



# Safeguarding nutrients from coral reefs under climate change

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**The sustainability of coral reef fisheries is jeopardized by complex and interacting socio-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 these responses are probably affected by both direct (metabolism and trophodynamics) and indirect (habitat and 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<sup>1</sup> and up to 90% of animal protein in some countries across the Pacific and Indian Oceans<sup>2–4</sup>. Small-scale reef fisheries are particularly crucial in coastal and rural areas, where they often provide the majority of fish consumed<sup>5</sup>, and are socially and culturally important<sup>6</sup>. Aquatic foods are a unique dietary source of iodine, vitamin D and the long-chained n-3 fatty acids eicosapentaenoic acid and docosahexaenoic acid, and are also a valuable source of bioavailable micronutrients, including iron, zinc and vitamins A and B<sub>12</sub><sup>7</sup>. Deficiencies of these micronutrients are linked to a growing triple burden of malnutrition, which refers to the coexistence of overnutrition, undernutrition and micronutrient deficiencies that are responsible for impaired cognitive development and account for 1 million premature deaths per year<sup>8–10</sup>. Fish therefore hold the potential to help address these deficiencies, particularly where nutrient intakes are inadequate<sup>8,11</sup> (Fig. 1a). However, coral reefs are highly vulnerable to both overfishing<sup>12</sup> and climate change<sup>13</sup>, stressing the need to better understand the current and potential future contributions of coral reef fisheries to human health<sup>11</sup>.

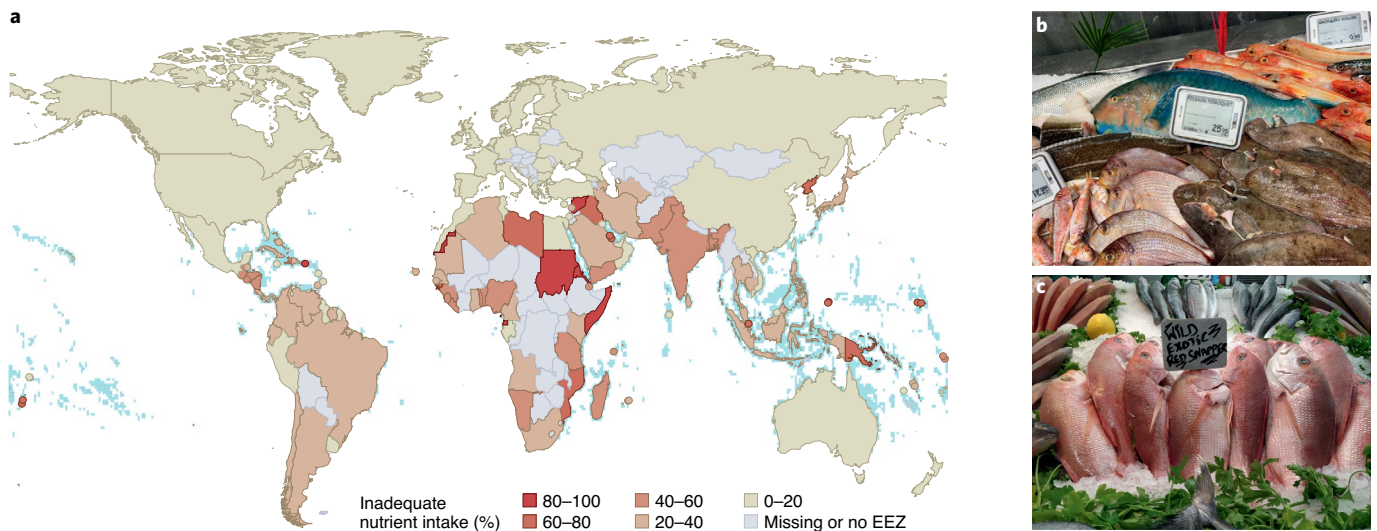
Global development has led to complex shifts in food supply and demand through increases in wealth, human population size, urbanization and the globalization of trade and transport. Through the global fish trade, reef fish can now be sold at high prices in European seafood markets and luxury restaurants<sup>14</sup> (Fig. 1b,c), while the aquarium trade can target species caught by small-scale fishers,

some of which would have been consumed locally<sup>15</sup>. These globalizing markets erode reef fish biomass, resulting in catch decreases 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<sup>16</sup>. Global demand for reef fish through trade also drives market prices up, which can make fish unaffordable for local consumers<sup>17</sup>. 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<sup>18,19</sup>, potentially heightening the risk of metabolic diseases and micronutrient deficiencies<sup>11,19</sup>. Together, the rapidly changing socio-economic context, as is characteristic in tropical regions, simultaneously exacerbates decreases in nutrient-rich foods, particularly where nutrient gaps (for example, East Africa)<sup>8</sup> and increases in diet-related diseases (for example, Pacific islands)<sup>10</sup> are apparent<sup>11</sup>.

## Essential ecosystem services under pressure from climate change

Socio-economic 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 (for example, tropical cyclones and 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,

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**Fig. 1 | Addressing inadequate micronutrient intake in countries with coral reefs requires policies that integrate the global fish trade dynamics with food and nutrition security policy.** **a**, The risk of inadequate micronutrient intake (averaged across seven nutrients; reproduced with permission from ref. <sup>11</sup>, Springer Nature Limited) in coastal countries is often high for countries with coral reefs (data from UNEP-WCMC<sup>21</sup>; light blue). Countries with no maritime exclusive economic zone (EEZ) are shown in light grey and countries smaller than 25,000 km<sup>2</sup> are shown as dots. **b,c**, Blue-barred parrotfish (*Scarus ghobban*) sold in France (**b**) and red snapper (*Lutjanus* species) sold in London (**c**), both more than 3,500 km from their closest potential point of capture (based on the shortest great-circle distance to the Red Sea). Photo in **b** is provided by E.M.; photo in **c** is provided by J.P.W.R.

with foundational species such as reef-building corals among the most affected taxa<sup>20</sup>. Although algal growth following coral loss can support higher biomass<sup>21–23</sup> and productivity<sup>24</sup> of herbivorous species under moderate fishing pressure, the resulting catch instability that can arise from spatiotemporal variation in reef recovery<sup>21</sup> 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 function (Fig. 2). For example, herbivore depletion through overharvesting can impede post-bleaching coral recovery<sup>13</sup>, especially on reefs where structural complexity has been degraded<sup>25</sup>. In turn, the loss of reef structural complexity can reduce the recruitment of juvenile fishes and the replenishment of fish stocks<sup>26</sup>. The consequences of interactions between climate change and other human-driven processes range from the collapse of reef structure and associated fish stocks<sup>27</sup> to novel benthic communities dominated by stress-tolerant and weedy taxa, where some ecological functions can persist to some extent<sup>28,29</sup>, to an increased prevalence of toxic microalgae and ciguatoxins<sup>30</sup>.

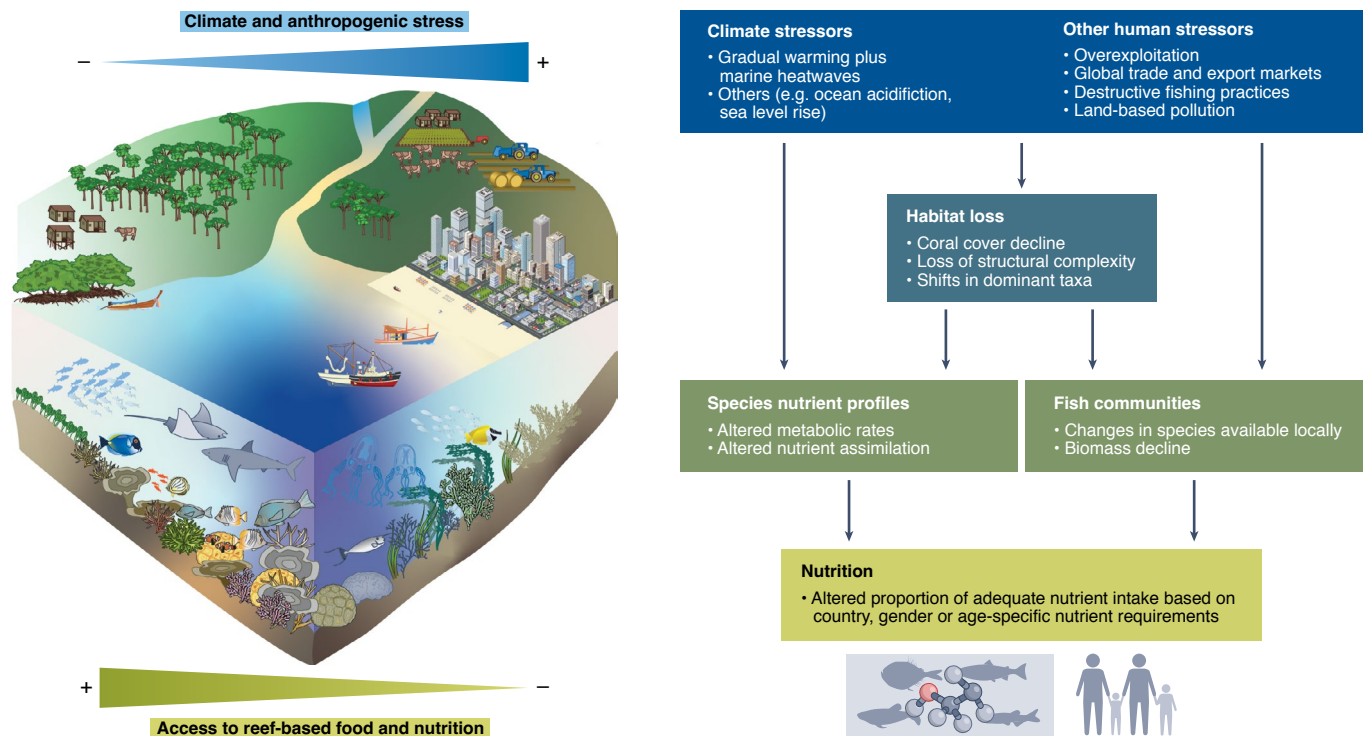
Future climate projections unanimously predict that without immediate intervention to reduce harmful greenhouse gas emissions, most ecosystem services provided by coral reefs will be severely degraded by the end of the century<sup>31</sup>. Such detrimental effects of climate change on seafood production 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<sup>32</sup>. Understanding how nutrient availability from coral reef fisheries responds 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 will probably apply to all coral reef fisheries (that is, 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<sup>33</sup>. We argue that coral reef management practices currently focusing on fish stocks must be reorientated to sustain and protect nutritional benefits as well. This will require robust projections for the species that are the most likely to provide essential nutrients in warmer oceans, as well as knowledge of the functional traits that characterize them. Achieving this objective will require understanding of 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 (for example, diet, energetic demand and thermal regime)<sup>34</sup>, shedding light on the determinants of interspecific variability in nutrient quality. However, the extent to which nutrient profiles differ intra-specifically over space (for example, 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 and metabolism) and



**Fig. 2 | Impacts of climate change and other human stressors on access to reef-based food and nutrition.** Amplification of socio-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 gradient), safeguarding food and nutrition security traditionally supported by healthy coral reefs (green gradient) will require adaptation to novel coral reef communities and the identification of winners versus losers among fish species, not only in terms of biomass but also nutritional value. Images from Shutterstock.com; used with permission.

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<sup>35</sup>. 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<sup>36</sup> and microphytobenthos, including *Gambierdiscus toxicus*, the ciguatera-producing dinoflagellate<sup>37</sup>. 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<sup>38</sup>. Changes in the nutrient profiles of primary and secondary producers can propagate through the food web to higher trophic levels<sup>39</sup> and, in turn, have consequences for the structure and nutrition profile of fish populations and fishery stocks<sup>40</sup>. For example, warmer temperatures reduce fatty acid production in phytoplankton<sup>40–42</sup>. 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<sup>43</sup>.

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<sup>44,45</sup>. Likewise, some tropical species are moving towards temperate areas as oceans warm<sup>46–48</sup>, 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<sup>49</sup>), probably 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<sup>50</sup>. 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<sup>51</sup>. 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 probably important role in the way 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 suggested high regional variability in fish gastrointestinal microbial composition and associated nutritional outcomes<sup>52</sup>. 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<sup>53</sup>. 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.



**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, algae-dominated states, which reroute nutrient pathways in reef food webs<sup>92</sup> and alter the productivity and composition of fish communities<sup>24</sup>. 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 species (changes in the energy sources that determine an individual's nutrient content).

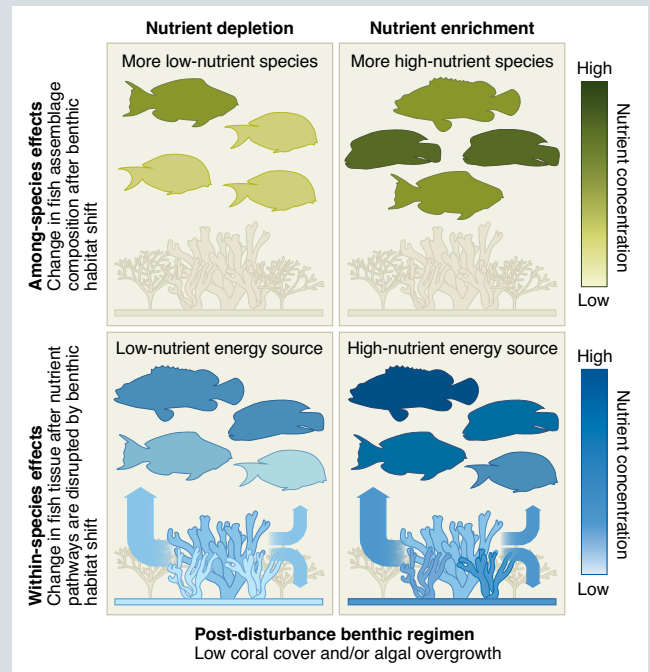
Fish gain micronutrients from their diet, implying that nutrient levels in fish will be influenced by changes to nutrient pathways (within-species effects), while the availability of nutritious target species will depend on the productivity and composition of reef fish communities in post-bleaching reef habitats (among-species effects). Evidence from the Seychelles suggests that disruption of nutrient pathways may have a greater influence on nutrient levels than species compositional changes<sup>54</sup>. In the Seychelles, a mass coral bleaching event in 1998 caused >95% coral mortality, collapsing reef habitat and, on some reefs, provoking macroalgal regime shifts<sup>13</sup>. Such benthic turnover altered trophic pathways<sup>14</sup>, probably 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<sup>93</sup> to primary production.

Reef fish communities also became less diverse after bleaching, forming bottom-heavy trophic pyramids<sup>13,21,73</sup> with enhanced biomass of herbivorous scrapers (Scarinae) and browsers (Siganidae), which are targeted by small-scale trap fisheries<sup>22</sup>. Although browsers were abundant on macroalgal reefs, scraping herbivores dominated fish communities on most reefs both before and after bleaching, suggesting that the 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 (that is, more fishable biomass).

Scraping herbivores contain higher levels of calcium, iron and zinc than most animal-source foods<sup>55,56</sup> and often respond positively to decreases in coral coverage<sup>24</sup>. 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.<sup>54</sup>.



**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<sup>54</sup> (Box 1). This is influenced by compositional shifts in fish communities, with some species decreasing in abundance (losers) in response to marine heatwaves and other climate drivers while others increase (winners) due to more abundant and better-quality food resources<sup>21,24</sup>, greater stress tolerance, competitiveness or better ability to recolonize habitats after a disturbance<sup>49</sup>. The species composition of fisheries catches determines their nutritional quality according to predictable interspecific variation in fish nutrient levels<sup>34</sup>, 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 such as rabbitfishes (family Siganidae) are relatively rich in iron, whereas piscivores have the highest omega-3 concentrations among reef fishes<sup>55,56</sup>. Therefore, iron content may increase in fishery catches following climate-driven increases in herbivore biomass, whether through (1) increased algal productivity after coral mortality<sup>22</sup> or (2) an increase in temperature placing herbivorous species closer to their thermal optima (for example, in higher-latitude reefs and sub-tropical regions) and thus optimal fitness<sup>23,57</sup>. In contrast, size-based food web models predict decreases

in piscivore productivity following the collapse of coral habitat structure and subsequent decreases in prey populations<sup>27</sup>, 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<sup>58</sup>). By 2050, the combination of poleward species redistributions, decreases in habitat suitability, reduced species richness along the equator (as some species exceed maximum thermal limits)<sup>59</sup> and reduced primary productivity is expected to decrease global fisheries catch potential<sup>60</sup>, diminishing nutrient yields from coral reefs<sup>61</sup>. 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 intraspecific shifts in reef fish nutritional quality is fundamental to understanding the effects of environmental change on nutrient production from coral reef fisheries.

**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 us to understand the variability in the nutrient content of fish. Warming experiments (for example, ref. <sup>94</sup>) and feeding trials (for example, ref. <sup>95</sup>) 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 our understanding of future climate-driven variability in nutritional profiles. The close ties between fish traits and nutrient profiles<sup>34</sup>, as well as the extensive literature detailing traits of coral reef fishes<sup>96</sup>, could be leveraged to use trait-based approaches<sup>97</sup> 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 provide a powerful method with which to explore the effect of environmental variability on the trophodynamics and ultimately nutrient content of fishes. However, the extreme ecological complexity and range of primary production sources<sup>98</sup> on coral reefs present a challenge in the study of trophic pathways. Compound-specific stable isotope analyses, which target specific essential amino acids rather than the bulk muscle tissue used for traditional isotope analysis<sup>99</sup>, provide a potential, albeit expensive, solution. Essential amino acids undergo little modification through trophic transfer, so forms synthesized by the primary producer persist as they move up the food chain, permitting researchers to track sources of dietary carbon more accurately<sup>100</sup> and to interpret trophic dynamics, even where basal samples are not available<sup>101</sup>. Lastly, recent developments in next-generation sequencing<sup>52</sup> and metagenomics<sup>53</sup> 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/populations to reef communities**

The use of size-based models to evaluate the impacts of fishing and environmental change is well established<sup>102</sup> and has recently been applied to coral reef systems<sup>27</sup>. Such models, if forced using climate change projections at fisheries-relevant spatial scales, would allow exploration of the effects 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 (for example, algae and invertebrates), which have been generally neglected but can be a major source of nutrition through gleaning (mostly by women) in many coastal communities<sup>103</sup>. Such comprehensive, multispecies reef fisheries models that incorporate nutritional benefits<sup>84</sup> would provide decision makers with an effective framework with which to anticipate future patterns in nutrient production from reef fisheries, enabling them to be proactive in managing fisheries for nutritional outcomes in a changing world.

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<sup>62</sup>.

Biological traits relevant to diet, thermal regime or energetic demand are strong predictors of the nutrient profile of fish species<sup>34</sup>. Furthermore, the response of fish communities to changes in coral composition and associated structural complexity probably depends on species traits rather than taxonomic composition *per se*. Species traits represent a suite of essential biodiversity variables<sup>63</sup> that can reflect trophic ecology, metabolic theory or life history strategy, and thereby provide novel indicators with which 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<sup>64</sup> (but see, for example, Maire *et al.*<sup>65</sup>) (Table 1).

Understanding how changes in reef habitats will impact nutrient supply requires quantification of the degree to which each species (or trait) relies on healthy coral reefs, as well as their ability to cope with alternative reef ecosystem states. Reef health assessments have typically focused on total live hard coral cover—an essential indicator<sup>66</sup> 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 (for example, 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<sup>29</sup>). 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<sup>49</sup>. Therefore, an important remaining question is whether the extent of habitat specialization, potentially inducing diet specialization, can also predict fish nutrient profiles. If so, a community-weighted mean of the species generalization index<sup>49</sup> could provide an important tool with which 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<sup>67</sup> 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<sup>68</sup>. 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 5 years<sup>69</sup>. Subsequent loss of structural complexity can drive decreases in fish diversity by 50%<sup>70</sup>, homogenize community composition among habitat types<sup>71</sup> and change fish size structure by depleting abundances of small-bodied individuals<sup>72</sup>. Size-based food web models predict that such changes to benthic structure could result in a 35% decrease in fisheries productivity<sup>27</sup>. Moreover, turf and macroalgae can proliferate after coral mortality and loss of reef structure, forming alternative benthic regimes that typically support bottom-heavy trophic pyramids<sup>73</sup>. Nonlinear relationships between algal cover and herbivore biomass<sup>74</sup> 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).

**Table 1 | Key knowledge gaps and potential solutions towards food and nutrition security from coral reef fisheries under climate change**

| ID | Category        | Key knowledge gap   | Potential solution   | Prerequisite <sup>a</sup> |
|----|-----------------|---|--|---------------------------|
| 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 (for example, sex or 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 (for example, household income and expenditure)  |                           |
| c  |                 | Proportion of total nutrient yield that is exported through the global and regional fish trade versus retained for domestic consumption in different countries with coral reefs | Couple nutrient databases with data on fish production, export and local consumption (especially 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 the potential nutrient supply from coral reef fisheries  | Assess the nutritional and catch contribution of species and functional groups under varying levels of exploitation and climate stress                                       | a and 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 and e                |
| g  | Policy need     | Appropriate incentives and mechanisms for managing reef fisheries for nutrition security, and the identification of relevant spatial scales                                     | Incorporate reef fish as a micronutrient source in national dietary guidelines and public nutrition programmes (for example, in schools)                                     | 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 and 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 in trade negotiations and implement economic incentives and/or subsidies for retaining local fish production                               | a–i                       |

<sup>a</sup>Other elements listed in the table and identified by the ID column.

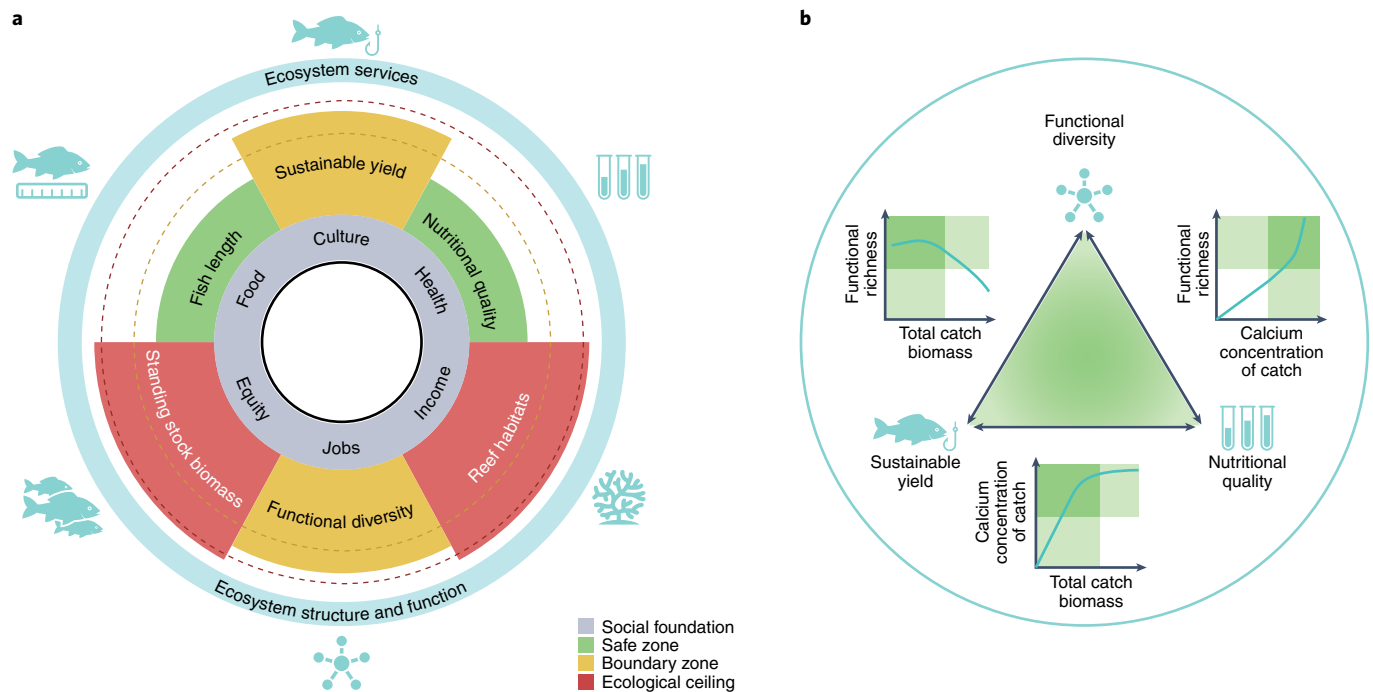
While evidence suggests that higher functional redundancy (that is, a higher number of species with similar ecological functions) can initially buffer communities against the detrimental impact of disturbances<sup>75,76</sup>, the general trend over time is a loss of functional redundancy<sup>75</sup> and biotic homogenization<sup>49,71</sup> 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 and Table 1). While nutrient profiles have been predicted from phylogeny<sup>77</sup> and traits<sup>34</sup>, only one study has related nutrient profiles to traits that reflect species vulnerability to environmental changes<sup>65</sup>. 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 a changing climate<sup>78</sup>, in particular those relevant to future food and nutrition security from coral reef fisheries<sup>34</sup> (Box 2). It will also help to prioritize the indicators that long-term monitoring programmes should focus on in the future and to 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<sup>56,79</sup> to identify the most reliable

and cost-effective ecological indicators of fish community nutritional responses to climate change (Box 2 and Table 1).

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

The ecological management of multispecies fisheries on tropical reefs is challenging because fisheries and landing sites are widely dispersed, catches are often unreported<sup>80</sup> and formal governance, monitoring and management are often lacking<sup>81</sup>. However, the need for sustainable reef fisheries has motivated the search for solutions through alternative fisheries-independent, biomass-based models, showing that fishing can be compatible with the maintenance of key ecosystem functions<sup>82</sup>. These approaches have typically aggregated fish communities into either total biomass<sup>82</sup> or trophic group biomass<sup>12</sup> 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  $\sim 1,000 \text{ kg ha}^{-1}$  (ref. 12), fishing down to approximately 50% of total unfished biomass tends to maintain important reef ecosystem structure and function<sup>82</sup> and that there are clear benefits from having some form of reef management in place<sup>12,83</sup>.

Maximizing sustainable production while maintaining ecosystem function 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<sup>34</sup> are



**Fig. 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. The colours of the different dimensions of coral reef fisheries correspond to their status in relation to the boundaries. For example, reef habitats are shaded red as in this example they have crossed the ecological ceiling (the level at which ecological goals are unlikely to be met and irreversible change may have occurred; red boundary) and are now in such a depauperate state that irreversible changes have occurred. Safe zones (the level at which both social and ecological goals may be met; green) and boundaries (where there is uncertainty around the capacity to meet ecological goals; orange) need to be jointly defined for multiple interacting dimensions, as illustrated in **b**. The social foundation (blue) represents the level below which social goals are unlikely to be met. **b**, Examples of interactions between the indicators of three dimensions include trade-offs (for example, decreases in functional richness with increasing catch biomass), synergies (for example, increases in the mean calcium concentration of the catch with increasing functional richness) and scale-dependent interactions (for example, higher mean calcium concentrations of catches at intermediate levels of catch biomass). The status of each dimension (**a**) and relationships between indicators and green safe zones (**b**) are illustrative only.

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, raise 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 the indicators and targets relevant to each goal, and comparison with safe zone boundaries, will be necessary to assess the overall performance and sustainability of coral reef fisheries and will ultimately support efforts to maximize synergies and minimize 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<sup>84</sup>.

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<sup>85</sup>. These multispecies 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, for example, increasing levels of methylmercury in warmer oceans<sup>86</sup>.

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 countries with coral reefs.

Temperature-dependent models<sup>87</sup> that also account for species range shifts<sup>88</sup> and life history traits<sup>89</sup> will then be needed to project future changes in fisheries contributions to food and nutrition security, 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 are sensitive to factors such as taxonomy, ecoregion and life history<sup>87</sup>, providing promising insights for coral reef fisheries. Together, a combination of these approaches and their spatially explicit extensions will help to identify which target species are most susceptible (losers) to negative impacts and which 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, to harness the species that will thrive to their fullest nutritional potential (Table 1). Enhancement of the contribution coral reefs can make to future food and nutrition security will ultimately require a holistic approach that incorporates improved local



management of small-scale domestic fisheries<sup>83</sup> and agriculture with integrated and targeted programmes that provide vulnerable societies with healthy and sustainable diets<sup>18</sup>, such as socio-economic incentives, nutrition-sensitive policies and integration into education<sup>18</sup>, as well as public nutrition programmes (for example, in schools)<sup>90</sup>. At larger scales, inclusion of food and nutrition security experts in the development of international trade agreements will be essential to ensure that nutrient-rich catches are retained for vulnerable populations<sup>17</sup> and to 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 socio-ecological stressors is increasingly impacting reef ecosystem structure and function, 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, as well as how these changes will propagate from individual fish to entire communities throughout food webs. Transdisciplinary approaches (from the collection of baseline data on catches and the domestic consumption of reef-based seafoods to the identification of safe operating spaces for future coral reef fisheries) are required to fill knowledge gaps and inform fisheries management policies, and to ensure their uptake in the management of local fisheries and the 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 the 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. and G.J.E. expanded on the ideas and engaged in discussion and editing of the final manuscript. All authors contributed to writing, editing, and approving the final manuscript.

**Competing interests**

The authors declare no competing interests.

**Additional information**

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