

Impacts of nutrient enrichment on coral reefs: new perspectives and implications for coastal management and reef survival[☆]

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Anthropogenic nutrient enrichment is often associated with coral reef decline. Consequently, there is a large consent that increased nutrient influxes in reef waters have negative longterm consequences for corals. However, the mechanisms by which dissolved inorganic nutrients can disturb corals and their symbiotic algae are subject to controversial debate. Herein, we discuss recent studies that demonstrate how nutrient enrichment affects the heat and light stress tolerance of corals and their bleaching susceptibility. We integrate direct and indirect effects of nutrient enrichment on corals in a model that explains why healthy coral reefs can exist over a rather broad range of natural nutrient environments at the lower end of the concentration scale and that anthropogenic nutrient enrichment can disturb the finely balanced processes via multiple pathways. We conceptualise that corals can suffer from secondary negative nutrient effects due to the alteration of their natural nutrient environment by increased phytoplankton loads. In this context, we suggest that phytoplankton represents a likely vector that can translate nutrients effects, induced for instance by coastal run-off, into nutrient stress on coral reefs in considerable distance to the site of primary nutrient enrichment. The presented synthesis of the literature suggests that the effects of nutrient enrichment and eutrophication beyond certain thresholds are negative for the physiological performance of the coral individual and for ecosystem functioning. Hence, the immediate implementation of knowledge-based nutrient management strategies is crucial for coral reef survival.

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Introduction

The presence of humans in the proximity of coral reefs usually results in an elevated input of nutrients into reef waters. Nutrients associated with human activities, importantly nitrogen and phosphorus compounds, are introduced in various forms: they reach the marine environment as organic and inorganic compounds, they can be dissolved in the water or contained in sediments or in particulate organic matter and can enter reef ecosystems via riverine influx, via diffuse discharge or as aeolian dust [1,2[☆],3[☆],4,5]. Consequently, the decline of coral reefs close to urbanised areas or to agriculturally or industrially exploited regions has been considered to be promoted by anthropogenic nutrient enrichment of reef waters [3[☆],6[☆],7[☆],8].

However, it has proven unexpectedly difficult to provide experimental evidence for the negative effects of nutrient enrichment, particularly of dissolved inorganic nutrients, on coral physiology. Hence, the mechanisms by which nitrification might promote coral reef decline became subject to intense and controversial debate [9[☆],10[☆]]. The lack of scientific consensus was considered responsible for wrong management decisions that resulted in regional coral reef degradation [10[☆],11]. In some areas, for instance in the Great Barrier Reef, nutrient management has been improved, but even there, water quality still remains a largely unresolved issue [1,2[☆]]. Elsewhere, major problems persist and the increasing human population will further aggravate the situation by continued coastal development, land and fertiliser usage. For instance, modelling suggests that human deforestation might outweigh future climate change impacts of sedimentation on major coral reef ecosystems in Madagascar [12]. Unfortunately, the most desirable nutrient management, namely the reduction of the nutrient input to natural levels will often be technically impossible or cost prohibitive. Therefore, knowledge-based optimisation of nutrient management becomes crucial for coral reef conservation [2[☆],13]. As we will discuss in this paper, recent scientific results show that increased nutrient levels can reduce the heat stress tolerance of corals, which assigns critical importance to local management of water quality in order to mitigate the pressure of global warming and climate change. We will revisit some longstanding problems of coral nutrient biology and discuss them in the light of these recent findings, focussing mostly on issues associated with dissolved inorganic nutrients (*Dissolved Inorganic Nitrogen* [DIN: NH₄⁺, NO₂⁻, NO₃⁻] and phosphate [PO₄³⁻]). Although the discussion of various other forms of nutrients, especially in particulate form or dissolved as organic

nitrogen or phosphorus compounds is not within the scope of this review, we point out that they deserve further attention since some are readily taken up by corals and can contribute significantly to coral reef nutrient budgets [14–17]. Also, nutrient issues are often closely related to sedimentation, a topic that is reviewed by Risk in the present volume.

Here, we introduce conceptual models with the intention to promote a constructive progress in understanding the immensely complex nutrient biology of coral reefs. Considering a broad diversity of potential nutrient effects that might vary dramatically over space and time will certainly be key to the development of successful nutrient management strategies.

Direct and indirect effects of dissolved inorganic nutrients

Hermatypic scleractinian corals, the habitat forming species of shallow, warm water coral reefs, depend vitally on the symbiotic relationship with dinoflagellate algae (zooxanthellae) contained in the host tissue [18,19]. The demand of zooxanthellae for the typical plant nutrients, importantly nitrogen and phosphorus compounds, makes the coral holobiont responsive to the nutrient environment [20]. Corals and other cnidarians seem able to restrict the access of nutrients such as phosphate to their zooxanthellae [21,22], but this capacity appears to be limited since zooxanthellae have been often shown to react to nutrient enrichment of the water [3,23]. While there is a general consent that certain nutrient levels are required for coral growth [20], the effects of elevated concentrations of dissolved inorganic nutrients on coral reefs, however, are subject to intense debate. One reason for the controversy is the fact that coral reefs can exist over a range of nutrient concentrations and are not necessarily restricted to extremely oligotrophic waters [9,24]. Here we show that conflicts arising from apparently contradictory findings can often be avoided by strictly separating the discussion of direct effects of nutrient enrichment on coral physiology and the indirect effects provoked by nutrient-driven processes outside of the coral.

Direct effects of nutrient enrichment

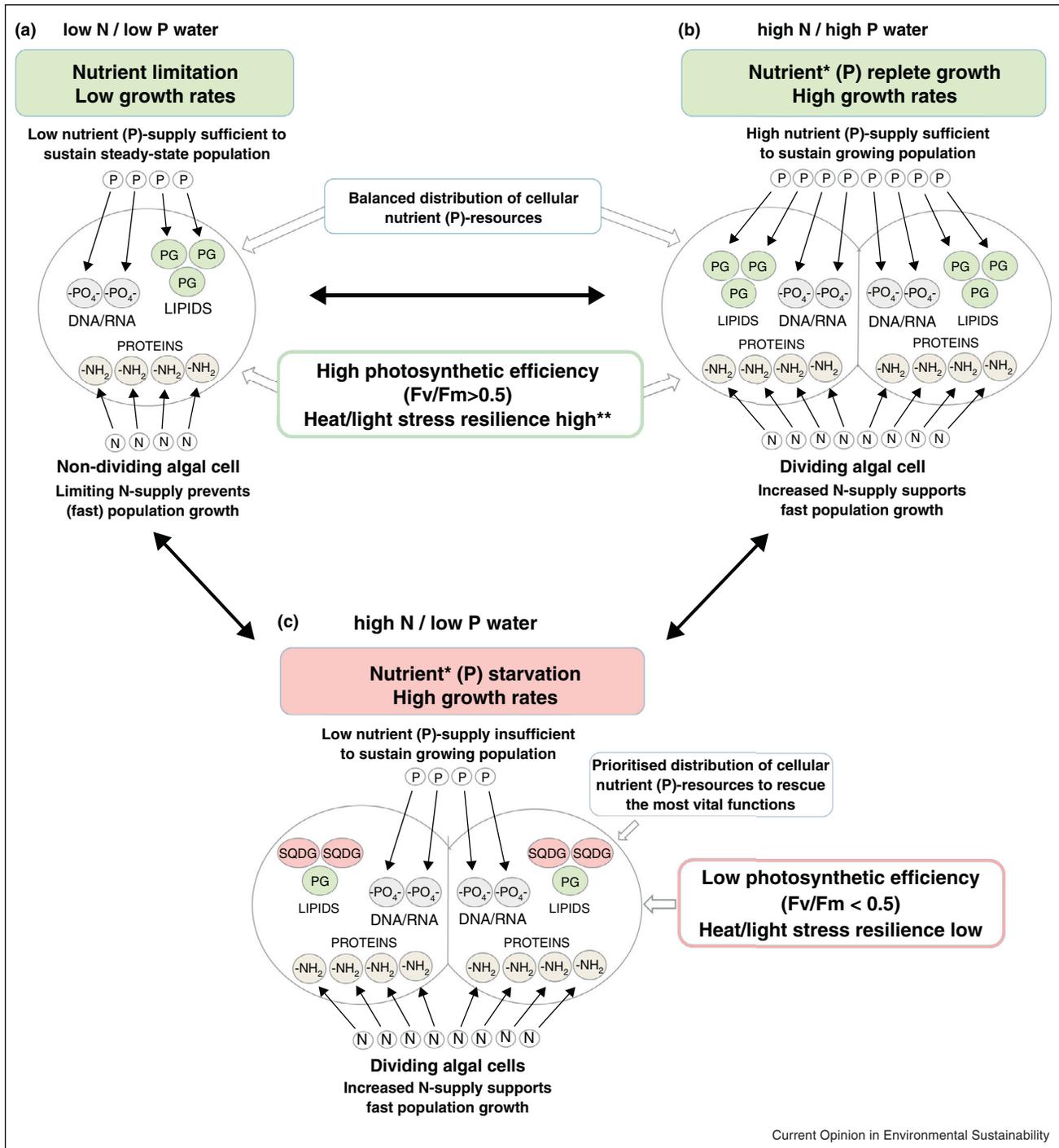
Experimental exposure to elevated nutrient concentrations can induce a number of negative responses of corals such as reduced reproductive success, calcification rates, skeletal density or linear extension [3,23,25,26,27]. However, several studies did not reveal direct negative effects of increased nutrient levels on coral physiology or found them only at unnaturally high concentrations [3,9]. We have recently shown that increased nutrient levels might not negatively affect the physiological performance of zooxanthellae as long as all essential nutrients are available at sufficient concentrations to ensure their chemically balanced growth [28]. These results could explain why some reefs and the nutritional

status and metabolism of their inhabitants do not always show negative responses to eutrophication [29,30], at least in the absence of temperature and light stress.

In yet some other cases, corals responded positively to the addition of nutrients, for instance by increased growth [25,31,32] or by a reduced susceptibility to the end-of-summer bleaching, the seasonal loss of corals' zooxanthellae [33]. Refuges from heat stress-mediated bleaching were found in regions with small-scale upwelling [34]. The water from greater depths might not only provide cooling effects [34], but may also supply dissolved inorganic nutrients [35].

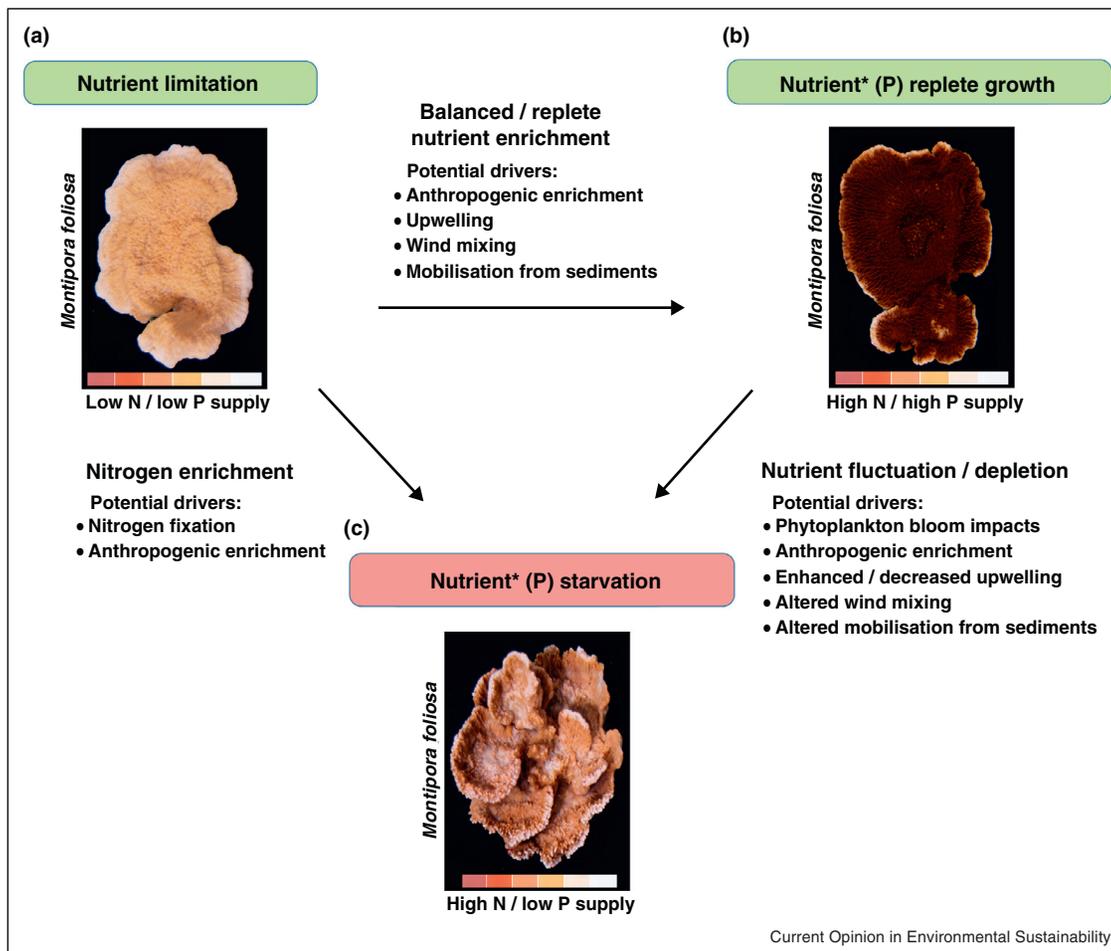
A number of studies found that elevated nitrogen levels in the water promoted zooxanthellae growth and resulted in higher zooxanthellae densities without obvious negative effects on the corals (see review by Fabricius [3]). Most recently, however, we could demonstrate that corals exposed to elevated nitrogen levels were more susceptible to bleaching when exposed to heat and light stress [28]. Interestingly, the detrimental effects observed in these experiments could be attributed to the relative undersupply of phosphorus that resulted from the enhanced demand of the proliferating zooxanthellae population rather than to the elevated nitrogen levels themselves (Figures 1 and 2). While we established this nutrient starvation syndrome for high nitrogen/ambient phosphorus conditions, we postulate that negative effects might also arise from other forms of chemically imbalanced zooxanthellae growth during which vital compounds become undersupplied, including trace elements or micronutrients such as iron. This view is supported by a previous study that showed that experimental iron depletion reduced the photosynthetic efficiency of zooxanthellae from *Stylophora pistillata*, in particular under heat stress [36]. Another study showed that high zooxanthellae densities that might result from nutrient enrichment render corals more susceptible to bleaching [37]. Mechanistically, bleaching of corals harbouring nutrient-starved zooxanthellae or high algal stocks is thought to be mediated by reactive oxygen species (ROS). An increased ROS production may be associated with a nutrient-driven alteration of the lipid compositions of zooxanthellae membranes (e.g. by higher sulfolipid [sulphoquinovosyldiacylglycerol, SQDG] to phospholipid [phosphatidylglycerol, PG] ratios) (Figure 1) [28] or result from a larger number of ROS producing units (algal cells) [37]. Higher algal densities might also facilitate bleaching by increasing the light absorption and consequently, the temperature of the coral colony [38,39]. Furthermore, enhanced zooxanthellae growth rates promoted by elevated nutrient levels were suggested to promote coral bleaching by inducing a CO₂-limitation of the symbiotic algae [40]. Elevated nitrogen levels can stimulate zooxanthellae growth with the potential downstream effects discussed

Figure 1



Negative direct effects of high nitrogen availability on zooxanthellae growth and heat and light stress resistance of corals according to Wiedenmann *et al.* [28*]. **(a)** Under nutrient limitation in a steady-state population where the growth rate is determined by the rate of nutrient supply, zooxanthellae are fully acclimated and show no signs of photosynthetic stress ($F_v/F_m > 0.5$). **(b)** Under nutrient-replete conditions, growth rates are increased. Since all essential nutrients including iron/trace elements (*) and phosphorus (P) are supplied in sufficient amounts, the cellular biochemical composition remains stable and under experimental conditions, the photosynthetic capacity and stress resistance are normal. (**) Possible negative side-effects of high zooxanthellae densities are discussed in the text. **(c)** Undersupply of growing zooxanthellae populations with P or other essential nutrients including iron/trace elements (*) can result in nutrient starvation of the algae. P starvation, can be induced by the transition of zooxanthellae from a nutrient-limited to a nutrient starved state due to an increased cellular P demand caused by growth rates being accelerated by elevated nitrogen supply. Under this condition, zooxanthellae replace phospholipids [phosphatidylglycerol, PG] by sulfolipids [sulphoquinovosyldiacylglycerol, SQDG]. P starvation reduces the photosynthetic capacity ($F_v/F_m < 0.5$) and renders the corals susceptible to heat/light stress. Alternatively, P starvation might result when zooxanthellae growing under nutrient replete conditions are deprived of P while nitrogen levels remain high.

Figure 2



Potential anthropogenic and natural drivers of transitions between water conditions that might cause nutrient limitation (a), nutrient replete growth (b) or nutrient starvation (c) of zooxanthellae. References are given in the text. Nutrients include phosphorus (P), iron and trace elements (*). Photographs show the appearance of *Montipora foliosa* cultured under the respective nutrient conditions. The coral colour is dominated by variation in the zooxanthellae density [28*]. Colour scales are provided under the coral images to facilitate the comparison of their colours.

here. On the other hand, increased phosphate concentrations can accelerate, for instance, coral growth, but also reduce skeletal density, rendering the corals more brittle and susceptible to mechanical damage [25]. Hence, it is important to consider that direct effects of nitrogen or phosphorus enrichment may be substantially different (see also [3*] for review). Several natural and anthropogenic drivers have the potential to alter the nutrient environment (see [41] and references therein) and induce shifts between nutrient limited, nutrient replete and nutrient starved conditions (Figure 2). Relevant processes include changes in upwelling and water mixing regime [35,42,43], alterations in the mobilisation from sediments (e.g. by trawling, dredging, storm mixing) [44,45], production (nitrogen fixation) or removal (denitrification, assimilation) by organisms such as bacteria and phytoplankton [46,47] and various forms of anthropogenic disturbances [3*]. Summarising the direct effect

of nutrients on corals, the results of different studies clearly suggest that very low nutrient levels are not necessarily optimal for all aspects of their physiological performance. However, levels beyond certain thresholds can have fatal direct effects on the physiology of the coral holobiont, especially under heat and light stress.

Indirect effects of nutrient enrichment

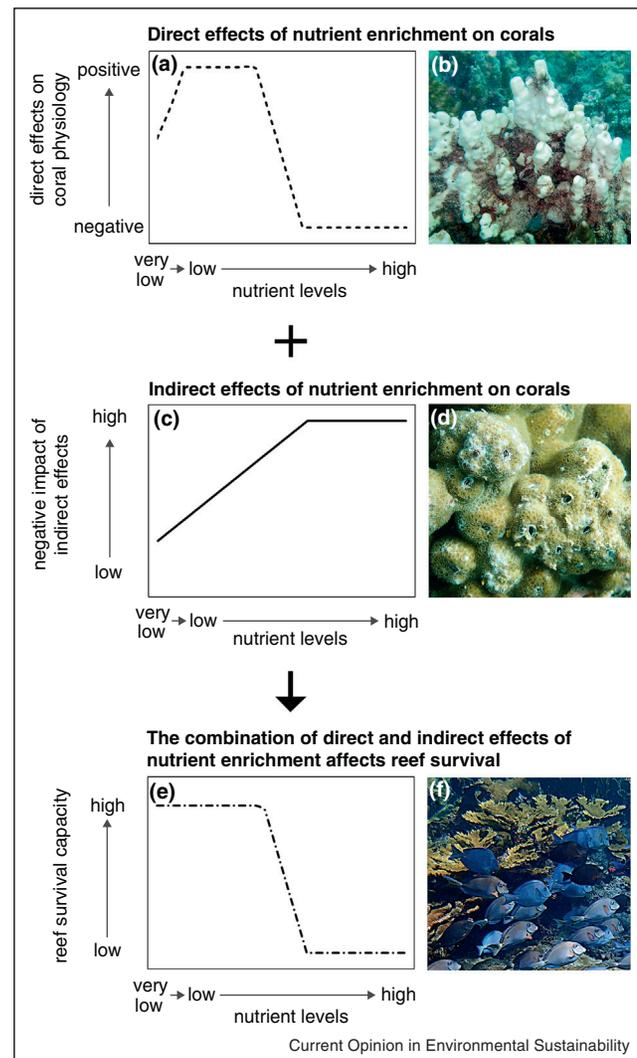
On the positive side, the increased productivity of nutrient enriched waters might benefit corals for instance by an increased availability of particulate food [3*,14,48,49]. Moreover, the sun screening provided by phytoplankton in the water column might potentially help corals in situations during which their functioning is negatively affected by light stress [50]. However, several studies from recent years have demonstrated that a range of indirect negative effects of elevated nutrient levels can contribute to coral reef decline. For example, nutrient

enrichment can increase the productivity of coral reef macroalgae [51], and has been consequently associated with increases in macroalgal densities on coral reefs [52,53*,54,55]. While the replacement of corals by macroalgae may often indicate previous coral mortality due to external drivers rather than competitive overgrowth, once established, the algal cover can lead to competitive inhibition of coral recruitment [56]. Furthermore, macroalgae can negatively affect corals by shading/overtopping, reducing water exchange, and causing mechanical abrasion or chemical disturbance [56,57]. Unusually strong upwelling of nutrient-rich waters in the Gulf of Eilat induced algal blooms and resulted in thick mats of filamentous algae covering of the reef and in extensive coral death [57]. A nutrification-mediated increase in phytoplankton abundance can supply more food for larvae of the crown-of-thorns starfish (*Acanthaster planci*), thereby promoting devastating invasions by the corallivorous adults [58*,59]. At the same time, the increased plankton load stimulates the proliferation of filter feeders and bioeroders that can represent space competitors for corals or endanger their structural integrity [53*,60–61] but see [62]. This can be of particular concern when the corals' growth rates are reduced due to elevated nutrient levels [23*], weakening those parts of their innate immune response that rely on active overgrowth of epizoic and endolithic competitors [63]. High phytoplankton densities may impose light limitation to zooxanthellae and result in reduced calcification rates (see [27] and references therein). Finally, the increase of nutrient levels in reef waters can be considered to contribute to the spread of coral diseases [64–66]. All indirect negative effects can potentially be subject to top-down control, but as the reef health becomes more and more dependent on such control mechanisms it also becomes more susceptible to disturbances. Insufficient top-down control may have catastrophic consequences for reef ecosystems as exemplified by the removal of grazers by overfishing or die-outs [67].

Synthesis of direct and indirect effects of nutrient enrichment

We have integrated both, the direct and indirect effects of nutrification in a conceptual model of reef resilience and survival (Figure 3). This model considers that in very oligotrophic waters, corals' physiological performance may not be at their highest levels in all aspects, for example, coral growth rates may not be at their maximum [25] (Figure 3a). However, under these conditions, the reef benefits from the absence of many negative indirect nutrient effects and the associated higher independence from top-down control processes. The abundance of corallivorous *Acanthaster*, for instance, would also be restricted by the lack of phytoplankton as food for its larvae [58*] and not only by its predators (Figure 3b). Moreover, low nutrient levels could limit the growth of macroalgae, in addition to top-down control by herbivores

Figure 3



Conceptual model of reef coral resilience and survival under the combined impact of direct and indirect effects of elevated nutrient levels. (a) The performance of corals can be sub-optimal at very low nutrient levels and benefits from a slight enrichment. However, higher concentrations of nutrients in the water can have direct negative effects on the corals, for example, by increasing their susceptibility to heat stress. (b) Coral bleaching in waters influenced by urban pollution and coastal development, Saadiyat Reef, UAE, September 2012. (c) With higher nutrient levels, the coral reef ecosystem becomes more dependent on the top down control of indirect negative nutrient effects and accordingly vulnerable to disturbances. (d) Increased nutrient input stimulates plankton loads that promote filter feeders and bioeroders. These can represent space competitors for corals or endanger their structural integrity. Here, *Porites* sp. is deformed by a high load of filter feeding parasitic barnacles, Gulf of Oman, September 2012. (e) Direct and indirect effects act together to define coral reef resilience and survival. The individual contribution of these components will probably vary depending, for instance, on the regional nutrient environment, the species assemblage and seasonal changes. Importantly, both direct and indirect effects become negative at higher nutrient levels and put reef survival at risk. (f) In healthy coral reefs, top down control processes can restrict the potential negative impacts of elevated nutrient levels. The image shows a coral (*A. palmata*) – herbivoric fish assemblage in Curaçao, May 2013.

[52]. Slightly increased nutrient levels may result in a better physiological performance of corals, for instance, in increased growth [25]. At the same time the stronger impact of indirect negative effects and the increasing dependence on top-down control might neutralise the positive direct nutrient effects on coral physiology in the context of the overall reef performance [68]. Importantly, at higher nutrient concentrations, direct nutrient effects may also provoke negative responses such as an increase in bleaching susceptibility [28^{*}]. Together with the indirect negative effects that prevail at higher nutrient concentrations, the direct high-nutrient driven negative effects act together to promote coral reef decline (Figure 3c). This model can help to explain why healthy coral reefs can exist over a relatively broad range of natural nutrient environments at the lower end of the concentration scale and that anthropogenic nutrient enrichment can disturb the finely balanced processes via multiple pathways.

Primary and secondary effects of nutrient enrichment on the nutrient environment of reef corals

The fast assimilation of nutrients by phytoplankton limits the geographical range of direct effects of newly introduced nutrients on coral reefs [69^{*}]. Accordingly, it has been difficult to correlate negative effects of increased dissolved inorganic nutrients on coral communities beyond local scales [3^{*}]. Hence, the impression might be generated that nutrient enrichment may not affect coral communities further away from the nutrient source. Here, we discuss why this is not always the case and why we consider phytoplankton to be an important key to the understanding of long-range nutrient effects on coral reefs.

Primary effects of newly introduced dissolved inorganic nutrients

Newly introduced dissolved inorganic nutrients are often taken up rapidly and turned over by plankton communities [69^{*}]. Consequently, the phytoplankton density, usually measured as chlorophyll concentration in the water column, represents a robust indicator of increased nitrification [69^{*},70]. The fast removal of nutrients may suggest that the direct effects of nutrient enrichment on coral physiology are only relevant within a short range from the source. However, recent findings from the Great Barrier Reef demonstrate that nutrients in flood plumes can be transported over distances >50 km, exposing even distant reefs to temporally elevated nutrient spikes. This long-range transport is facilitated when high sediment loads of the plume impose light limitation to the nutrient-enriched water body and prevent the assimilation of nutrients by phytoplankton [2^{*}]. Corals take up nitrogen compounds effectively within hours [71,72] and their phosphate uptake rates (half-saturation constants ~0.38–1.08 μM) [73,74] fall in the same range, for

instance, as those of the bloom-forming cyanobacterium *Trichodesmium* spp. (0.1–0.6 μM ; [75]). Hence, if coral reefs are located in an area in which the primary introduction of nutrients promotes phytoplankton growth, it is likely that these conditions will also, at least to a certain extent, stimulate the proliferation of zooxanthellae. This assumption is supported by the finding that corals from habitats with lower water quality hosted higher numbers of algal symbionts [60,105]. As discussed above, the accelerated zooxanthellae proliferation can result in a higher susceptibility to heat and light stress-mediated bleaching [28^{*},37^{*}] and other direct negative effects on coral physiology. In fact, the studies by Wagner *et al.* and Wooldridge [6^{*},7^{*}] correlate elevated nitrogen levels and increased phytoplankton densities with higher coral bleaching prevalence at the regional scale.

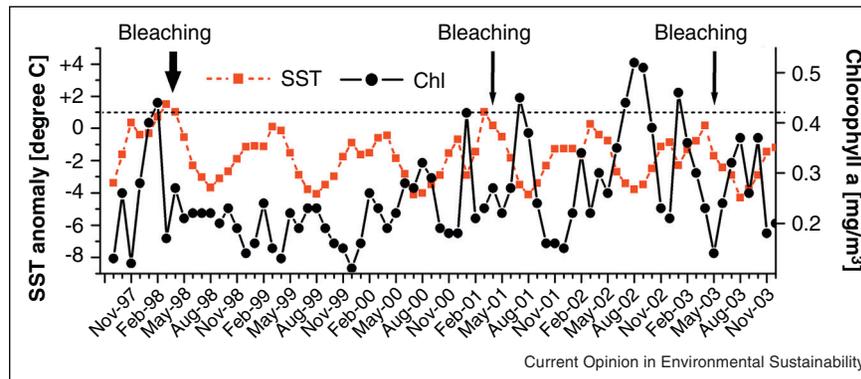
Secondary nutrient effects mediated by phytoplankton: a key to the understanding of nutrient enrichment

Increased nutrient loads and altered nitrogen to phosphorus ratios due to human activities in river catchment areas frequently result in algal blooms and altered phytoplankton communities in coastal waters [47,76,77]. As shown for the Great Barrier Reef and the so-called “blackwater events” in Florida bight, phytoplankton blooms induced by coastal run-off can drift over large distances before they reach coral reefs [2^{*},78^{*},79^{*}]. In the Florida bight, coral communities were impacted by phytoplankton blooms and their decay products [78^{*},79^{*}]. In 2002, the region was affected for more than two months, resulting in increased coral mortality [78^{*}].

As a consequence of coastal algal blooms, primary production can become limited by single or multiple nutrients or can be affected by nutrient ratios shifting over time and space. For example, a depletion of dissolved inorganic phosphorus in coastal waters can be observed in the aftermath of phytoplankton blooms that were induced by enhanced concentrations of DIN [47,76,77]. Hence, the pelagic algae might temporarily reduce DIN, phosphate or iron concentrations below normal levels, resulting in a reduced availability of these essential nutrients for the benthic corals. Both the absolute and the relative depletion of iron and phosphate were recently shown to increase the stress susceptibility of zooxanthellae and to promote coral bleaching [28^{*},36]. Moreover, a recent experimental study yielded the counterintuitive finding that nitrate enrichment in the presence of phytoplankton resulted in lower measurable nitrate concentrations in the water and increased coral mortality as compared to un-enriched controls [80].

In the Great Barrier Reef, some phytoplankton blooms, promoted by increased iron and phosphate influx in coastal waters, are formed by nitrogen-fixing *Trichodesmium* spp. that might release newly formed bioavailable nitrogen [46,70], especially towards the end of a bloom.

Figure 4



Time courses of monthly averages of chlorophyll *a* concentration (Chl) and sea surface temperature (SST) deviations from the long-term average of the warmest month in waters surrounding the coral reefs of Kenya. The local bleaching threshold [103] is indicated by a dashed line. Documented bleaching events [85] are highlighted by arrows (fat arrows symbolise severe bleaching). Monthly composites of sea surface temperature (SST) and the average chlorophyll *a* concentrations for each site were calculated from products of the Advanced Very High Resolution Radiometer Sensor (AVHRRS) and the Sea-Viewing Wide Field-of-View Sensor (SeaWiFS).

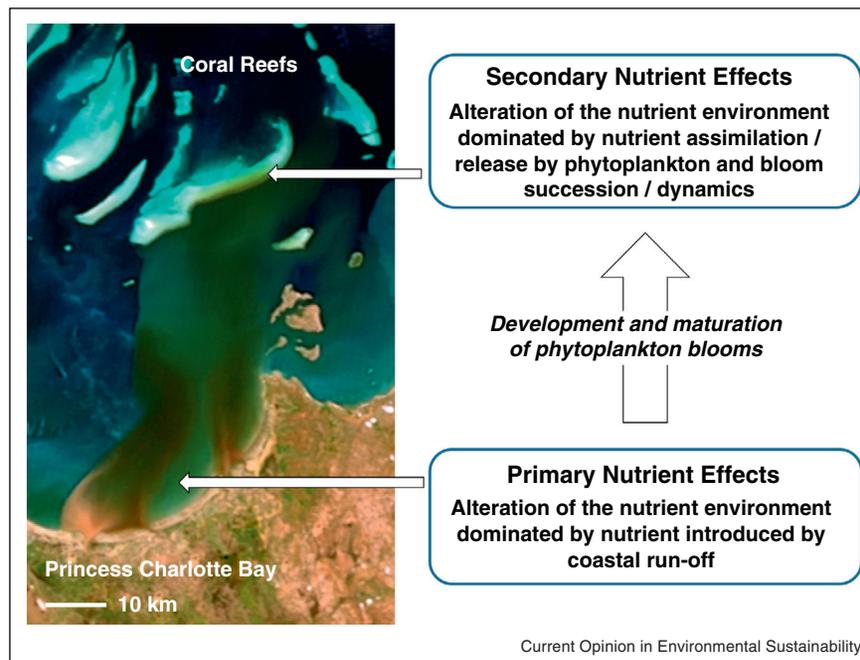
Studies around Fiji and Tonga correlated *Trichodesmium* blooms with a mesoscale decrease of surface phosphate [81]. We analysed remote sensing data of the Kenyan coast to further assess whether phytoplankton blooms can be associated with coral bleaching. *Trichodesmium* blooms have been recorded from East African waters [82,83,84] and corals in this region were severely affected by mass bleaching in 1998 and over the following years [85,86]. We aligned changes in the chlorophyll *a* concentration with the local sea surface temperature and the reported bleaching events (Figure 4). The data suggest that bleaching occurred when high temperatures followed a steep decline of previously elevated chlorophyll *a* levels indicative of a breakdown of phytoplankton blooms. These blooms reached their maximum in January–February, around the time when *Trichodesmium* spp. is most abundant in East-African coastal waters [82,83,84]. Interestingly, the remote sensing data of the sea surface temperature suggest that bleaching in 2003 occurred after temperatures had risen, but not above the local bleaching threshold temperature. The *Trichodesmium* blooms reported for the East African coast were correlated with elevated nitrate levels in the water, which persisted unusually long in the mass bleaching year 1998 [82,83]. In contrast, phosphate levels showed less pronounced seasonal variations, but tended to be reduced when nitrate levels were elevated [83]. As described above, water conditions featuring elevated nitrogen levels together with low phosphorus (or iron) concentrations, were experimentally shown to induce nutrient starvation of zooxanthellae and increase bleaching susceptibility [28]. Hence, these data are consistent with our hypothesis that the alteration of the nutrient environment associated with phytoplankton blooms may increase susceptibility of corals to heat stress and consequent

bleaching. We conceptualise that corals can suffer from secondary negative nutrient effects due to the alteration of their natural nutrient environment by increased phytoplankton loads that result from an initial introduction of dissolved inorganic nutrients (Figure 5). However, we note that high phytoplankton densities can disturb corals also by other mechanisms such as smothering with mucus derived from algal cells, the release of algal toxins, oxygen depletion and high amounts of decomposing organic material [87] that may increase the risk of bacterial and fungal infections [88]. The above discussed extensive coral mortality in the Gulf of Eilat caused by an upwelling event that increased the nutrient levels in the surface waters was also accompanied by large phytoplankton blooms. The negative effects for the reefs, though, were dominated by the covering of the corals with benthic algal mats [57].

Future challenges of coral reefs nutrient biology

Defining nutrient concentrations or nutrient ratios that represent thresholds for the different direct and indirect nutrient effects on coral reefs and to introduce optimised target values that promote reef resilience are important tasks for nutrient biology research. When assessing the impact of nutrient enrichment on coral physiology in the field, it should be considered that some effects could be subtle and might become detectable only after long-term exposure or under distinct circumstances, for example, during periods of stress. Importantly, many effects may vary locally depending on the regional reef water biogeochemistry. In the Great Barrier Reef, for instance, many processes are nitrogen-limited [69], whereas phosphorus availability seems to be limiting in other sites such as Discovery Bay, Jamaica [52]. The data reported by

Figure 5



Conceptual model of primary and secondary nutrient effects on coral reef ecosystems. The potential disturbances of the natural nutrient environment of coral reefs resulting from phytoplankton blooms triggered by coastal run-off are superimposed to a NASA satellite image that reveals that even the outer areas of the Great Barrier Reef can be exposed to land-based pollution carried offshore by river plumes [104]. Depending on environmental factors such as the sediment load of the bloom, the nutrients in the plume will be sooner or later taken up by phytoplankton [2^{*}]. At a later stage, the nutrient environment of the receiving water will be affected by the dynamics and successions of the phytoplankton bloom and its decay products. NASA image courtesy of the MODIS Rapid Response Team, Goddard Space Flight Center.

Lugomela *et al.* [83^{*}] suggest that in yet another case, the East African waters, nutrient limitation might switch seasonally between nitrogen and phosphorus. Accordingly, the effects of nutrients on different coral reef ecosystems may vary significantly and need to be assessed individually.

Further experimental studies are required to refine the mechanistic understanding of nutrient effects on the physiology of the coral holobiont and to characterise secondary nutrient stress caused by elevated phytoplankton densities. In particular, the understanding of the combined effects of the disturbance of nutrient levels induced by phytoplankton blooms and other post-bloom changes including increases of decomposing organic matter and bacterial load and altered oxygen levels needs to be furthered. Such studies, including remote sensing approaches, should consider reefs from different geographical locations to evaluate the influence of the above mentioned regional conditions. It will be crucial to maintain long-term monitoring programs of nutrient levels in order to establish baselines and to assess the efficiency of management activities. The data sets are mandatory to correlate the physiological status of corals (especially during disturbance events such as bleaching) with the underlying water chemistry. The results of nutrient

monitoring will also be required to ground truth the output of remote sensing products that record chlorophyll concentrations as measure of nutrient fluctuations.

Future assessment of nutrient effects on coral reefs will strongly involve the optimal utilization of bioindicators. Recently, a substantial array of water quality indicators was evaluated and yielded promising candidates [53^{*},60,89]. Among others, changes in macroalgal cover and the colouration/symbiont density of *Porites* colonies showed good correlations with water quality [53^{*},60,89]. The photosynthetic pigment content of zooxanthellae is often modulated by light intensity whereas zooxanthellae growth rates and densities can be nutrient dependent [20^{*}]. Since the latter can be mechanistically related to coral stress susceptibility, the determination of zooxanthellae numbers of suitable model corals, their mitotic indices and photosynthetic pigment levels can serve as “high-content” bioindicators. Enzymatic markers such as phosphatase activity along with the photosynthetic capacity of zooxanthellae (Fv/Fm) promise to be helpful in characterising the nutrient status of individual corals [22,28^{*},90]. As exemplified by the mass spectrometric analysis of the zooxanthellae lipidome from nutrient stressed corals [28^{*}], advanced molecular analyses can provide biomarkers for distinct nutrient conditions.

Finally, the green-fluorescent protein-like pigments of the coral host represent excellent markers of environmental conditions [63,91] and might be potentially useful to characterise the nutrient status of corals by non-invasive monitoring.

Implications for coral reef management and the future of coral reefs

We have discussed recent findings that demonstrate that elevated levels of dissolved inorganic nutrients can have severe negative effects on the physiology of corals, in particular when the balance between different types of nutrients is shifted [28]. Imbalanced nutrient levels can result, for instance, from nitrogen loaded run-off in areas of pronounced fertiliser usage or by enhanced nitrogen fixation due to elevated phosphate influxes and have severe direct effects on the thermal bleaching threshold of corals. Here, we have presented a model that integrates direct nutrient effects on the coral performance and indirect negative impacts that result from eutrophication of the reef waters. Importantly, high nutrient levels negatively affect corals concerning both, direct and indirect effects. Hence, management strategies should aim for sustaining top-down control processes as well as reducing the nutrient influx in seawater, closely considering that the balance between different nutrients has a strong influence on coral physiology. Top-down control processes that can reduce the impact of negative indirect effects of elevated nutrient levels involve distinct fish assemblages [92,93]. Consequently, the implementation of sustainable fishing practices, the specific protection of fish species fulfilling ecological key roles along with the establishment of no-take-zones to promote species diversity are important management actions to support reef health [92,94–96]. Also, other groups of reef animals including sea urchins, holothurians, crustaceans, and molluscs can positively contribute to reef health as grazers of benthic algae, detritivores, or predators of corallivorous species such as *Acanthaster planci* and should be considered for specific protection [67,97,98]. Phytoplankton blooms induced by the anthropogenic introduction of nutrients can be suspected to alter the nutrient environment of coral reefs in a negative way and may not simply “neutralise” the impact of nutrients by taking them up from the water column. Depending on the involved algal species, phytoplankton blooms might, for instance, convert elevated phosphate levels into higher nitrogen levels or deplete essential nutrients including iron that are required by the corals for normal functioning. Hence, future management strategies should consider the differences between primary nutrient effects and secondary direct nutrient effects induced by the resulting increase in phytoplankton biomass. Regionally, the reduction of either DIN or phosphate pollution might have different effects [99] and hence, management strategies should evaluate whether the reduction of one or the other or of both types of nutrients is most effective in promoting

coral reef resilience. In some cases, corals might already benefit from controlling the nutrient load before and during seasons with high levels of heat stress. Management action should cover all dominant sources of anthropogenic nutrient enrichment, considering that there might be large distances between the source (e.g. a river catchment area) and the impacted reefs [2,78,79]. Measures to reduce the nutrient influx in reef waters can include the reduction of urban pollution by tertiary waste water treatment, changes in agricultural practice such as reduction of fertiliser usage, the control of deforestation and land use for grazing and finally, the restoration of wetlands and riparian buffers [1,2,12,13,99,100]. Moreover, aquaculture practices in the proximity of coral reefs need to be evaluated for their impact on the nutrient environment [26]. A close collaboration between multidisciplinary teams of researchers, engineers, coral reef management and policy makers is required to refine and develop a range of efficient nutrient management strategies that will be of utmost importance for coral reef survival. Since coral reefs are declining at a fast rate [101,102], it is important that action is taken immediately. Otherwise, there might be no reefs left that could benefit from the efforts.

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