**Supplementary Material**

Positive feedbacks in coastal reef social-ecological systems can maintain coral dominance

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Appendix 1: Key papers used in initial literature search

Allgeier, J.E., Burkepile, D.E. & Layman, C.A. (2017) Animal pee in the sea: consumer‐mediated nutrient dynamics in the world’s changing oceans. *Global Change Biology* **23**, 2166–2178.

Allgeier, J.E., Layman, C.A., Mumby, P.J. & Rosemond, A.D. (2014) Consistent nutrient storage and supply mediated by diverse fish communities in coral reef ecosystems. *Global Change Biology* **20**, 2459–2472.

Allgeier, J.E., Valdivia, A., Cox, C. & Layman, C.A. (2016) Fishing down nutrients on coral reefs. *Nature Communications* **7**, 12461.

Allgeier, J.E., Wenger, S.J., Rosemond, A.D., Schindler, D.E. & Layman, C.A. (2015) Metabolic theory and taxonomic identity predict nutrient recycling in a diverse food web. *Proceedings of the National Academy of Sciences* **112**.

Burkepile, D.E., Allgeier, J.E., Shantz, A.A., Pritchard, C.E., Lemoine, N.P., Bhatti, L.H. & Layman, C.A. (2013) Nutrient supply from fishes facilitates macroalgae and suppresses corals in a Caribbean coral reef ecosystem. *Scientific Reports* **3**, 1493.

Cyronak, T., Andersson, A.J., Langdon, C., Albright, R., Bates, N.R., Caldeira, K., Carlton, R., Corredor, J.E., Dunbar, R.B., Enochs, I., Erez, J., Eyre, B.D., Gattuso, J.-P., Gledhill, D., Kayanne, H., et al. (2018) Taking the metabolic pulse of the world’s coral reefs. *PLOS ONE* **13**, e0190872.

Larned, S.T. (1998) Nitrogen- versus phosphorus-limited growth and sources of nutrients for coral reef macroalgae. *Marine Biology* **132**, 409–421.

Mumby, P.J. & Steneck, R.S. (2018) Paradigm Lost: Dynamic Nutrients and Missing Detritus on Coral Reefs. *BioScience* **68**, 487–495.

Pawlik, J.R., Burkepile, D.E. & Thurber, R.V. (2016) A Vicious Circle? Altered Carbon and Nutrient Cycling May Explain the Low Resilience of Caribbean Coral Reefs. *BioScience* **66**, 470–476.

Pawlik, J.R. & McMurray, S.E. (2020) The Emerging Ecological and Biogeochemical Importance of Sponges on Coral Reefs. *Annual Review of Marine Science* **12**, 315–337.

Saba, G.K., Burd, A.B., Dunne, J.P., Hernández‐León, S., Martin, A.H., Rose, K.A., Salisbury, J., Steinberg, D.K., Trueman, C.N., Wilson, R.W. & Wilson, S.E. (2021) Toward a better understanding of fish‐based contribution to ocean carbon flux. *Limnology and Oceanography* **66**, 1639–1664.

Shantz, A.A., Ladd, M.C., Schrack, E. & Burkepile, D.E. (2015) Fish-derived nutrient hotspots shape coral reef benthic communities. *Ecological Applications* **25**, 2142–2152.

Villéger, S., Ferraton, F., Mouillot, D. & de Wit, R. (2012) Nutrient recycling by coastal macrofauna: intra- versus interspecific differences. *Marine Ecology Progress Series* **452**, 297–303.

Appendix 2: Description of literature search process to build causal loop diagram

Once we had built an initial causal loop diagram with the most relevant variables explaining nutrient and carbon cycling in CRSES, using the key papers provided in Appendix 1, we performed a secondary search. In this secondary search, we used a search engine (Google Scholar) with variable names as search terms, as well as broader search terms including: “ocean nutrient cycling”; “marine nutrient cycling”; “reef nutrient cycling”; “nitrogen cycling”; “marine nitrogen cycling”; “reef nitrogen cycling”; “ocean phosphorus cycling”; “marine phosphorus cycling”; “reef phosphorus cycling”; “quantifying carbon cycling”; “marine carbon cycling”; and “reef carbon cycling”. We searched for additional papers related to the influence of human activities on nutrient and carbon cycling in reefs. We included direct anthropogenic interventions on the nutrient and carbon cycles, i.e., either the addition or removal of nutrients or carbon to or from the system. Search terms included “anthropogenic nutrient inputs to reefs”, “anthropogenic carbon inputs to reefs”, “fishing and nutrient cycles” and “nutrients removal fishing”. Our literature search was primarily focused on processes occurring at the local scale (i.e., within a reef). From each of these searches, we read article titles, abstracts, and key words, and identified and read those papers that contained information about key drivers (both biotic and abiotic) that contribute to nitrogen, phosphorus, and carbon cycling in reefs.

From these selected papers, we extracted information about key variables and causal interactions most relevant to nutrient and carbon cycling in CRSES and built a causal loop diagram to represent them. We started with a very simple diagram including only key biological and environmental variables. We then iteratively added complexity to the diagram, in the form of additional variables and links, during the literature search process. In cases where different literature suggested opposite interaction signs between pairs of variables, we performed further literature search to find additional evidence that would help support our decision of which interaction sign to include in the causal loop diagram. The sign was selected which received more support from the literature.

As a first step, we described the role of biotic and abiotic drivers in nutrient and carbon cycles. We did this by investigating biologically related fluxes, storages and transformations of nutrients and carbon. Thus, the resulting causal loop diagram described how the different biological and environmental variables affect one another through nutrient- and carbon-related processes. In a second step, we incorporated anthropogenic variables and their interactions with the nutrients and carbon cycles in CRSES through their impact on both environmental and biological variables. The result was a conceptual causal loop diagram which depicts the primary variables and mechanisms of the nutrient and carbon cycling in CRSES.

Appendix 3: Description of the variables and mechanisms of nutrient and carbon cycling in CRSES as identified through literature search and captured in the causal loop diagram.

Here we describe the variables and mechanisms of nutrient and carbon cycling in CRSES as identified through literature search and captured in the causal loop diagram. A summary of links and references can be found in Table S1. Subsections are organized as follows: (1) nutrient cycling internal to ecosystems; (2) carbon cycling internal to ecosystems; (3) anthropogenic inputs and effects on both nutrient and carbon cycles. Throughout, we refer to links in the causal loop diagram in Fig. 1 in the main text.

#### **Table S1**. Summary table of links and reference literature.

|  |  |  |
| --- | --- | --- |
| **Link** | **Variables** | **References** |
| 1 | Size-selective fishing – Ratio of small-bodied to large-bodied fishes | Graham *et al.*, 2005; 2017 ; Edgar *et al.*, 2018 ; Bosch *et al.*, 2022 |
| 2 | Size-selective fishing – Population density of reef fishes and invertebrates | Graham *et al.*, 2017; Edgar *et al.*, 2018 |
| 3 | Benthic community – Population density of reef fishes and invertebrates | Bellwood *et al.*, 2004; Hoey and Bellwood, 2008 |
| 4 | Population density of reef fishes and invertebrates – Rate of herbivory | Bellwood *et al.*, 2004; Hoey and Bellwood, 2008 |
| 5 | Ratio of small-bodied to large-bodied fishes – Ambient N :P ratio | Moody *et al.*, 2015 |
| 6 | Ratio of small-bodied to large-bodied fishes – Nitrogen and phosphorus stored in biomass | Moody *et al.*, 2015 |
| 7 | Population density of reef fishes and invertebrates – Nitrogen and phosphorus stored in biomass | Allgeier *et al.*, 2014 ; 2017 |
| 8 | Population density of detrivivores – Population density of reef fishes and invertebrates | de Goeij *et al.*, 2013 |
| 9 | Ambient N :P ratio – Population density of corals | Muscatine and Porter, 1977 ; Allgeier *et al.*, 2014; Ezzat *et al.*, 2015; Rosset *et al.*, 2017 |
| 10 | Nitrogen and phosphorus stored in biomass – Ambient concentration of dissolved nutrients | Allgeier *et al.*, 2017 |
| 11 | Nitrogen and phosphorus stored in biomass – Ambient concentration of particulate nutrients and carbon | Allgeier *et al.*, 2017 |
| 12 | Ambient concentration of particulate nutrients and carbon – Population density of detritivores | de Goeij *et al.*, 2013 |
| 13 | Nutrient density of macroalgae – Rate of herbivory | Shantz *et al.*, 2015 |
| 14 | Rate of herbivory – Population density of macroalgae | Bellwood *et al.*, 2004; Hoey and Bellwood, 2008 |
| 15 | Ambient concentration of dissolved nutrients – Nutrient density of macroalgae | Meyer *et al.*, 1983; Meyer and Schultz, 1985a, 1985b |
| 16 | Ambient concentration of dissolved nutrients – Population density of corals | Stambler *et al.*, 1994; Dubinsky and Stambler, 1996; Koop *et al.*, 2001; Szmant, 2002; Shantz and Burkepile, 2014 |
| 17 | Ambient concentration of dissolved nutrients – Population density of macroalgae | Allgeier *et al.*, 2013 ; Burkepile *et al.*, 2013 |
| 18 | Ambient concentration of dissolved nutrients – Population density of sponges | Diaz and Ward, 1997; Southwell *et al.*, 2008; Archer *et al.*, 2021 |
| 19 | Ambient concentration of dissolved nutrients – Population density of phytoplankton | Burkepile *et al.*, 2013 |
| 20 | Ambient concentration of particulate nutrients and carbon – Population density of sponges | de Goeij *et al.*, 2013 |
| 21 | Ambient concentration of particulate nutrients and carbon – Population density of microbes and zooplankton | de Goeij *et al.*, 2013 |
| 22 | Ambient concentration of DOC – Population density of sponges | de Goeij *et al.*, 2013 |
| 23 | Ambient concentration of DOC – Population density of microbes and zooplankton | de Goeij *et al.*, 2013 |
| 24 | Population density of corals – Ambient concentration of DOC | de Goeij et al. 2007 |
| 25 | Population density of corals – Population density of macroalgae | Muscatine and Porter, 1977 ; D’Angelo and Wiedenmann, 2014 ; Burkepile *et al.*, 2013; Faizal *et al.*, 2020 |
| 26 | Population density of macroalgae – Ambient concentration of DOC | de Goeij *et al.*, 2007 ; 2013 |
| 27 | Population density of corals – Population density of sponges | Muscatine and Porter, 1977 ; López-Victoria *et al.*, 2006; González-Rivero *et al.*, 2011; D’Angelo and Wiedenmann, 2014 ; Perry *et al.*, 2014 ; Pawlik *et al.*, 2016 ; Pawlik & McMurray, 2020 |
| 28 | Population density of macroalgae – Population density of sponges | Pawlik *et al.*, 2016 |
| 29 | Population density of sponges – Turbidity | Mumby and Steneck, 2018 |
| 30 | Population density of phytoplankton – Population density of sponges | de Goeij *et al.,* 2013 |
| 31 | Population density of phytoplankton – Concentration of organic matter (POC and DOC) | de Goeij *et al.*, 2007 ; 2013 |
| 32 | Turbidity – Population density of corals | Hallock and Schlager, 1986 ; Fabricius, 2011 ; Mumby and Steneck, 2018 |
| 33 | Turbidity – Population density of macroalgae | Hallock and Schlager, 1986 |
| 34 | Population density of phytoplankton – Turbidity | D’Angelo and Wiedenmann, 2014 |
| 35 | Concentration of dissolved inorganic nutrients – Population density of corals | Allgeier *et al.*, 2017 |
| 36 | Concentration of dissolved inorganic nutrients – Population density of macroalgae | Allgeier *et al.*, 2017 |
| 37 | Concentration of dissolved inorganic nutrients – Population density of sponges | Allgeier *et al.*, 2017 |
| 38 | Concentration of sediments – Population density of corals | Fabricius, 2005, 2011 ; Wenger *et al.*, 2016 ; Faizal *et al.*, 2020 |
| 39 | Concentration of sediments – Population density of macroalgae | Goatley and Bellwood, 2012 ; Faizal *et al.*, 2020 |
| 40 | Concentration of sediments – Turbidity | Hallock and Schlager, 1986 ; Faizal *et al.*, 2020 |
| 41 | Concentration of sediments – Population density of sponges | Faizal *et al.*, 2020 |
| 42 | Concentration of sediments – Population density of microbes and zooplankton | Faizal *et al.*, 2020 |
| 43 | Concentration of particulate nutrients – Turbidity | Hallock and Schlager, 1986 |
| 44 | Concentration of particulate nutrients – Population density of sponges | Bell et al. 2013 ; 2018 |
| 45 | Concentration of organic matter (POC and DOC) – Turbidity | Mumby and Steneck, 2018 |
| 46 | Concentration of organic matter (POC and DOC) – Population density of sponges | Goeij *et al.*, 2013; Pawlik *et al.*, 2016 |
| 47 | Concentration of organic matter (POC and DOC) – Population density of microbes and zooplankton | de Goeij *et al.*, 2013 ; den Haan *et al.*, 2016 |
| 48 | Runoff from sewage, agriculture, and aquaculture – Ambient N :P ratio | Ferrier-Pagès *et al.*, 2000; Webster *et al.*, 2012; D’Angelo & Wiedenmann, 2014; Kroon, Schaffelke & Bartley, 2014; den Haan *et al.*, 2016 |
| 49 | Runoff from sewage, agriculture, and aquaculture – Concentration of dissolved inorganic nutrients | Ferrier-Pagès *et al.*, 2000; Webster *et al.*, 2012; D’Angelo & Wiedenmann, 2014; Kroon, Schaffelke & Bartley, 2014 |
| 50 | Coastal development and land-use change – Concentration of sediments | Burke *et al.*, 2011 |
| 51 | Coastal development and land-use change – Concentration of particulate nutrients | Burke *et al.*, 2011 |
| 52 | Coastal development and land-use change – Concentration of organic matter (POC and DOC) | Burke *et al.*, 2011; Dai *et al.*, 2012; Pawlik *et al.*, 2013 |
| 53 | Population density of macroalgae – Organic carbon in macroalgae | de Goeij *et al.*, 2013 |
| 54 | Organic carbon in macroalgae – Population density of reef fishes and invertebrates | de Goeij *et al.*, 2013 |

(a) Nutrient cycling

Animals like reef fishes and invertebrates play key roles in reef ecosystems, contributing to both the stocks and flows of matter. Fishes contribute to the retention of nutrients in the ecosystem by storing large amounts of nutrients in their biomass (Allgeier *et al.*, 2017). Indeed, they represent the largest source of biomass in reefs (Newman *et al.*, 2006), and store both nitrogen and phosphorus (link 7) (Allgeier *et al.*, 2014), potentially storing up to 1,167 gigatons of nitrogen worldwide (Allgeier *et al.*, 2017). In turn, higher stores of nutrients in fish biomass have a positive effect on fish stocks via trophic interactions across the reef fish food web (link 7). Reef fish not only concentrate nutrients within reefs, but also play a role in importing nutrients from other systems, contributing to benthic-pelagic coupling (Morais and Bellwood, 2019). However, as many reefs are oligotrophic environments where natural inputs of new nutrients are scarce, the ability of fishes to retain nutrients within the ecosystem is crucial to the maintenance of high biological production.

In addition to their role in nutrient storage, reef fishes also shape reef ecosystems through both top-down and bottom-up processes (Munsterman et al. 2021). As consumers, reef fishes and invertebrates are involved in herbivory and corallivory (links 3 and 4), which influence the abundance of macroalgae and corals within reef systems (Bellwood *et al.*, 2004; Hoey and Bellwood, 2008). Bottom-up processes are also important drivers of ecosystem functioning through the ability of organisms to generate resource flows in the ecosystem via nutrient and carbon cycling (Williams and Carpenter, 1988; Villéger *et al.*, 2012; Vanni *et al.*, 2013; Allgeier *et al.*, 2014; Peters *et al.*, 2019). Fishes and invertebrates can supply nutrients through two main processes: excretion and egestion (links 10 and 11) (Allgeier *et al.*, 2017). The nutrients released via excretion are usually considered more bioavailablethan those released via egestion. Indeed, excreted nutrients are dissolved inorganic nutrients (mainly NH4+ for nitrogen and PO43- for phosphorus) that can be used by primary producers and other benthic organisms (links 16, 17, 19, 35, 36 and 37; Allgeier *et al.*, 2017). In contrast, egested nutrients released by reef fishes and invertebrates in the form of particulate organic matter which contains particulate organic carbon and nutrients (link 11), can be consumed by detritivores, sponges, and microbes (links 12, 20, and 21). Fish communities can be a major source of nutrient flow in reefs, via the pathways described above. Indeed, one study found that in a Caribbean reef, the amount of nutrients supplied by fishes through excretion was estimated to be 25 times greater than all other natural sources of nutrients combined (Burkepile *et al.*, 2013). This reflects the importance of fish-mediated nutrient cycling, especially in nutrient-poor reefs. The total rate and amount of nutrients provided by fishes and invertebrates is the sum of individual contributions. At the ecosystem level, the supply of nutrients from non-anthropogenic sources, and the rate of nutrient cycling, will thus depend on the abundance and composition of the reef biotic community. For individual reef fish, nutrient supply and cycling rates are determined by a combination of several traits, most notably body mass and taxonomic identity which affect e.g., stoichiometry and metabolism (Allgeier *et al.*, 2015).

Benthic organisms also play an important role in nutrient cycling. Notably, sponges may be important sources of dissolved inorganic nitrogen (DIN) through their release of ammonium, nitrate, and nitrite as metabolic waste (link 18) (Diaz and Ward, 1997; Southwell *et al.*, 2008; Archer *et al.*, 2021). Sponges may also consume PO43- and store phosphorus in polyphosphate granules produced by their symbionts (link 18). However, the contribution of sponges to the nitrogen and phosphorus cycle remains poorly quantified and understood (Pawlik and McMurray, 2020) and represents a gap in current knowledge.

The nutrients cycled via excretion and egestion by reef fishes and invertebrates are critical to reef function. As they provide bioavailable nutrients in the environment, this benefits to primary producers, including phytoplankton in the water column and benthic primary producers like corals and macroalgae (links 16, 17, and 19). Several field studies showed a positive correlation between fish density and seagrass growth rate (Allgeier *et al.*, 2013) and algal abundance (Burkepile *et al.*, 2013). Enhanced coral growth and resistance to thermal stress has also been reported at reef sites where schools of fish aggregate (Meyer *et al.*, 1983; Meyer and Schultz, 1985a; Shantz *et al.*, 2015, 2023). Therefore, the effect of fish-derived nutrients on benthic primary producers is significant, but is likely spatially heterogeneous. For example, fish-mediated fertilization has been reported in areas where fishes aggregate (Meyer and Schultz, 1985b; Shantz *et al.*, 2015), and higher concentrations of nutrients have been found in areas with high fish density (Allgeier *et al.*, 2013; Shantz *et al.*, 2015). Thus, reef fishes may create ‘nutrient hotspots’ in the areas of reefs where they are most present and abundant.

Beyond the growth of primary producers, fish-mediated supply of nutrients also impacts the nutrient content of seagrass, macroalgae and corals (via link 15) (Meyer *et al.*, 1983; Meyer and Schultz, 1985a, 1985b). A positive correlation between nutrient supply by fishes and the nutrient content of seagrass and algae tissues has been shown (Allgeier *et al.*, 2013; Burkepile *et al.*, 2013). This direct effect of fish-mediated fertilization may have further consequences for ecosystem functioning, including an increase in herbivory rate in fertilized areas, as fishes predominantly graze in highly nutritive areas (link 13) (Shantz *et al.*, 2015). This creates a double positive feedback effect by fishes on corals; on the one hand, nutrients supplied by fishes (via links 7 and 10) enhance coral growth (link 16), and on the other, high nutrient content leads to an increased herbivory rate in the fertilized area (via links 13 and 15), thus decreasing algal cover and reducing space competition for corals (via link 25).

(b) Carbon cycling

The organic carbon cycle is closely linked to the nutrient cycles and is key to the functioning of reef ecosystems, notably through the role of sponges. Sponges are filter feeding organisms, and therefore consume particulate nutrients and carbon egested by fish and invertebrates in the water column (via links 11 and 20). Sponges and certain microbes are also able to use dissolved organic carbon (DOC) produced by macroalgae. Indeed, one study found experimental evidence for DOC cycling performed by sponges, the so-called ‘sponge-loop’ (de Goeij *et al.*, 2013). Primary producers release fixed carbon as DOC (link 26), which is consumed by sponges (link 22), microbes and zooplankton (link 23). Corals (via link 24) also serve as sinks for DOC (de Goeij and van Duyl, 2007). Sponges then convert DOC into detritus and POC (link 20) that can be consumed by detritivores (link 12). Energy and nutrients then move up the food web to higher trophic levels (link 8). The organic carbon in primary producers is also taken up by herbivores through herbivory (link 53), and moves up the food chain (link 54). Herbivores also egest POC, which is taken up by filter feeders and sponges. This process cannot be generalized to all reef ecosystems, as it fundamentally depends on the abundance and composition of the sponge community. Reefs with high abundance of heterotrophic sponges should experience a stronger ‘sponge loop’ than reefs in very poor nutritive environments with a higher proportion of autotrophic sponges, such as Caribbean reefs, which tend to have a high sponge abundance and a large number of heterotrophic species (Pawlik *et al.*, 2016).

(c) Anthropogenic inputs and effects

Anthropogenic activities alter the natural cycles of nutrients and carbon in shallow reefs by both removing biomass and shifting population size structure of fishes (links 1 and 2) (Edgar *et al.*, 2018; Bosch *et al.*, 2022), as well as providing inputs of nutrients and carbon through pollution and runoff (links 48-52) (den Haan *et al.*, 2016) [(den Haan et al., 2016)](https://www.zotero.org/google-docs/?FqYlU5). Fisheries can profoundly affect ecosystem functioning via top-down processes (Zaneveld *et al.*, 2016), notably through the removal of herbivorous fishes, which can trigger algae dominance via the release of grazing pressure (Bozec *et al.*, 2016; Ruttenberg *et al.*, 2019). However, fisheries also impact reef ecosystems via the disturbance of fish-mediated nutrient cycling (Allgeier *et al.*, 2016). By extracting biomass (links 1 and 2), fisheries affect both the storage and the supply of nutrients through changes in reef fish communities (links 6 and 7). Allgeier and colleagues (2016) investigated the impacts of fisheries on fish-mediated nutrient processes on 43 reefs across a wide gradient of fishing pressures, from no-take, well-enforced protected areas to heavily-fished areas which are characterized by the absence of large predators and relatively small body size. They showed that fishing can reduce the nutritive capacity (the amount of nutrients stored in the ecosystem and the rate of its recycling) of reef ecosystems by nearly 50%. A loss of nutrient capacity in the ecosystem mediated by fish exploitation can weaken the fertilization of primary producers (i.e., coral, algae, seagrass) at the bottom of the food web (Burkepile *et al.*, 2013; Shantz *et al.*, 2015; Munsterman *et al.*, 2021).

Fisheries can also alter fish community size-structure (Graham *et al.*, 2005; Bosch *et al.*, 2022) and composition (Soler *et al.*, 2015; D’agata *et al.*, 2016; Loiseau *et al.*, 2021) since they are often both species and size selective (link 1). Fisheries often target species at higher trophic levels or large herbivorous fishes and the largest individuals (Graham *et al.*, 2017; Edgar *et al.*, 2018), shifting fish populations towards smaller species and individuals which generally have higher N:P ratio excretions due to their higher metabolic rates. Thus, fisheries can cause changes in the nitrogen to phosphorus (N:P) ratio of fish excretion (link 5). Phosphorus excretion by fishes is mainly related to diet composition; herbivorous species usually excrete at a higher N:P ratio than predators due to a diet that is poorer in phosphorus (Moody *et al.*, 2015). However, the N:P ratio of supply is very consistent across reefs and their fish communities (usually around 20:1) (Allgeier *et al.*, 2014). This ratio may facilitate coral growth, possibly resulting from co-evolution between coral symbionts and reef fishes (Howarth, 1988; Allgeier *et al.*, 2014). Several studies testing the effect of changes in the ambient N:P ratio on coral growth and calcification showed that a N:P ratio shifting away from its optimum value (around 20:1) may be deleterious to corals (via link 9) (Allgeier *et al.*, 2014; Ezzat *et al.*, 2015; Rosset *et al.*, 2017). Selective fishing could thus potentially affect coral health through changes in the reef fish community.

Another major anthropogenic pressure on coastal reefs is the input of pollutants (links 47 and 48) (den Haan *et al.*, 2016). Nutrient pollution can drastically affect reef nutrient cycles, in some cases leading to ecosystem degradation (Herbert, 1999). Anthropogenic inputs of nutrients to reefs have various origins and different chemical and physical forms: they can be supplied in dissolved or particulate forms, and be organic or inorganic. They can also be introduced with other kinds of pollutants, for example, toxic chemicals and heavy metals (Ramos *et al.*, 2004), which cause physiological stress to corals (Howard and Brown, 1984). The characteristics of nutrient pollutants influence their bioavailability and ultimately, the biological responses of reef organisms. Table S2 provides a summary of the primary types and sources of anthropogenic nutrient pollutants, their characteristics in terms of chemical form, supply rate and scale, associated pollutants, and possible mitigation strategies, where possible.

**Table S2**. Descriptions of the main types of anthropogenic nutrient pollutants associated with links 48-52 in Fig. 1. Information is provided on the sources and characteristics of each type of pollutant, including supply rate and scale, associated co-pollutants, and possible mitigation strategies.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Pollutant type and characteristics | Anthropogenic source(s) | Supply rate and scale | Co- pollutants | Notes relevant to management and possible mitigation strategies | References |
| Dissolved inorganic nutrients  (Chemical forms of dissolved inorganic nitrogen include nitrate, nitrite, and ammonium;  Chemical forms of dissolved inorganic phosphorus include phosphate) | Sewage from housing, infrastructure, pleasure boats: intensity of the nutrient load depends on the population density and the treatment of waste waters.  Fertilizers from agriculture and golf courses, which leach into runoff, especially with heavy rainfall.    Waste waters from animal husbandry and aquaculture. | Dissolved inorganic nutrients have local-scale effects as they are quickly taken up by primary producers. However, when they are carried simultaneously with a high load of particles and sediments, the increased water turbidity will reduce nutrient uptake by primary producers, thus such nutrients may be carried longer distances.    Nitrogen concentration measured in runoff is up to 20 Kg N/ha/year. | Pesticides, antibiotics and hormones | Highly bioavailable for primary producers.  Bodies of water with a short retention time of water may be less sensitive to this pressure.  Mitigation may include better treatment of runoff, wastewater and sewage. | (Ferrier-Pagès *et al.*, 2000; Webster *et al.*, 2012; D’Angelo and Wiedenmann, 2014; Kroon *et al.*, 2014) |
| Particulate nutrients and sediments | Human activities like deforestation, agriculture, pasture plowed and tillage increase the particulate matter load in rivers.  Coastal development, including construction or beach nourishment (also known as sand replenishment) can increase sediment load in coastal waters. | Particulate nutrients have regional-scale effects.  Sediments are carried by rivers over long distances, and when they reach coastal areas, they may extend up to 100km out to sea from the plume of the river mouth. | Toxic chemicals and heavy metals | Less bioavailable; particulate nutrients are often bound up in sediments.  Restoration and maintenance of riparian zones, and avoidance of infrastructure like dams that modify natural flow regimes, can help to mitigate coastal impacts by allowing the catchment of anthropogenic inputs before they reach coastal ecosystems.  Restoration of coastal ecosystems like mangrove and wetlands may buffer particulate nutrients before they reach reefs. | (Burke *et al.*, 2011) |
| Organic matter  (particulate or dissolved) | Organic matter leaches from soil and is carried as runoff to bodies of water.  Human activities like deforestation, agriculture, and plowing or tilling pastures decrease the retention of organic matter in the soil and increase organic matter load in rivers, which ends up in coastal waters. | The rivers that discharge into the Caribbean have among the highest dissolved organic carbon (DOC) flux in the world, with estimates of 30.7, 4.3, and 2.3 teragrams of carbon per year (TgC/year) for the Amazon, Orinoco, and Mississippi, respectively. | No significant co-pollutants | Restoration and maintenance of riparian zones, and avoidance of infrastructure like dams that modify natural flow regimes, can help to mitigate coastal impacts by allowing the catchment of anthropogenic inputs upstream from coastal ecosystems.  Restoration of coastal ecosystems like mangrove and wetlands may buffer organic matter before it reaches reefs. | (Burke *et al.*, 2011; Dai *et al.*, 2012; Pawlik *et al.*, 2013) |

Anthropogenic inputs of organic matter, in both particulate and dissolved forms, can affect mechanisms of the carbon cycle (links 48-52). Land-use changes like deforestation and agricultural tilling can decrease the retention of organic matter in soils, causing it to runoff into rivers, which eventually empty into the ocean (link 52) (see Table S2 for details on pollutant types and origins). The increase in dissolved and particulate organic carbon (DOC and POC) can benefit sponges, microbes, and plankton (links 31 and 46). In addition to the direct benefits to sponges from increased POC (link 46), dissolved nutrients from anthropogenic sources, can indirectly benefit sponges through the enhancement of picophytoplankton (link 37). Generally, the anthropogenic supply of organic matter in coral reefs is positively correlated with the abundance of sponges (de Goeij *et al.*, 2013; Pawlik *et al.*, 2016). Yet, an increase in sponge abundance has deleterious consequences on corals (González-Rivero *et al.*, 2011). Indeed, despite certain positive interactions between sponges and corals, for example, the ability of sponges to hold rubble together and improve water clarity, both of which benefit corals (Wulff, 2017), several negative impacts of sponges on corals have been documented, including physical damage to corals from excavating sponges, negative effects on coral recruitment, and competition for space (López-Victoria *et al.*, 2006; González-Rivero *et al.*, 2011; Perry *et al.*, 2014).

It has also been hypothesized that high sponge abundance can trigger a feedback loop between sponges, algae and corals (links 25, 27, and 28), negatively impacting the latter: the reciprocal cycling of carbon and nutrients between sponges and macroalgae may enhance the growth of both sponges and macroalgae to the disadvantage of corals, through both direct spatial competition and changes to the coral microbiome (Pawlik *et al.*, 2016). Moreover, the enhanced production of detritus by sponges or decomposing seaweeds may increase coral stress by increasing turbidity (link 29) (Mumby and Steneck, 2018). Sponges’ ability to take advantage of anthropogenic inputs, as well as their greater temperature and pH tolerance, may allow them to become the dominant benthic species in reefs of the future (Bell *et al.*, 2013). The ecosystem functioning in sponge-abundant, coral-depauperate reefs is expected to accompany a loss of complexity, a shift in reef fish community composition toward generalist and sponge-eating species, reductions in biodiversity and a loss of resilience to future threats (Bell *et al.*, 2018).

Dissolved inorganic nutrients from anthropogenic sources also have local effects on reefs as they are highly bioavailable and incorporated quickly by primary producers (links 35, 36, and 37). Since phytoplankton have the fastest generation time, they will often be the primary beneficiary of this type of nutrient enrichment (link 37). Therefore, one of the first expected responses to nutrient enrichment in reefs is an increase of phytoplankton abundance (D’Angelo and Wiedenmann, 2014). Increased phytoplankton abundance may lead to an increase in water turbidity (link 34). Particulate nutrients and sediments from anthropogenic sources may further increase water turbidity (links 40 and 43) and subsequent light attenuation that can affect the growth and survival of benthic phototrophic organisms (i.e., coral, macroalgae, seagrass) (via links 32 and 33) (Hallock and Schlager, 1986). High levels of turbidity can reduce both growth and calcification rates of corals (Fabricius, 2011). In severe cases of eutrophication, seagrass and phytoplankton proliferation produces a large amount of dead organic matter that can lead to increased demand for O2 by bacteria for remineralization. This can lead to hypoxia, “dead zones” and ecosystem collapse (Roman *et al.*, 2019; Johnson *et al.*, 2021).

The addition of nutrients from anthropogenic sources can also alter the competitive interactions between space-limited benthic organisms (links 25, 27, and 28). Corals have a competitive advantage in nutrient-poor environments thanks to the efficient internal recycling of nutrients by their symbionts (Muscatine and Porter, 1977). However, corals may lose this competitive advantage under high nutrient-concentration conditions (D’Angelo and Wiedenmann, 2014). Under such conditions, other benthic primary producers, like algae and seagrass, may outcompete corals for space and increase in abundance following nutrient enrichment (Burkepile *et al.*, 2013; Faizal *et al.*, 2020). The effect of the addition of dissolved nutrients on coral growth and calcification rates has been experimentally tested in numerous studies (Stambler *et al.*, 1994; Dubinsky and Stambler, 1996; Koop *et al.*, 2001; Szmant, 2002; Shantz and Burkepile, 2014). Fabricius (2005) reviewed the impact of nutrient additions on corals and concluded that even though nutrient enrichment can significantly change coral physiology (i.e., calcification, growth rate, and photobiology), it is not necessarily damaging to corals. However, high levels of dissolved organic compounds increase coral susceptibility to pathogenic microbes and viruses (Kuntz *et al.*, 2005; Kline *et al.*, 2006; Ban *et al.*, 2014; D’Angelo and Wiedenmann, 2014; Zaneveld *et al.*, 2016). Moreover, particulate nutrients and sediments can have deleterious effects on corals (link 38) through sedimentation (Faizal *et al.*, 2020), which can cause burial and abrasion of corals and may affect the regeneration of the coral community by impeding coral settlement and recruitment (Fabricius, 2005, 2011), even in marine protected areas (Wenger *et al.*, 2016). Sedimentation can alter key ecosystem functions performed by fishes like herbivory, which controls algal growth (Goatley and Bellwood, 2012). We conclude that anthropogenic activities, by providing additional nutrient inputs to reefs and by altering biotic populations and the cycling they mediate, can alter the competitive interactions between space-limited benthic organisms, including coral, macroalgae, and sponges. Under high nutrient-concentration conditions, as corals may lose their competitive advantage (D’Angelo and Wiedenmann, 2014), the reef may shift to a macroalgal- or sponge-dominated benthic state.

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