Safeguarding nutrients from coral reefs under climate change

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Abstract

The sustainability of coral reef fisheries is jeopardized by complex and interacting social-ecological stressors that undermine their contribution to food and nutrition security. Climate change has emerged as one of the key stressors threatening coral reefs and their fish-associated services. How fish nutrient concentrations respond to warming oceans remains unclear but is likely affected by both direct (metabolism, trophodynamics) and indirect (habitat, species range shifts) effects. Climate-driven coral habitat loss can cause changes in fish abundance and biomass, revealing potential 'winners' and 'losers' among major fisheries targets that can be predicted using ecological indicators and biological traits. A critical next step is to extend research focused on the quantity of available food (fish biomass) to also consider its nutritional quality, which is relevant to progress in the fields of food security and malnutrition. Biological traits are robust predictors of fish nutrient content, and thus potentially indicate how climate-driven changes are expected to impact nutrient availability within future food webs on coral reefs. Here we outline future research priorities and an anticipatory framework towards sustainable reef fisheries contributing to nutrition-sensitive food systems in a warming ocean.

The world's coral reefs support extraordinary biodiversity and provide essential ecosystem services, including food and income to over 500 million people[1], and up to 90% of animal protein in some countries across the Pacific and Indian Oceans[2-4]. Small-scale reef fisheries are particularly crucial in coastal and rural areas where they often provide the majority of fish consumed[5], and are socially and culturally important[6]. Aquatic foods are a unique dietary source of iodine, vitamin D, and the long-chained n-3 fatty acids eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), and are also a valuable source of bioavailable micronutrients, including iron, zinc, vitamin A, and B_{12}[7]. Deficiencies of these micronutrients are linked to a growing 'triple burden of malnutrition', which refers to the coexistence of overnutrition, undernutrition, and micronutrient deficiencies, responsible for impaired cognitive development and accounting for a million premature deaths per year[8-10]. Fish therefore hold potential to help address these deficiencies, particularly where nutrient intakes are inadequate[8,11] (Fig. 1A). However, coral reefs are highly vulnerable to both overfishing[12] and climate change[13], stressing the need to better understand the current, and potential future, contributions of coral reef fisheries to human health[11].

Global development has led to complex shifts in food supply and demand through increases in wealth, human population size, urbanisation, and the globalization of trade and transport. Through the global fish trade, reef fish can now be sold at high prices in European seafood markets and luxury restaurants[14] (Fig. 1B, C), while the aquarium trade can target species caught by small-scale fishers, some of which would have been consumed locally[15]. These globalising markets erode reef fish biomass, resulting in catch declines that can force fishers to travel further offshore, increasing inequalities between those who can afford larger and more powerful boats to maintain production and those who cannot[16]. Global demand for reef fish through trade also drives market prices up, which can make fish unaffordable for local consumers[17]. In parallel, diets in these countries can be influenced by preferences shifting towards a greater demand for meat and a reliance on imported, often processed or high-starch root crop foods characterized by lower nutrient quality[18,19], potentially heightening the risk of metabolic diseases and micronutrient deficiencies[11,19]. Together, the rapidly changing socioeconomic context, as is characteristic in tropical regions, simultaneously exacerbates declines in nutrient-rich foods, particularly where nutrient gaps (e.g., East Africa)[8] and increases in diet-related diseases (e.g., Pacific islands)[10] are apparent[11].

Essential ecosystem services under pressure from climate change

Socioeconomic pressures on coral reefs, including overfishing and the global fish trade, are exacerbated by climate-driven coral bleaching and other ongoing environmental stresses, including extreme weather events (e.g., tropical cyclones, tsunamis), sea level rise, reduced water quality, ocean acidification, and invasive species (Fig. 2). Of particular concern, increasingly frequent and severe marine heatwaves disrupt the provision of ecosystem services, with foundational species such as reef-building corals among the most affected taxa[21]. Although algal growth following coral loss can support higher biomass[22-24] and productivity[25] of herbivorous species under moderate fishing pressure, the resulting catch instability that can arise from spatiotemporal variation in reef recovery[22] has the potential to negatively impact local market supply chains, including fisher incomes and consumer access to seafood, with potential implications for food and nutrient intakes.

Importantly, climate change and human activities interact in many ways, reinforcing pressures on coral reefs that ultimately threaten both ecosystem structure and functioning (Fig. 2). For example, herbivore depletion through overharvesting can impede post-bleaching coral recovery[13], especially on reefs where structural complexity has been degraded[26]. In turn, the loss of reef structural complexity can reduce recruitment of juvenile fishes and the replenishment of fish stocks[27]. The consequences of interactions between climate change and other human-driven processes range from the collapse of reef structure and associated fish stocks[28] to novel benthic communities dominated by stress-tolerant and 'weedy' taxa, where some ecological functions can persist to some extent[29,30], to increased prevalence of toxic microalgae and ciguatoxins[31].

Future climate projections unanimously predict that without immediate intervention to reduce harmful greenhouse gas emissions, most ecosystem services provided by coral reefs will be severely degraded by the end of the century[32]. Such detrimental effects of climate change on seafood production in the world's poorest countries will not be counteracted by agricultural production, since 90% of the world's population are projected to experience losses of food production in both sectors simultaneously[33]. Understanding how nutrient availability from coral reef fisheries respond to environmental change will offer potential pathways for maintaining and even boosting access to nutrient-dense seafood under climate change. Managing these fisheries so that they sustain or even increase the nutritional value of harvested stocks in the face of global warming will have many benefits for human health. These potential benefits likely apply to all coral reef fisheries, not only those targeting coral reef finfish (the focus of this paper) but also those including other reef organisms such as algae and invertebrates, for which data are severely lacking.

Here, we outline the key ecological knowledge gaps and research priorities required to support the future potential contribution of coral reef fisheries to food and nutrition security under climate change. We focus on the impacts of a warming ocean, including both gradual warming and acute marine heatwaves, which have been identified as the primary drivers of coral reef habitat loss[34]. We argue that coral reef management practices currently focusing on fish stocks must be reorientated to sustain and protect nutritional benefits as well. This needs robust projections for the species that are the most likely to provide essential nutrients in warmer oceans and the knowledge of functional traits that characterize them. Achieving this objective requires understanding the environmental factors and trophic pathways that underpin macro- and micronutrient concentrations in fishes, and how these are likely to change in a warmer ocean with degraded coral reefs. Looking forward, we propose an anticipatory approach for defining safe operating spaces for multiple ecological and social objectives. These much-needed advances are now ready for development and will form the cornerstone of future management interventions to minimize impacts, and to improve the adaptive capacity of human societies that rely on coral reef fisheries for food and nutrition.

Unlocking the trophic pathways behind fish nutrient quality in warmer oceans

Environmental determinants of fish nutrient profiles

Recent research has revealed the environmental and biotic correlates of fish nutrient content at the species level (e.g., diet; energetic demand; thermal regime)[35], shedding light on the determinants of interspecific variability in nutrient quality. However, the extent to which nutrient profiles differ intra-specifically over space (e.g., at biogeographic scales) or time (in response to global warming) is still poorly known. A better understanding is required of the potential mechanisms by which fishes accumulate their nutrients, and how these mechanisms respond to thermal stress and habitat loss, both directly (trophodynamics, metabolism) or indirectly (fish microbiome). Trophodynamics determine the flow of energy and nutrients through food webs, and thus can predict how fish assimilate bioavailable nutrients or synthesize them from other precursors[36]. Importantly, fish diet composition and metabolic rates, two major determinants of the nature and strength of trophic pathways, might both be affected by global warming.

Fishes primarily derive nutrients from diet, and diet composition is impacted by climate-driven changes in food composition and availability across multiple pathways, including primary and secondary producers. Ocean biogeochemical dynamics such as changes in light, temperature and nutrient availability can differentially affect the composition and abundance of phytoplankton communities[37], and microphytobenthos, including *Gambierdiscus toxicus*, the ciguatera-producing dinoflagellate[38]. Secondary producers may also respond to changing habitats independently from changes in primary producers. For example, dominant epifaunal crustacean taxa vary massively between live coral habitats and dead coral rubble, especially in terms of size structure and productivity[39]. Changes in nutrient profiles of primary and secondary producers can propagate through the food web to higher trophic levels[40] and, in turn, have consequences for the structure and nutrition profile of fish populations and fishery stocks[41]. For example, warmer temperatures reduce fatty acid production in phytoplankton[41-43]. Because plankton is the main source of omega-3 for fishes, this would ratchet down the omega-3 levels in most species, including apex predators[44].

Most fish species are characterized by mixed diets, suggesting a degree of versatility and opportunism as available food sources change in response to coral bleaching and habitat loss[45,46]. Likewise, some tropical species are moving towards temperate areas as oceans warm[47-49], leading to novel biotic interactions including potential competition between temperate, sub-tropical, and tropical species. This implies a degree of adaptability in fish diet for at least some fish species, in particular ecological generalists[50], likely driving a shift in their nutrient concentration. This also suggests the existence of dynamic spatial gradients in fish nutrient profiles at biogeographic scales, which have so far remained largely unexplored.

Metabolism is predominantly driven by temperature, which determines the rate at which food is processed and assimilated by biological organisms, and further translates to somatic growth[51]. Warmer temperatures induce faster exothermic biogeochemical reactions and higher metabolic rates, and thus faster and less efficient biomass transfer across the food web, especially in tropical ecosystems[52]. This is because, at each trophic level, large energy losses are induced by respiration and metabolic processes that scale with temperature. Yet, whether nutrient assimilation efficiency at each trophic level will similarly be affected by warmer temperatures remains unknown.

Microbiomes can also play an indirect yet likely important role in the way that fish assimilate nutrients but remain a key gap in our understanding of reef trophodynamics. In particular, little is known regarding the environmental drivers of fish hindgut microbiome composition, although a recent study suggests high regional variability in fish gastrointestinal microbial composition and associated nutritional outcomes[53]. For corals, microbial community composition can be affected by thermal stress, leading to a metabolic shift from autotrophy to heterotrophy, and altered metabolism of fatty acids, contributing to a deterioration in coral health[54]. Altogether, these examples suggest that microbiomes can be influenced by environmental variation at various stages of trophodynamic pathways that determine fish nutrient profiles, but more research is required to assess the generality of these results and embed them into trophodynamic ecosystem models.

Climate impacts on potential nutrient yields from multispecies fisheries

Nutrient changes at the species level scale up to determine community-level nutrient concentrations, with the potential to globally affect the nutritional quality of multispecies fisheries, for instance through enriched iron and zinc concentrations in fish living on regime-shifted macroalgal reefs[55] (Box 1). This is influenced by compositional shifts in fish communities, with some species declining in abundance (losers) in response to marine heatwaves and other climate drivers, while others can increase (winners) due to more abundant and better-quality food resources[22,25], greater stress tolerance, competitiveness or better ability to recolonize habitats after a disturbance[50]. The species composition of fisheries catches determines their nutritional quality, according to predictable interspecific variation in fish nutrient levels[35], implying that climate-driven compositional shifts are likely to impact the potential of fisheries to supply key nutrients in support of human health. For example, browsing herbivores (e.g., rabbitfishes, family Siganidae) are relatively rich in iron, whereas piscivores have the highest omega-3 concentrations among reef fishes[56,57]. Therefore, iron content may rise in fishery catches following climate-driven increases in herbivore biomass, whether through (*i*) increased algal productivity after coral mortality[23] or (*ii*) increased temperature placing herbivorous species closer to their thermal optima (e.g. in higher latitude reefs and subtropical regions) and, thus optimal fitness[24,58]. In contrast, size-based food web models predict declines in piscivore productivity following the collapse of coral habitat structure and subsequent declines in prey populations[28], which may reduce omega-3 fatty acids in fishery catches.

The long-term implications of climate change for nutrients supplied by reef fisheries will ultimately depend on how fish populations from different species collectively respond to the combination of warming (gradual and more frequent extreme events) and habitat changes (including reductions in primary production, ocean acidification and deoxygenation[59]). By 2050, the combination of poleward species redistributions, declines in habitat suitability, reduced species richness along the equator (as some species exceed maximum thermal limits)[60], and reduced primary productivity is expected to decrease global fisheries catch potential[61], diminishing nutrient yields from coral reefs[62]. Collectively, gradual warming and more frequent marine heatwaves will modify the rates at which fish assimilate energy and nutrients, influencing the quantity and quality of multispecies catches in warmer oceans, and substantially altering the future contribution of reef fisheries to both food and nutrition security.

Indicators of nutrient availability from climate-impacted reefs

Information on inter and intra-specific shifts in reef fish nutritional quality is fundamental to understanding the effect of environmental change on nutrient production from coral reef fisheries. However, our capacity to effectively monitor shifts in fisheries nutrient production will rely on careful selection of biological traits and ecological indicators that can reveal the vulnerability of coral communities to climate impacts and subsequent responses of fish communities[63].

Biological traits relevant to diet, thermal regime or energetic demand are strong predictors of the nutrient profile of fish species[35]. Furthermore, the response of fish communities to changes in coral composition and associated structural complexity likely depends on species traits rather than taxonomic composition *per se*. Species traits represent a suite of 'Essential Biodiversity Variables'[64] that can reflect trophic ecology, metabolic theory, or life history strategy, and thereby provide novel indicators to monitor the capacity of reef ecosystems to support essential ecological functions linked to ecosystem services such as food and nutrition security (Box 2). Yet, many of the potential relationships between biological traits, pressures and habitat types, and consequences on the nutritional quality of reef fisheries remain to be explored, particularly from the perspectives of sustainability and resilience of ecosystem processes and services[65] (but see e.g. Maire et al. 2021[66]) (Table 1).

Understanding how changes in reef habitats will impact nutrient supply requires quantifying the degree to which each species (or trait) relies on healthy coral reefs, and their ability to cope with alternative reef ecosystem states. Reef health assessments have typically focused on total live hard coral cover, an essential indicator[67] of reef condition that allows for cross-comparisons among regions and ecosystems when measuring the impact of chronic and acute disturbances on coral reefs. However, climate-induced changes in total hard coral cover can obscure changes in coral community composition, e.g., from the dominance of fast-growing, branching and tabular species that are important providers of three-dimensional habitat, to depauperate communities dominated by taxa with simpler morphologies and slower growth rates[30]. It follows that fish species that are not particularly reliant on a specific coral habitat tend to have a competitive advantage over habitat specialists as benthic communities shift in composition[50]. Therefore, an important remaining question is whether the extent of habitat specialisation, potentially inducing diet specialisation, can also predict fish nutrient profile. If so, a community-weighted mean of the species generalisation index[50] could provide an important tool to track nutritional changes at the community level in response to changes in benthic habitats.

The structural complexity of a coral reef, built by the living coral veneer and sustained by the underlying old reef matrix, is a key determinant of reef fish abundance and diversity[68] with potentially important implications in terms of nutrition. For example, the scale of complexity in hard reef structure affects where abundance peaks occur in the size spectrum of fish present on the reef[69]. Following coral mortality, reef structure can remain intact in the short-term, sustaining fish communities aside from specialist species that require live coral for food or shelter. However, reef structures dominated by dead corals are vulnerable to physical and biological erosion, and may begin to collapse within five years[70]. Subsequent loss of structural complexity can drive declines in fish diversity by 50%[71], homogenise community composition among habitat types[72], and change fish size structure by depleting abundances of small-bodied individuals[73]. Size-based food web models predict that such changes to benthic structure could result in a 35% decline in fisheries productivity[28]. Moreover, turf and macroalgae can proliferate after coral mortality and loss of reef structure, forming alternate benthic regimes that typically support bottom-heavy trophic pyramids[74]. Non-linear relationships between algal cover and herbivore biomass[75] suggest the existence of benthic thresholds triggering shifts in fish community composition, which may help to better predict the biomass, productivity and nutritional quality after coral mortality (Box 1).

While evidence suggests that higher functional redundancy (i.e., higher number of species with similar ecological functions) can initially buffer communities against the detrimental impact of disturbances[76,77], the general trend over time is a loss of functional redundancy[76] and biotic homogenisation[50,72] in response to habitat degradation under increasing disturbance regimes. However, the consequences for nutritional quality at the community level remain unknown, and future research will need to assess which species traits matter most for predicting winners and losers from a nutrition perspective (Box 2; Table 1). While nutrient profiles have been predicted from phylogeny[78] and traits[35], only one study has related nutrient profiles to traits that reflect species vulnerability to environmental changes[66]. This information is necessary to determine how coral and fish traits can be used to derive conservation and resource management policies in the face of changing climate[79], in particular those relevant to future food and nutrition security from coral reef fisheries[35] (Box 2). It will also help prioritize the indicators that long-term monitoring programs should focus on in the future and determine the taxonomic scope and resolution required for making such inferences. For example, collecting data on benthic cover at the species level can be extremely difficult and time consuming, whereas automated image analysis might provide a cost-effective proxy of habitat condition for predicting nutritional outcomes. A key priority for future research should thus focus on using existing, extensive datasets[57,80] to identify the most reliable and cost-effective ecological indicators of fish community nutritional responses to climate change (Box 2; Table 1).

Balancing food security, ecosystem functioning and other socio-ecological goals

The ecological management of multi-species fisheries on tropical reefs is challenging because fisheries and landing sites are widely dispersed, catches are often unreported[81], and formal governance, monitoring, and management are often lacking[82]. However, the need for sustainable reef fisheries has motivated the search of solutions through alternative fisheries-independent biomass-based models, showing that fishing can be compatible with the maintenance of key ecosystem functions[83]. These approaches have typically aggregated fish communities into either total biomass[83] or trophic group biomass[12] and used space-for-time substitutions of large observational datasets to infer temporal dynamics. Consistently, such work has shown that, out of a total unfished biomass averaging ~1000 kg/ha[12], fishing down to approximately 50% of total unfished biomass tends to maintain important reef ecosystem structure and function[83] and that there are clear benefits from having some form of reef management in place[12,84].

Maximizing sustainable production while maintaining ecosystem functioning is a major goal in coral reef fisheries science, but it is not the only one. Maximizing economic yield, incorporating socio-cultural dimensions, and addressing nutrient deficiencies[35] are important goals that also need to be considered where coral reef fisheries operate. This broad range of objectives and the potential for synergies and trade-offs among them, raises the importance of defining a safe operating space for coral reefs informed by multiple social and ecological dimensions (Fig. 3). Within this framework, boundaries that delineate safe operating spaces need to be jointly defined based on indicators for multiple dimensions. For example, a safe zone is one that allows for sustainable yield while delivering nutritional quality, and still preserving functional diversity. Monitoring of indicators and targets relevant to each goal, and comparison to safe zone boundaries will be necessary to assess the overall performance and sustainability of coral reef fisheries and will ultimately support efforts to maximise synergies and minimise trade-offs. The combination of maximum sustainable yield, maximum economic yield, and recent developments in modelling maximum nutrient yield for fisheries now provides an interdisciplinary framework for comparing nutritional outcomes with other ecological and socio-economic objectives[85].

A key question for reef fisheries management is how models of reef fisheries and biomass-based targets should be adapted to incorporate potential nutritional benefits while handling uncertainty surrounding the future composition and abundance of reef fish communities impacted by ongoing environmental changes[86]. These multi-species models will need to account for future changes in fish nutritional content as well as food safety parameters that, while beyond the scope of this paper, are likely to change with e.g., increasing levels of methylmercury in warmer oceans[87]. A critical first step will be to collate comprehensive food composition and safety databases from small-scale domestic fisheries, along with country-specific statistics on catches, local consumption, and consumer preferences (Table 1), which are still crucially lacking in many coral reef countries.

Temperature-dependent models[88] that also account for species range shifts[89] and life history traits[90] will then be needed to project future changes in fisheries contributions to food and nutrition security, and accounting for associated uncertainty (Box 2). For example, work from temperate ecosystems has shown that the direction and magnitude of the expected maximum sustainable yield is sensitive to factors such as taxonomy, ecoregion, and life history[88], providing promising insights for coral reef fisheries. Together, a combination of these approaches and their spatially explicit extensions will help identify which target species are most susceptible (losers) to negative impacts and which ones will thrive (winners) under future environmental changes (Box 1).

This knowledge will contribute to a better understanding of how future environmental changes will alter the ecological capacity of coral reef fisheries, their associated nutrient supply, and the flows of these nutrients to consumers. These data will allow fisheries management to be governed not only by ecological and economic priorities, but also through the lens of human nutritional vulnerability and needs, in order to harness the species that will thrive to their fullest nutritional potential (Table 1). Enhancing the contribution coral reefs can make to future food and nutrition security will ultimately need a holistic approach that incorporates improved local management of small-scale domestic fisheries[84] and agriculture with integrated and targeted programs that provide vulnerable societies with healthy and sustainable diets[18], such as socio-economic incentives, nutrition-sensitive policies, and integration into education[18], as well as public nutrition (e.g. schools) programs[91]. At larger scales, inclusion of food and nutrition security experts into the development of international trade agreements will be essential to ensure nutrient-rich catches are retained for vulnerable populations[17] and provide a key resource in addressing nutrient deficiencies (Table 1).

Conclusion

Coral reef fisheries represent an important resource for addressing micronutrient deficiencies, particularly in countries where reef dependency is high, and these deficiencies are most acute. Yet, the complex interplay between climate change and other social-ecological stressors are increasingly impacting reef ecosystem structure and functioning, with major consequences for ecosystem services that support food provision and nutrition. Our capacity to adapt to novel fish communities based on fewer or different coral reefs will rely on a better understanding of the modified trophic pathways that will affect the nutrient profiles of fished species, and how these changes will propagate from individual fish to entire communities, throughout food webs. Transdisciplinary approaches are required to fill knowledge gaps and inform fisheries management policies, from the collection of baseline data on catches and domestic consumption of reef-based seafoods, to the identification of safe operating spaces for future coral reef fisheries, and their uptake in the management of local fisheries and regulation of trade and export markets. Addressing such key priorities will provide important opportunities towards much needed “nutrition-sensitive” approaches to fisheries management and conservation.

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Author contributions

C.M. conceptualized the structure and content of the manuscript after discussion with C.C.H. and N.A.J.G. C.M. wrote an initial draft. D.A.F., C.D.G., M.K., M.A.M., E.M., S.M., D.M., K.L.N., J.O.O., J.P.W.R., R.D.S.-S., J.Z.-M., G.J.E. expanded upon the ideas, and engaged in discussion and editing of the final manuscript.

Competing interests

The authors declare no competing interests.

Figure legends

Figure 1. **Addressing inadequate micronutrient intake in coral reef countries requires policies that integrate the global fish trade dynamics with food and nutrition security policy**. (a) Risk of inadequate micronutrient intake (%) (average across seven nutrients and reproduced from Golden et al. 2021[11]) in coastal countries is often high for countries with coral reefs (data from UNEP-WCMC[20]; in cyan). Countries with no maritime Exclusive Economic Zone are shown in light grey, and countries smaller than 25,000km^2 are shown as dots. (b) Blue-barred parrotfish (*Scarus ghobban*) sold in France and (c) red snapper (*Lutjanus spp.*) sold in London, both more than 3,500-km from their closest potential point of capture (based on the shortest great-circle distance to the Red Sea; photos from J. Robinson and E. Maire).

Figure 2. **Impacts of climate change and other human stressors on access to reef-based food and nutrition.** Amplification of social-ecological stressors linked to global change (blue) disrupts the provision of ecosystem services provided by coral reefs (green) in support of food and nutrition security. As human activities continue to increase greenhouse gas emissions, pollution and overharvesting (blue arrow), safeguarding food and nutrition security traditionally supported by healthy coral reefs (green arrow) will require adaptation to novel coral reef communities and the identification of 'winners' vs. 'losers' among fish species, not only in terms of biomass but also nutritional value. Images from Shutterstock.com; used with permission.

Figure 3. Safe operating spaces for coral reef fisheries and interactions between multiple indicators. (a) Safe operating spaces for multiple dimensions of coral reef fisheries, including ecosystem structure and function, ecosystem services, and social goals. Colours of the different dimensions of coral reef fisheries correspond to their status in relation to the boundaries, e.g., reef habitats are shaded red as in this example they have crossed the ecological ceiling (red boundary) and are now in such a depauperate state that irreversible changes have occurred. Safe zones (green) and boundaries (orange) need to be jointly defined for multiple interacting dimensions, as illustrated in (b). (b) Examples of interactions between indicators of three dimensions include trade-offs (e.g., functional richness declines with increasing catch biomass), synergies (e.g., mean calcium concentration of the catch increases with increasing functional richness), or scale dependent interactions (e.g., mean calcium

concentration of the catch is higher at intermediate levels of catch biomass). Status of each dimension (a), relationships between indicators and green 'safe' zones (b) are illustrative only.

Box 1: Pathways to nutritional gains and losses on climate-impacted coral reefs

Climate-driven loss of coral habitat is expected to change the nutritional value of coral reef fisheries. Coral bleaching and mortality following heat stress can transform reef habitats into low complexity, algal-dominated states, which reroute nutrient pathways in reef food webs[92] and alter the productivity and composition of fish communities[25]. Nutrient yields on climate-impacted reefs will thus be determined by the effects of these processes on fish nutrient content, both among (changes in species compositions) and within (changes in the energy sources that determine an individual's nutrient content) species.

Fish gain micronutrients from their diet, implying that nutrient levels in fish will be influenced by changes to nutrient pathways (within-species effects), while the availability of nutritious target species will depend on the productivity and composition of reef fish communities in post-bleaching reef habitats (among-species effects). Evidence from Seychelles suggests that disruption of nutrient pathways may have a greater influence on nutrient levels than species compositional changes[55]. In Seychelles, a mass coral bleaching event in 1998 caused >95% coral mortality, collapsing reef habitat and, on some reefs, provoking macroalgal regime shifts[13]. Such benthic turnover altered trophic pathways[45], likely because macroalgae replaced plankton as the primary energy nutrient input to the reef food web. Fish on regime-shifted macroalgal reefs had greater iron and zinc concentrations than fish caught on nearby recovering coral reefs, possibly due to greater contributions of mineral-rich tropical seaweeds[93] to primary production.

Reef fish communities also became less diverse after bleaching, forming bottom-heavy trophic pyramids [13,22,74] with enhanced biomass of herbivorous scrapers (Scarinae) and browsers (Siganidae) that are targeted by small-scale trap fisheries[23]. Although browsers were abundant on macroalgal reefs, scraping herbivores dominated fish communities on most reefs both before and after bleaching, suggesting that average micronutrient concentrations of the target fish community were largely unaffected by changes in reef fish composition. Greater post-bleaching herbivore productivity also increased micronutrient availability to fishers (i.e., more fishable biomass). Scraping herbivores contain higher levels of calcium, iron and zinc than most animal-source foods[56,57] and often respond positively to coral declines[25]. If fishing pressure is managed sustainably, these species may be nutrition 'winners', sustaining micronutrient contributions from climate-impacted reefs.

[Figure redrawn with permission from Robinson et al. 2022[55]]

Box 2. Looking ahead: Future research priorities towards nutrition security from coral reef fisheries.

(i) Determine the nutritional vulnerability of fish species under increased temperatures.

Combining experimental, observational and modelling approaches would help understand the variability in nutrient content of fish. **Warming experiments** (e.g., [94]) and **feeding trials** (e.g., [95]) will provide fundamental knowledge of causal relationships between food availability, temperature and nutritional value. Field-based **space-for-time analyses** of intraspecific variability in fish nutrient content along temperature gradients will build understanding of future climate-driven variability in nutritional profiles. The close ties between fish traits and nutrient profiles[35], and the extensive literature detailing traits of coral reef fishes[96] could be leveraged to use **trait-based approaches**[97] for predicting spatial and temporal trends in the nutrient content of fishes, notably including when species-specific information is lacking.

(ii) Understand the direct and indirect trophic pathways that affect fish nutritional content.

Stable isotope analyses (SIA) provide a powerful method to explore the effect of environmental variability on trophodynamics and ultimately nutrient content of fishes. However, the extreme ecological complexity and range of primary production sources[98] on coral reefs present a challenge for studying trophic pathways. **Compound-specific SIA**, which targets specific essential amino acids rather than the bulk muscle tissue used for traditional isotope analysis[99], provides a potential, albeit expensive, solution. Essential amino acids undergo little modification through trophic transfer, so forms synthesised by the primary producer persist as they move up the food chain, permitting researchers to track sources of dietary carbon more accurately[100] and interpret trophic dynamics, even where basal samples are not available[101]. Lastly, recent developments in **next-generation sequencing**[53] and **metagenomics**[54] will allow indirect trophic links to be inferred that involve the role of the microbiome associated with fish gastrointestinal tracts as well as fish habitats.

(iii) Establish how nutritional changes propagate from species/population to reef communities.

Use of **size-based models** to evaluate the impacts of fishing and environmental change is well established[102], and has recently been applied to coral reef systems[28]. Such models, if forced using **climate change projections** at fisheries-relevant spatial scales, would allow to explore the effect of fishing and environmental change scenarios on key fish traits and the flow of nutrients through entire reef communities. It is also important for multispecies reef fisheries models to expand and include other aquatic species(e.g., algae, invertebrates), which have been generally neglected but can be a major source of nutrition through gleaning (mostly by women) in many coastal communities[103]. Such comprehensive, **multispecies reef fisheries models** that incorporate nutritional benefits[85] would provide decision-makers with an effective framework to anticipate future patterns in nutrient production from reef fisheries, and to be proactive in managing fisheries for nutritional outcomes in a changing world.

Table 1. Key knowledge gaps and potential solutions towards food and nutrition security from coral reef fisheries under climate change. 'Pre-requisite' refers to other elements listed in the table and identified by the 'ID' column.

ID	Category	Key knowledge gap	Potential solutions	Pre-requisite
a.	Data deficiency	Baseline data on nutrient composition and food safety parameters for target species	Collate relevant, up-to-date nutrient data on reef fishes to be integrated in local food composition databases	
b.		Reliable and disaggregated (e.g., sex, ethnicity) statistics of reported catches, including from small-scale fisheries, and domestic consumption of reef-based seafood	Integrate fish catch and consumption into market and national surveys (e.g., household income and expenditure)	
c.		Proportion of total nutrient yield that is exported through the global and regional fish trade vs. retained for domestic consumption, in different coral reef countries	Couple nutrient databases with data on fish production, export, and local consumption (esp. from small-scale fisheries) accounting for differences in reporting format	a
d.	Analytical need	Sensitivity of fish nutritional composition (species level) to environmental variation	Combine experimental biology and nutritional analysis on fish sampled along environmental gradients (Box 2)	a
e.		Relative impact of overfishing and climate change on potential nutrient supply from coral reef fisheries	Assess nutritional and catch contribution of species and functional groups under varying levels exploitation and climate stress	a, d
f.		Ecological indicators of nutritional vulnerability in response to environmental change	Identify species and community traits that characterize, among fishery targets, nutritional 'winners' in response to environmental change (Box 2)	a, d, e
g.	Policy need	Appropriate incentives and mechanisms for managing reef fisheries for nutrition security, and identify relevant spatial scales	Incorporate reef fish as micronutrient source in national dietary guidelines and public nutrition (e.g., schools) programs	a

h.		Ecologically and socially sustainable thresholds for future reef fisheries that enhance nutritional outcomes while preserving ecosystem function	Develop socio-ecological models to identify critical thresholds and tipping points to inform management	a-f
i.		Key trade-offs and alternative solutions to simultaneously maximize fishery production, nutritional content, and functional diversity	Intersect policy frameworks typically used to govern and set goals for fishery production, nutrition, biodiversity	a-h
j.		How changes in the nutrient supply from coral reef fisheries should be integrated with larger scale policy decisions on fish trade and export markets	Include food and security experts into trade negotiations; implement economic incentives and/or subsidies for retaining local fish production	a-i

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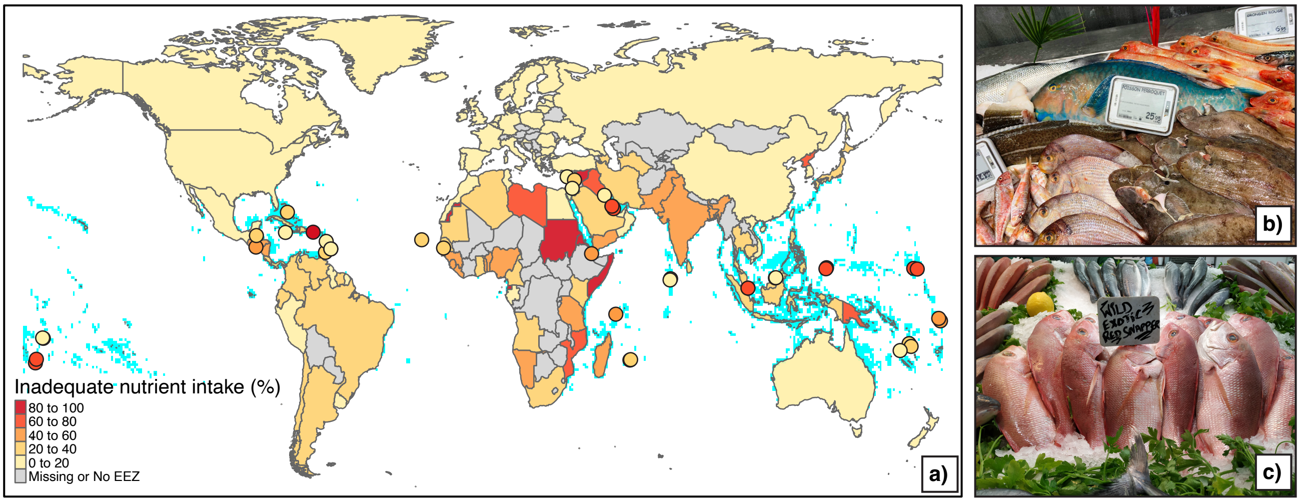
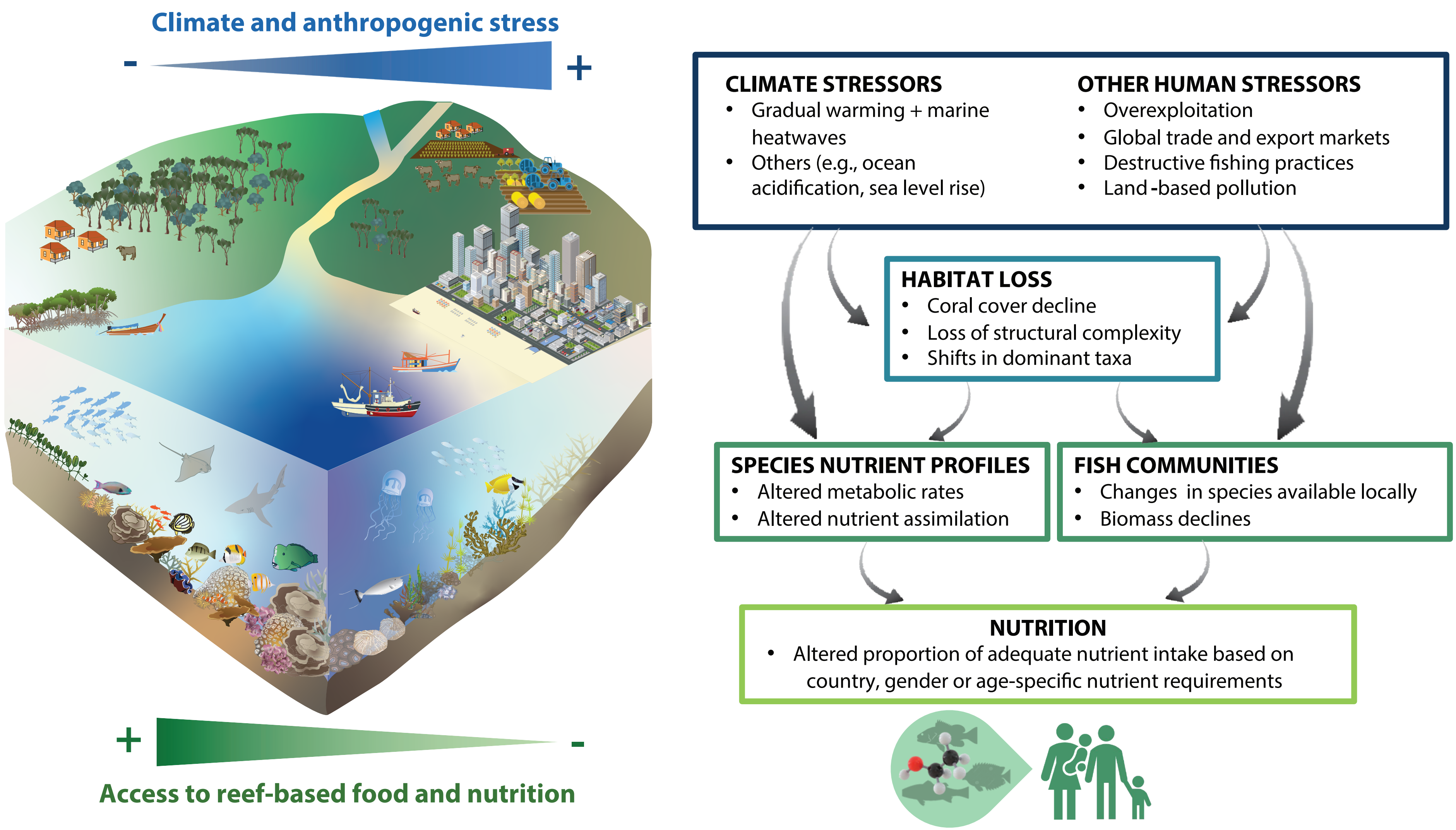
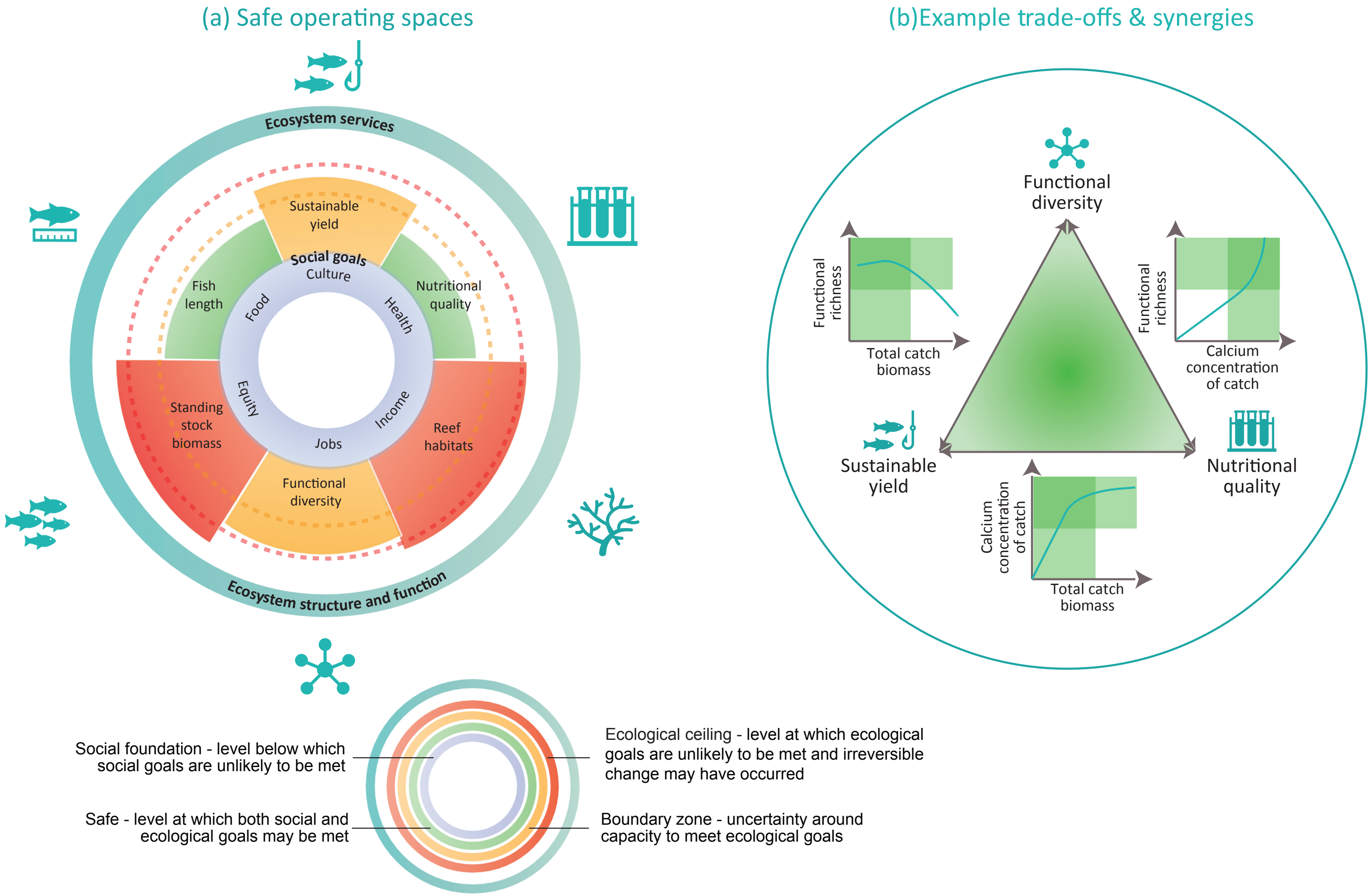
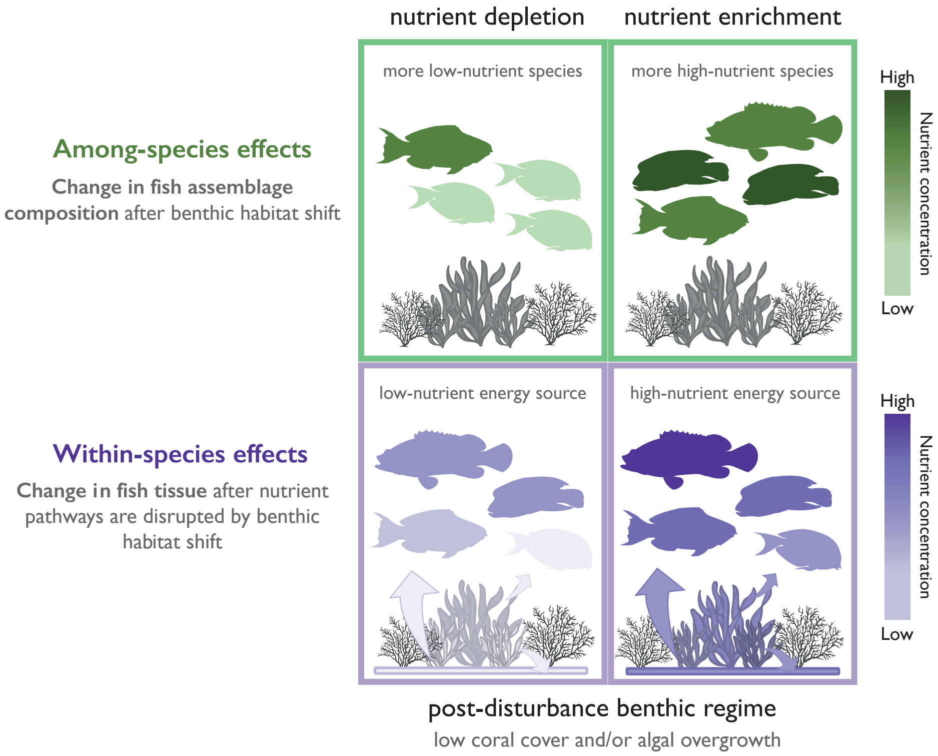

Inadequate nutrient intake (%)
80 to 100
60 to 80
40 to 60
20 to 40
0 to 20
Missing or No EEZ
a)
b)
WILD EXOTIC RED SNAPPER
c)


Climate and anthropogenic stress
-
+
+
-
Access to reef-based food and nutrition
CLIMATE STRESSORS
• Gradual warming + marine heatwaves
• Others (e.g., ocean acidification, sea level rise)
OTHER HUMAN STRESSORS
• Overexploitation
• Global trade and export markets
• Destructive fishing practices
• Land -based pollution
HABITAT LOSS
• Coral cover decline
• Loss of structural complexity
• Shifts in dominant taxa
SPECIES NUTRIENT PROFILES
• Altered metabolic rates
• Altered nutrient assimilation
FISH COMMUNITIES
• Changes in species available locally
• Biomass declines
NUTRITION
• Altered proportion of adequate nutrient intake based on country, gender or age-specific nutrient requirements


(a) Safe operating spaces
(b)Example trade-offs & synergies
Ecosystem services
Sustainable yield
Social goals
Culture
Fish length
Nutritional quality
Food
Health
Equity
Income
Jobs
Standing stock biomass
Reef habitats
Functional diversity
Ecosystem structure and function
Functional diversity
Functional richness
Total catch biomass
Calcium concentration of catch
Sustainable yield
Nutritional quality
Social foundation - level below which social goals are unlikely to be met
Safe - level at which both social and ecological goals may be met
Ecological ceiling - level at which ecological goals are unlikely to be met and irreversible change may have occurred
Boundary zone - uncertainty around capacity to meet ecological goals


nutrient depletion
nutrient enrichment
Among-species effects
Change in fish assemblage composition after benthic habitat shift
more low-nutrient species
more high-nutrient species
High
Nutrient concentration
Low
Within-species effects
Change in fish tissue after nutrient pathways are disrupted by benthic habitat shift
low-nutrient energy source
high-nutrient energy source
High
Nutrient concentration
Low
post-disturbance benthic regime
low coral cover and/or algal overgrowth