al.* 2008) or even benthic algae (Hughes 1994; McCook 1999; Diaz-Pulido and McCook 2002; Bellwood *et al.* 2006) with obvious negative effects on provisioning of three-dimensional surfaces and habitats for associated high biodiversity. Climate change will contribute to such 'phase shifts' and potentially to long-term destruction of reef framework and changes in reef functioning (Glynn 1993; Aronson and Precht 1997; Diaz-Pulido and McCook 2002; Aronson *et al.* 2004). Dead corals are rapidly colonised by a diverse community of algae (Diaz-Pulido and McCook 2002), and living corals are directly overgrown or damaged by macroalgae (Smith *et al.* 2006; Haas *et al.* 2010). Algal colonisation of surfaces of dead or impaired corals therefore likely influences the recovery of neighbouring corals from climate change-induced stress such as bleaching of the coral engineer. This may also include dramatic changes of biogeochemical processes such as the fixation of nitrogen via coral-associated cyanobacteria. On a reef-wide scale, within weeks of a major bleaching event and mass coral mortality, the production of new nitrogen can be 30-fold greater than that associated with living corals under undisturbed conditions (Davey *et al.* 2008). Thermally-induced mortality of the coral engineer therefore has the potential to significantly alter the reef systems' overall dynamics and integrity. In addition, the loss of live tissue will affect natural recycling of nutrients within the system.

On a smaller scale, this involves changes in the scleractinian coral community. Branching, framework-building scleractinian corals including the genera *Acropora*, *Seriatopora*, *Pocillopora*, and *Stylopora* are examples of morphologies that are more sensitive to thermal stress than massive and encrusting growth forms (Marshall and Baird 2000; Loya *et al.* 2001; McClanahan *et al.* 2002). In addition, large colonies of these genera were more susceptible to thermal stress than small colonies (Loya *et al.* 2001; Mumby *et al.* 2001; Nakamura and van Woesik 2001; Bena and van Woesik 2004). Therefore, climate change will reduce the framework-building and habitat-generation capacity of reef-coral communities.

Calcifying activities of reef-building corals ultimately result in a three-dimensional matrix that provides space, shelter, and food for a multitude of organisms (Srinivasan 2003; Sale *et al.* 2005; Raes *et al.* 2007). High reef rugosity, for example where large massive *Porites* coral colonies dominate the seascape, is associated with high abundances of reef fishes (McClanahan and Shafir 1990). Similarly, a high abundance of microstructures within coral colonies is strongly and positively correlated with high fish and invertebrate diversity (Nanami and Nishihira 2004; Nanami *et al.* 2005). Reduction in rugosity reduces the availability of habitat space at a variety of scales and leads to a considerable reduction in reef biodiversity (McClanahan and Shafir 1990). In the Caribbean, the architectural complexity of reefs has already declined non-linearly over the last 40 years (Alvarez-Filip *et al.* 2009) as a combined result of climate-change effects and local disturbances.

The fate of reef corals and their community composition is not only fundamental for future reefs to maintain their ability to accrete and form coastal barriers, but also in determining whether or not they will continue to support the plethora of coral-associated diversity through time. Loss of corals and shifts in species composition reduces the variety of habitats available at macro- and micro-scales, which likely leads to subsequent losses of habitat complexity and associated biodiversity of invertebrates and fish (Reaka-Kudla 1997; Loya *et al.* 2001; Wilson *et al.* 2006). This includes obligate associates such as corallivorous fishes in the short term, but also subsequent reductions in overall fish diversity 3–4 years following a thermal stress event (Pratchett 2007; Munday *et al.* 2008).

Control of biocatalytical sand filters

The commonly observed phase-shifts from the dominance of corals to that of fleshy algae will additionally decrease the production of inorganic material in the long term, but will increase sediment-forming erosion processes in the short term, because of the breakdown of the reef framework (Fig. 1). The extent of this reef degradation is obviously dependent on the functional group of algae involved in phase shift. In areas dominated by crustose coralline algae, fragmentation of the reef framework can be mitigated by cementation and binding of sediments and loose coral fragments (Kennedy *et al.* 2002; Payri 1988). Some coralline algae species can even induce coral larval settlement, thereby facilitating new recruitment and reef recovery (Fabricius and De'ath 2001; Harrington *et al.* 2004; Golbuu and Richmond 2007). This beneficial effect may, however, depend on the extent of climate change, as crustose coralline algae are particularly sensitive to ocean warming and acidification (Anthony *et al.* 2008). Calcareous green and articulated corallines contribute less to sediment binding, although their sediment production, in particular by calcareous green algae (e.g. *Halimeda* spp.), can be high (Bach 1979; Drew 1983; Payri 1988).

Carbonate production by *Halimeda* spp. is likely quantitatively lower than that by scleractinian corals (Bosence 1989). In addition, sand and coralline sediments derived from *Halimeda* spp. are different in density and chemistry from coral-derived sediments (Borowitzka and Larkum 1977; Braga *et al.* 1996; Bosence and Wilson 2003). Therefore, these algae-generated sediments will very likely have shorter residence times, and therefore will most likely not function as biocatalytical filter systems as described for coral-generated sediments (Wild *et al.* 2005*a*, 2009; Werner *et al.* 2006).

Generation and fate of coral-derived organic material

Under undisturbed conditions, scleractinian corals release particulate organic carbon (POC) in quantities of 0.3–7.1 mg POC m^{-2} coral surface h^{-1} (Wild *et al.* 2004*a*, 2005*b*; Naumann *et al.* 2010). To date, there are no available studies on the effect of acidification on coral-derived organic matter release. However, during thermal-induced bleaching, two different kinds of organic matter are released in increased quantities: (1) zooxanthellae, and (2) coral-derived particulate organic matter (POM) (Niggl *et al.* 2009). Degradation of these substrates by reef microbes differs considerably, with very low rates observed

for symbiotic dinoflagellates (<1% h^{-1}), and high rates for coral-derived POM (>5% h^{-1}) (Wild *et al.* 2005*a*). This could indicate that a major fraction of the symbiotic dinoflagellate-composed POM does not remain in the reef system long enough to be recycled, and thus likely involves a considerable loss of essential nutrients. In contrast, the coral-derived POM may function as an energy carrier and particle trap (Wild *et al.* 2004*a*; Huettel *et al.* 2006). This material potentially stays within the system and is recycled, particularly by the benthic community. A short-term pulse of labile organic matter can result, and studies have demonstrated that this organic matter can be recycled by the planktonic and benthic reef community within two weeks (Wild *et al.* 2004*c*, 2008; Eyre *et al.* 2008; Glud *et al.* 2008).

Histological analyses (Fitt *et al.* 2009), however, indicate that internal mucus reservoirs in the coral tissue are depleted during bleaching, so that mucus–POM release by corals is most likely only stimulated during the early phase of bleaching, dropping to low levels the longer the bleaching event lasts (Fig. 1). This dynamic flux of POM was confirmed by Piggot *et al.* (2009), who demonstrated that the number of mucus-producing cells (mucocytes) in the coral tissue increases with increasing sea-surface temperatures, but declines to low levels after the initial bleaching response.

Coral bleaching thereby largely reduces the metabolic exchange between corals and associated organisms, as well as reducing the capacity of corals to trap organic matter. This may lead to further loss of POM from the reef system. Therefore, not only are corals affected by thermal stress, but the entire reef system changes and functions differently during and after a bleaching event, particularly when bleaching results in extensive coral mortality. Corals can recover from bleaching, which allows for the return of the described reef engineering functions through production of organic matter by the coral engineer (Fig. 1). The respective recovery time scales range from weeks to months (Gates 1990; Jokiel and Coles 1990), so that short- to mid-term effects on biogeochemical processes can be expected from a brief impediment of the coral engineer. However, these effects may include long-term changes in the reef's recycling capacity.

Value of coral engineer-driven reef ecosystem goods and services

Reef-building corals act as ecosystem engineers because they provide the physical structure as well as biotic and biogeochemical services to reefs (Moberg and Folke 1999). Such services are functionally similar to other ecosystem engineers such as rainforest trees, mangroves or seagrasses (Guitierrez *et al.*, in press), but usually much more persistent because of the calcareous material of the coral skeleton. However, corals will most likely be the ecosystem engineers most affected by climate change because they are comparatively slow-growing, stenothermic and calcifying organisms, and therefore particularly susceptible to ocean warming and acidification. Global climate change, especially ocean warming that includes coral bleaching, impedes the engineering capacity of scleractinian corals (Fig. 1). This also includes the loss of reef ecosystem services for coastal protection, tourism, and productivity.

Protection of coastal areas and their high associated biodiversity strongly depend on the production of inorganic material by scleractinian corals. These reef structures can absorb 70–90% of wind-generated wave energy (Wells *et al.* 2006) and differentiate habitats and physical environments that influence biological diversity at all scales. The attraction of coral reefs for tourism is probably a reflection of such coral-driven biodiversity.

The total annual economic value of coral reefs via ecosystem services has been estimated at least USD100 000–600 000 km^{-2} (Wells *et al.* 2006). The impediment of corals as reef engineers will drastically reduce these economic values, even without consideration of the ecological values (e.g. high biodiversity) if reefs are further degraded under climate change.

Coral engineer-controlled reef biodiversity also has an increasing economic importance for the delivery of new biologically active molecules (e.g. Fung *et al.* 1997; Fung and Ding 1998) that are being developed as pharmaceuticals. Reef productivity and ensuing fishery biomass largely depend on the production of scleractinian corals, but also on their reef-engineering functions including the initiation of biogeochemical processes, leading to rapid recycling, and conservation of essential elements, such as nitrogen and phosphorus.

Conclusions

This review indicates that anthropogenic climate change has the potential to drive major changes across the entire reef ecosystem and indeed is already doing so (Fig. 1). These fundamental changes have the ability to cause both reversible and irreversible changes to reef ecosystem functioning. As part of these interactions, several related aspects are likely to feed back on the role that corals play as ecosystem engineers. Bleaching-induced death of the coral engineers includes the generation of bare skeletons that are particularly sensitive to physical, chemical and biological erosion processes (Stoddart 1969). In addition, colonisation of these stable surfaces by microbial biofilms, algae or other invertebrates may not only reduce recruitment success (e.g. Webster *et al.* 2004), but also change the biogeochemical processes such as nitrogen fixation (Davey *et al.* 2008).

The initiation of carbon and nutrient cycles by coral-derived organic matter will likely be significantly reduced in warmer oceans (Fig. 1), which may alter nutrient dynamics to favour other organisms such as cyanobacteria rather than corals.

Production of calcareous reef sands will probably increase immediately after bleaching-induced mass coral mortality as a result of increased erosion. However, this is a short-term effect lasting only until the carbonate supply diminishes. At large scales, a net loss in carbonate accretion will hypothetically influence the biocatalytic filter systems so that the processing of imported organic matter, for example via eutrophication or river discharge, is reduced (Fig. 1). This may ultimately decrease reef resilience and increase vulnerability of coral-reef ecosystems.

Similar, but not as pronounced, feedback effects on the coral engineer can be expected during and after sub-lethal bleaching (Fig. 1). As the energetic status of corals will be affected, less energy may be invested in the production of inorganic and

organic matter, including carbonates, secondary metabolites, and antibiotic substances (Ritchie 2006) that prevent overgrowth by other organisms and promote resistance against pathogens. Such reductions may change the diversity and activity of coral-associated organisms, which consequently may overgrow or infect corals so that recovery from bleaching is suppressed.

The impacts of global climate change on fundamental physiological processes such as scleractinian coral growth, calcification, defence, maintenance and reproduction result in broad-scale consequences for ecosystem functions and services provided by the reef-building coral engineers. Reduced growth and reproduction translate directly to a reduced resilience of coral-dominated reef communities. Similarly, compromised immune systems and reduction in competitive abilities (Mydlarz *et al.* 2009; Reed *et al.* 2010) lead to fundamental changes in the community structure of tropical benthic assemblages (Hoegh-Guldberg *et al.* 2007). The consequences of reduced calcification rates as a result of ocean warming and acidification will manifest as a reduction in skeletal extension (Jokiel *et al.* 2008), changes in skeletal crystal morphology (Cohen *et al.* 2009) or, hypothetically, the formation of less dense skeletons that are highly susceptible to rapid physico–chemical and biological erosion.

Such deleterious impacts of climate change will thereby modify the ability of scleractinian corals to maintain their engineering roles in coral-reef ecosystems. Global influences will also interact with more local and direct disturbances to exacerbate the adverse effects of overfishing and declining water quality (Hughes *et al.* 2007) that additionally impede the functioning of corals as reef ecosystem engineers.

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