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

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Abstract

Understanding the mechanisms underlying nutrient (nitrogen and phosphorus) and carbon cycling in reefs is critical for effective management. Research on reef nutrient and carbon cycling needs to account for (i) the contributions of multiple organisms, (ii) abiotic and biotic drivers, and (iii) a social-ecological perspective. In this paper, we review the mechanisms underlying nutrient and carbon cycling in reef social-ecological systems and analyse them using causal loop analysis. We identify direct and indirect pathways and feedback loops through nutrient and carbon cycles that shape the dominant benthic state of reefs: coral, algal, and sponge-dominated states. We find that two of three anthropogenic impact scenarios (size-selective fishing and land use change) have primarily negative consequences for coral and macroalgae via the nutrient and carbon cycles. A third scenario (runoff) has fewer negative impacts on sponges compared to other benthos. In all scenarios, frequent positive feedback loops (size-selective fishing: 7 of 12 loops; runoff: 6 of 9 loops; land use change: 8 of 11 loops) lead to system destabilization; however, the presence of multiple loops introduces avenues whereby reefs may retain coral dominance despite anthropogenic pressures. Context-specific information on the relative strength of loops will be necessary to predict future reef state.

Keywords: carbon cycling; causal loop analysis; coastal reefs; nutrient cycling; social-ecological systems

Introduction

Shallow tropical reefs (<50 m deep) are social-ecological systems (SESs) in which humans and marine ecosystems are inextricably intertwined (Liu et al. 2007, Sing Wong et al. 2022). Coastal reef ecosystems thrive in around 250 000 square kilometres around the world, mostly in tropical and subtropical environments, and are among the most productive and diverse ecosystems on earth (Burke et al. 2011). The ecosystem services they generate are foundational to the social and economic development of coastal human communities (Cinner et al. 2009, Eddy et al. 2021). Coastal reefs contribute to supporting ecosystem services through the cycling of carbon and nutrients like nitrogen and phosphorus (Schiettekatte et al. 2022). Reefs occur under a variety of different nutrient regimes; however, typical concentrations of nutrients in healthy reefs are low (Crossland et al. 1984). The presence of healthy reefs, marked by high percentage of coral cover, low levels of macroalgae, and high fish biomass (Díaz-Pérez et al. 2016), in low-nutrient areas is known as Darwin's Paradox (Muscatine and Porter 1977). This paradox suggests that high productivity in coral reefs is sustained by an efficient cycling of nutrients (Muscatine and Porter 1977), which takes place at the cellular scale in coral tissues (Morris et al. 2019), and by reef fish, invertebrates, and phytoplankton (Schiettekatte et al. 2022). In addition to nutrient cycling, reef systems also have complex carbon cycles (Cyronak et al. 2018). Inorganic carbon is predominantly found in coral skeletons, while organic carbon in coral reefs is mainly in fish biomass (Saba et al. 2021). Considering organic carbon cycling together with nutrients can contribute to a holistic understanding of reef biogeochemical cycles.

Previous work on nutrient and carbon cycling in reefs has (i) mostly focused on the contributions of a single type of organism, (ii) focused on either abiotic or biotic drivers of nutrient cycling, and (iii) not analysed cycling from a social-ecological perspective. Studies of the nutrient cycling by a single species or distinct group of organisms have focused on, e.g. microbes (Glaze et al. 2022), sponges (Southwell et al. 2008), or fishes (Burkepile et al. 2013, Allgeier et al. 2014, Shantz et al. 2015), and have restricted analyses to either biotic processes (Allgeier et al. 2017, Munsterman et al. 2021) or abiotic processes (Szmant 2002, Adam et al. 2021). While there is strong evidence that anthropogenic activities, including agriculture, sewage, and coastal development produce nutrient inputs to marine environments that may result in eutrophication and associated regime shifts in marine ecosystems (Herbert 1999, Adam et al. 2021), no studies to our knowledge have analysed nutrient and organic carbon cycling in reefs as part of complex social-ecological systems (SESs).

The SES concept recognizes the embeddedness of humans in the biosphere and emphasizes the role of humans in shaping ecological outcomes and the role of ecosystems in shaping people, culture, and society (Folke et al. 2016). Approaching nutrient and carbon cycling from an SES perspective allows us to consider how anthropogenic activities such as fishing and land use change interact with biotic and abiotic processes in reefs. Understanding the mechanisms underlying the cycling of nutrients and carbon in coastal reef social-ecological systems (CRSES), and identifying potential feedback loops between cycling and reef community composition, is needed if reef management is to consider strategies that optimize these and other ecosystem services. It is thus important to contextualize how nutrient and carbon cycling occurs in CRSES, how it changes under multiple conditions, and what this means for reef-generated ecosystem services.

The dynamics of nitrogen, phosphorus (hereafter referred to collectively as 'nutrients'), and carbon cycling in ecosystems are complex processes involving multiple ecological and anthropogenic drivers. Studying nutrient and carbon cycles in CRSES thus requires a systemic approach, combining biologically based processes of nutrient and carbon cycling with human-related inputs and outputs of carbon and nutrients in the system. Moreover, non-linear dynamics such as sudden collapses or state shifts can emerge from complex interactions within CRSES (Norström et al. 2009, Graham et al. 2013). Systems analysis is particularly well suited to study CRSES as it focuses on processes (e.g. fishing), and allows for system dynamics and outcomes to emerge from the interaction of these processes (Scheffer et al. 2001).

In this paper, we identify key drivers of nutrient and carbon cycling through literature search to understand: (i) the mechanisms underlying natural cycling processes resulting from interactions between biotic and abiotic variables in CRSES, and (ii) the effects of anthropogenic activities on nutrient and carbon cycles in reefs and resulting reef state. We then use qualitative systems analysis to build a conceptual causal loop model of CRSES (Williams and Hummelbrunner 2010), focusing on key variables and mechanisms associated with the cycling of nitrogen, phosphorus, and organic carbon, and including multiple biological, environmental, and anthropogenic drivers within CRSES. With a clearer understanding of reef systems, drivers, and processes, we then use causal loop analysis to qualitatively characterize the outcomes associated with three anthropogenic impact scenarios. This method allows us to study the mechanisms of nutrient and carbon cycling carried out via multiple abiotic and biotic drivers within CRSES, and to test how various scenarios are expected to affect coastal reef functioning. Finally, we place our results in the context of reef science and management, by discussing how a comprehensive overview of the mechanisms underlying cycling contributes to a holistic understanding of how best to manage reef systems to support the delivery of ecosystem services.

Materials and methods

Literature search and causal loop diagram

We performed a literature search on nutrient and carbon cycling within CRSES, starting with a set of key papers (Appendix 1 of Supplementary Material), and identified further articles from literature cited in or by those key papers. In our literature search, we included studies of both tropical and subtropical reefs. We used this ensemble to build an initial causal loop diagram including the most relevant variables explaining nutrient and carbon cycling in CRSES. We then engaged in an iterative process in which we searched for additional articles to clarify the relationships between variables and their roles in nutrient and carbon cycling. A full description of the literature search process can be found in Appendix 2 of Supplementary Material.

Causal loop diagrams are used in systems analysis to visualize key variables and the causal relationships, or links, between them (Williams and Hummelbrunner 2010). They are used to communicate the structure of a system dynamics model (Barbrook-Johnson and Penn 2022), and to analyse the current state of a system and clarify assumptions about system structure and dynamics (Williams and Hummelbrunner 2010). Causal loop diagrams have been employed in previous analyses of CRSES to identify drivers of marine regime shifts in coral reefs (Rocha et al. 2015), and evaluate how reef ecosystem services may change in response to climate change adaptation strategies (Hafezi et al. 2021).

In this study, we developed a causal loop diagram as a tool to explicitly represent various processes involved in the nutrient and carbon cycles within CRSES, as well as their relations to anthropogenic activities. We structured the information in the causal loop diagram using three types of variables (biological, environmental, and anthropogenic) and two types of links (positive or negative), which represent the processes by which variables influence one another. Key variables were differentiated into three types: (1) biological variables—in green—that represent biological components of the reefs that contribute to nutrient and carbon cycling (i.e. groups of organisms that we gathered because they have a similar function in terms of nutrient and carbon cycling), (2) environmental variables—in blue—that represent the concentration or presence of chemicals and physical elements that influence nutrient and carbon cycles, and (3) anthropogenic variables—in yellow—that represent human activities that influence biological or environmental variables. The links between the variables represented one or several underlying biologically based or human-based processes. Links were included only when they were considered relevant and represented a direct interaction, rather than merely a correlation *(link between A and B was considered significant because a change in A will result in a change in B)*. Positive links lead to a change in the same direction, and negative links lead to a change in the opposite direction. The resulting conceptual causal loop diagram depicts the primary variables and mechanisms of the nutrient and carbon cycling in CRSES.

Causal loop and pathway analysis

To understand how human activities affect nutrient and carbon cycles and the consequences for reef functioning, we developed three anthropogenic impact scenarios with the potential to alter the nutrient and carbon cycles in reefs.

We used a causal loop analysis to qualitatively analyse the outcomes associated with these three scenarios. Loop analysis is a systemic approach that allows researchers (1) to identify feedback loops and (2) to analyse their interactions and the possible effects of loops on the dynamic behaviour of the entire system (Williams and Hummelbrunner 2010). Similar to qualitative loop analysis systematically developed by Levins (1974), we use causal loop analysis to make qualitative predictions about changes in variables based on direct and indirect causal relations that are coded by sign only (i.e. increase or decrease). Feedback loops are system structures in which an initial change in one variable results in a chain reaction that ultimately results in additional change in the same initial variable (Meadows 2008). There are two types of feedback loops: reinforcing loops and balancing loops (Meadows 2008), both of which we include in our analysis. In

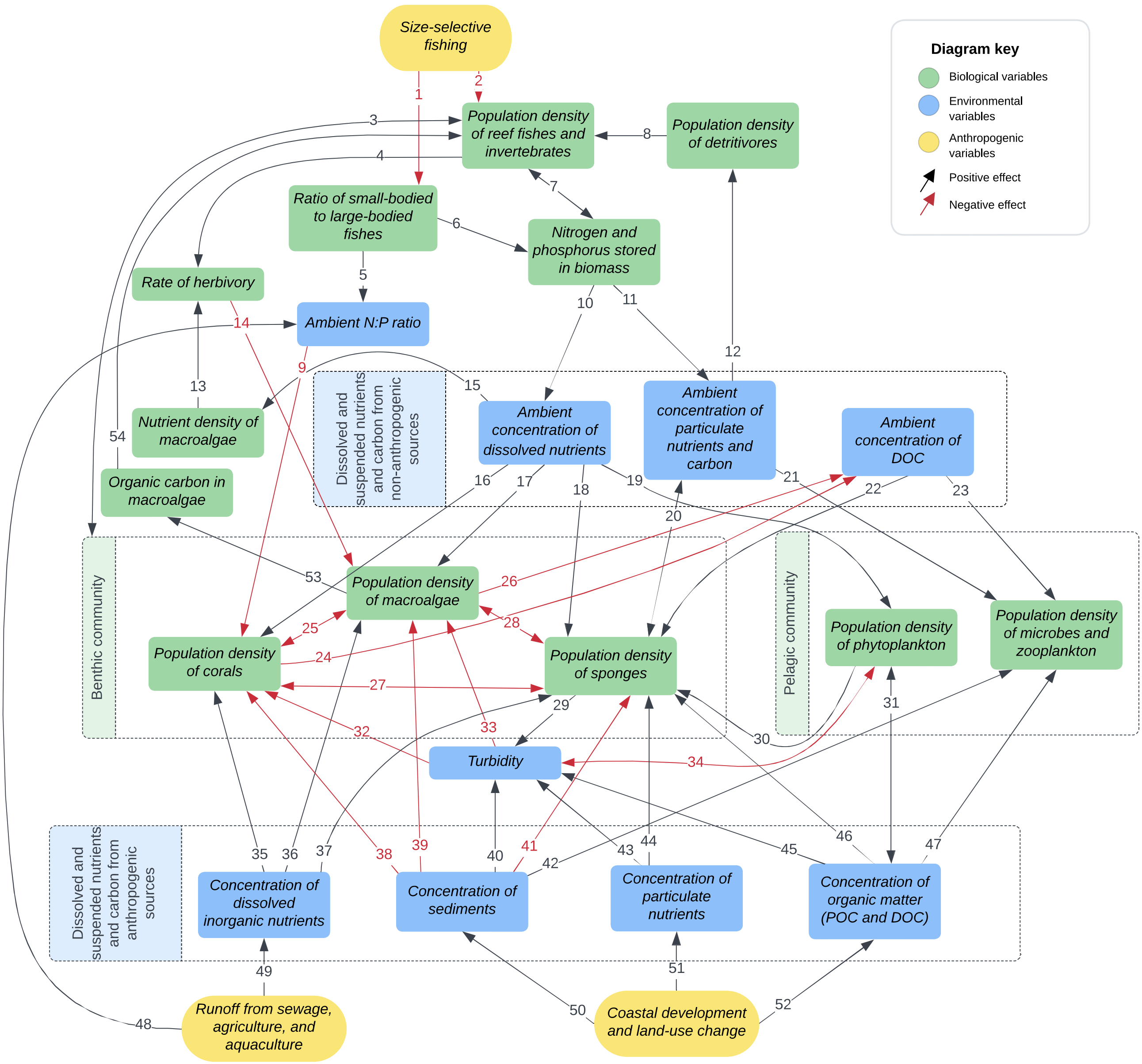

Figure 1. Causal loop diagram depicting variables and mechanisms involved in nutrient and carbon cycling in coastal reef SESs. Variables are simplified and, in some cases, represent groupings of multiple species or organisms that have the same or similar function in the nutrient and carbon cycles. A positive (negative) direct link from variable A to variable B means that an increase in the first variable will cause an increase (decrease) in the second variable, in the absence of effects from other links. A double-headed arrow indicates that interactions of the same sign flow in both directions between the two variables. Each link has a unique number identifier.

reinforcing loops, also called positive loops, a change in one direction results in additional changes in the same direction. Reinforcing loops produce changes that are compounded, thus leading to changes such as exponential growth or decay, which alter system state. On the other hand, with balancing loops, also called negative loops, a change in one direction results in a change in the opposite direction. Thus, balancing loops serve to regulate or balance a system, producing equilibrium and preventing significant changes in system state. The prevalence of either positive or negative feedback loops in the causal loop model provides us with a basic understanding of the dynamical stability of the system (Williams and Hummelbrunner 2010). Negative feedback loops enhance system stability, while positive loops are destabilizing and introduce the possibility of regime shifts (Williams and Hummelbrunner 2010).

We used loop analysis as a method to highlight important variables within the system and explore how the interactions among them contribute to system-level outcomes. We also explored the outcomes related to the expected benthic reef state (i.e. coral-, algal-, or sponge-dominant benthos) based on the balance of multiple linkages and loops in the causal loop diagram associated with each scenario. To do this, we identified pathways, or chains of interactions among variables. We also calculated the sign of each pathway as either positive or negative based on the effect of the first variable in the pathway on the last. The causal loop analysis of the different scenarios allowed us to assess the consequences of specific human

Table 1. Summary table of nodes, positive and negative links, positive and negative pathways, and loops for each scenario.

	Size-selective fishing	Agricultural runoff	Land use change
Total nodes	13	10	10
Negative links	6	11	13
Positive links	17	12	12
Total links	23	23	25
Negative pathways	5	1	13
Positive pathways	1	3	4
Total pathways	6	4	17
Negative loops	5	3	3
Positive loops	7	6	8
Total loops	12	9	11

pressures in terms of reef functioning, and also to identify potential implications for reef management.

Results

Literature search and causal loop diagram

From literature search we extracted information about key drivers and mechanisms (both biotic and abiotic) that contribute to nitrogen, phosphorus, and carbon cycling in reefs (Appendix 3) and built a causal loop diagram to represent them (Fig. 1). We identified three main groups of interactions: those related to nutrient cycling (nitrogen and phosphorus cycling), carbon cycling, and anthropogenic inputs. From our general causal loop diagram, we developed a pared-down version of the diagram containing relevant variables for each of the three scenarios. The general causal loop diagram contained 24 nodes, 19 negative links, and 41 positive links.

These links, or interactions give rise to multiple feedback loops, which are further explored in Tables 1–4. Negative loops provide stability to the reef system, while the presence of positive feedback loops introduces the possibility that the reef system may shift to a different dominant benthic state. The three primary stable states we identify through literature review are coral-dominated, macroalgae-dominated, and sponge-dominated states.

Qualitative analysis of anthropogenic impact scenarios

Through the development of three anthropogenic input scenarios, together with the qualitative loop analysis, we assessed the consequences of anthropogenic activities on reef functioning via the nutrient and carbon cycles. The three anthro-

Table 2. Pathways and loops for Scenario 1: Fishing effort selectively removes large-bodied individuals from reef systems.

Pathway or loop	Sign	Associated variables, in order
Pathway	−	Size-selective fishing—Ratio of small-bodied to large-bodied fish—Ambient N:P ratio—Population density of corals
Pathway	−	Size-selective fishing—Ratio of small-bodied to large-bodied fish—Nitrogen and phosphorus stored in biomass—Ambient concentration of dissolved nutrients—Population density of corals
Pathway	−	Size-selective fishing—Ratio of small-bodied to large-bodied fish—Nitrogen and phosphorus stored in biomass—Ambient concentration of dissolved nutrients—Population density of macroalgae
Pathway	+	Size-selective fishing—Population density of reef fishes and invertebrates—Nitrogen and phosphorus stored in biomass—Ambient concentration of dissolved nutrients—Nutrient density of macroalgae—Rate of herbivory—Population density of macroalgae
Pathway	−	Size-selective fishing—Population density of reef fishes and invertebrates—Nitrogen and phosphorus stored in biomass—Ambient concentration of dissolved nutrients—Population density of corals
Pathway	−	Size-selective fishing—Population density of reef fishes and invertebrates—Nitrogen and phosphorus stored in biomass—Ambient concentration of dissolved nutrients—Population density of macroalgae
Loop	+	Population density of reef fishes and invertebrates—Benthic community (population density of corals and population density of macroalgae)
Loop	+	Population density of reef fishes and invertebrates—Nitrogen and phosphorus stored in biomass
Loop	−	Population density of reef fishes and invertebrates—Rate of herbivory—Population density of macroalgae
Loop	−	Population density of reef fishes and invertebrates—Rate of herbivory—Population density of macroalgae—Organic carbon in macroalgae
Loop	−	Population density of reef fishes and invertebrates—Nitrogen and phosphorus stored in biomass—Ambient concentration of dissolved nutrients—Nutrient density of macroalgae—Rate of herbivory—Population density of macroalgae
Loop	+	Population density of reef fishes and invertebrates—Nitrogen and phosphorus stored in biomass—Ambient concentration of dissolved nutrients—Population density of corals
Loop	−	Population density of reef fishes and invertebrates—Nitrogen and phosphorus stored in biomass—Ambient concentration of dissolved nutrients—Population density of corals—Population density of macroalgae
Loop	+	Population density of reef fishes and invertebrates—Nitrogen and phosphorus stored in biomass—Ambient concentration of dissolved nutrients—Population density of macroalgae
Loop	−	Population density of reef fishes and invertebrates—Nitrogen and phosphorus stored in biomass—Ambient concentration of dissolved nutrients—Population density of macroalgae—Population density of corals
Loop	+	Population density of reef fishes and invertebrates—Nitrogen and phosphorus stored in biomass—Ambient concentration of dissolved nutrients—Population density of macroalgae—Organic carbon in macroalgae
Loop	+	Population density of reef fishes and invertebrates—Nitrogen and phosphorus stored in biomass—Ambient concentration of particulate nutrients and carbon—Population density of detritivores
Loop	+	Population density of macroalgae—Population density of corals

Only pathways that start with size-selective fishing and end in a benthic community variable are listed. Pathways via link 25 (representing benthic space competition) are omitted for brevity, but it is assumed that, for each pathway listed, there exist additional pathways from size-selective fishing to the other benthic community variables via link 25. For loops, the last variable given in the 'Associated variables' column interacts with the first variable in the 'Associated variables' column.

Table 3. Pathways and loops for Scenario 2: Runoff from sewage, agriculture, or aquaculture introduces dissolved inorganic nutrients into the reef system.

Pathway or loop	Sign	Associated variables, in order
Pathway	−	Runoff from sewage, agriculture, and aquaculture—Ambient N:P ratio—Population density of corals
Pathway	+	Runoff from sewage, agriculture, and aquaculture—Concentration of dissolved nutrients—Population density of corals
Pathway	+	Runoff from sewage, agriculture, and aquaculture—Concentration of dissolved inorganic nutrients—Population density of macroalgae
Pathway	+	Runoff from sewage, agriculture, and aquaculture—Concentration of dissolved nutrients—Population density of sponges
Loop	+	Population density of corals—Population density of macroalgae
Loop	−	Population density of corals—Population density of macroalgae—Population density of sponges
Loop	+	Population density of corals—Population density of sponges
Loop	+	Population density of macroalgae—Population density of sponges
Loop	+	Population density of macroalgae—Population density of sponges—Turbidity
Loop	+	Concentration of organic matter (POC and DOC)—Population density of phytoplankton
Loop	+	Turbidity—Population density of phytoplankton
Loop	−	Turbidity—Population density of phytoplankton—Concentration of organic matter (POC and DOC)
Loop	−	Concentration of organic matter (POC and DOC)—Population density of sponges—Turbidity—Population density of phytoplankton

Only pathways that start with runoff from sewage, agriculture, and aquaculture and end in a benthic community variable are listed. Pathways via link 25 (representing benthic space competition) are omitted for brevity, but it is assumed that, for each pathway listed, there exist additional pathways from runoff to the other benthic community variables via link 25. For loops, the last variable given in the 'Associated variables' column interacts with the first variable in the 'Associated variables' column.

pogenic scenarios were: (1) size-selective fishing; (2) runoff from sewage, agriculture, and aquaculture; and (3) coastal development and land use change. These three scenarios were selected based on their potential to alter the nutrient and carbon cycles in reefs, leading to changes in CRSES functioning and state. While we recognize that some land use changes also contribute to runoff (e.g. agriculture), we distinguish between multiple types of effects in our model. Our runoff scenario focuses on the inputs of dissolved, inorganic nutrients to reefs, while our land use change scenario focuses on inputs of sediments, particulate nutrients, and organic matter in the form of dissolved and particulate organic carbon.

Scenario 1: Size-selective fishing

Fishing tends to be size-selective, resulting in the removal of large-bodied species and individuals from the reef fish community (Fig. 2, link 1). Changes in reef fish community size structure and an increasing ratio of small-bodied to large-bodied fish alter the N:P ratio of nutrients excreted by fish, and thus, the N:P ratio in the water column (link 5), which has negative consequences for coral growth and survivorship (link 9). In addition, fishing activities extract fish biomass, leading to a decline in reef fish population density (link 2) and the total amount of nitrogen and phosphorus stored in fish biomass (link 7). Reductions in the total amounts of nitrogen and phosphorus stored in fish biomass also change the ambient concentration of dissolved nutrients (link 10), which is affected by fish egestion and excretion. This has negative consequences for both corals and macroalgae (links 16 and 17), which partly rely on the input of these nutrients from fish.

All three pathways from size-selective fishing to coral, and one of two pathways from size-selective fishing to macroalgae are negative (Table 2). Declining nutrient concentrations in the water column reduce nutrient content in algae and seagrass tissues (link 15), which reduces local herbivory as remaining herbivorous reef fish move elsewhere to graze in nutrient-rich areas (link 13). A decline in local herbivory, particularly at sites with low nutrient concentrations, may lead to a recovery of, and increase in, macroalgae cover at those sites (link 14).

The presence of multiple negative loops (5 of 12 loops), e.g. the negative feedback that results from the effect of population density of reef fishes and invertebrates on the rate of herbivory, which, in turn, affects population density of macroalgae, and thus, the available food for reef fish populations (via links 4, 14, and 3), may contribute to stabilizing reef dynamics under a fishing effort scenario. On the other hand, the presence of positive loops (7 of 12 loops), e.g. the positive feedback facilitated by benthic space competition between macroalgae and corals (link 25), may destabilize reef dynamics under a fishing effort scenario. Our qualitative analysis reveals that there are potential trade-offs between size-selective fishing activities and reef health, introducing the possibility of a shift away from a coral-dominated benthos to one dominated by macroalgae.

Scenario 2: Terrestrial runoff from sewage, agriculture, and aquaculture

Three separate pathways lead to increasing effects of runoff on sponges, coral, and macroalgae (Fig. 3). Terrestrial runoff from sewage, agriculture, and aquaculture introduces dissolved nutrients nitrogen and phosphorus into the reef system. The runoff from human activities may increase nitrogen and phosphorus supply in the water column (Fig. 3, link 49), which has a potential positive effect on both macroalgae and corals (links 35 and 36), since reefs are typically phosphorus-limited. A disruption in the N:P ratio in the water column (link 48) is also likely to negatively affect coral growth (link 9), forming the only negative pathway between runoff and benthic variables. An increase in the concentration of organic matter is also likely to lead to the growth of phytoplankton (link 31), increasing turbidity (via link 34 and via links 31 and 45) to the detriment of photosynthesis for both corals and macroalgae (links 32 and 33). Phytoplankton, which may initially bloom under high nutrient conditions, will also be negatively affected

Table 4. Pathways and loops for Scenario 3: Coastal development and land use change introduce sediments and particulate nutrients into reef systems.

Pathway or loop	Sign	Associated variables, in order
Pathway	–	Coastal development and land use change—Concentration of sediments—Population density of corals
Pathway	–	Coastal development and land use change—Concentration of sediments—Population density of macroalgae
Pathway	–	Coastal development and land use change—Concentration of sediments—Turbidity—Population density of corals
Pathway	–	Coastal development and land use change—Concentration of sediments—Turbidity—Population density of macroalgae
Pathway	–	Coastal development and land use change—Concentration of sediments—Population density of sponges
Pathway	+	Coastal development and land use change—Concentration of sediments—Population density of sponges—Turbidity—Population density of corals
Pathway	+	Coastal development and land use change—Concentration of sediments—Population density of sponges—Turbidity—Population density of macroalgae
Pathway	–	Coastal development and land use change—Concentration of particulate nutrients—Turbidity—Population density of corals
Pathway	–	Coastal development and land use change—Concentration of particulate nutrients—Turbidity—Population density of macroalgae
Pathway	+	Coastal development and land use change—Concentration of particulate nutrients—Population density of sponges
Pathway	–	Coastal development and land use change—Concentration of particulate nutrients—Population density of sponges—Turbidity—Population density of corals
Pathway	–	Coastal development and land use change—Concentration of particulate nutrients—Population density of sponges—Turbidity—Population density of macroalgae
Pathway	–	Coastal development and land use change—Concentration of organic matter (POC and DOC)—Turbidity—Population density of corals
Pathway	–	Coastal development and land use change—Concentration of organic matter (POC and DOC)—Turbidity—Population density of macroalgae
Pathway	+	Coastal development and land use change—Concentration of organic matter (POC and DOC)—Population density of sponges
Pathway	–	Coastal development and land use change—Concentration of organic matter (POC and DOC)—Population density of sponges—Turbidity—Population density of corals
Pathway	–	Coastal development and land use change—Concentration of organic matter (POC and DOC)—Population density of sponges—Turbidity—Population density of macroalgae
Loop	+	Ambient concentration of particulate nutrients and carbon—Population density of sponges
Loop	–	Ambient concentration of DOC—Population density of sponges—Population density of macroalgae—Population density of corals
Loop	+	Ambient concentration of DOC—Population density of sponges—Population density of macroalgae
Loop	+	Ambient concentration of DOC—Population density of sponges—Population density of corals
Loop	–	Ambient concentration of DOC—Population density of sponges—Population density of corals—Population density of macroalgae
Loop	+	Population density of macroalgae—Population density of corals
Loop	–	Population density of corals—Population density of macroalgae—Population density of sponges
Loop	+	Population density of sponges—Population density of corals
Loop	+	Population density of macroalgae—Population density of sponges
Loop	+	Population density of sponges—Turbidity—Population density of corals
Loop	+	Population density of sponges—Turbidity—Population density of macroalgae

Only pathways that start with coastal development and land-use change and end in a benthic community variable are listed. Pathways via link 25 (representing benthic space competition) are omitted for brevity, but it is assumed that, for each pathway listed, there exist additional pathways from coastal development and land-use change to the other benthic community variables via link 25. For loops, the last variable given in the 'Associated variables' column interacts with the first variable in the 'Associated variables' column.

by the turbidity generated (link 34), leading to a negative, stabilizing feedback loop (Table 3). Initial increases in nutrient supply from runoff may result in an initial period of growth for macroalgae, corals, and phytoplankton, but increasing turbidity is likely to result in declines in all photosynthetic organisms over time.

With the pathways largely symmetric, feedback loops triggered by differences in pathway strengths are likely to determine the dominant benthic state. The presence of a negative loop (between links 25, 27, and 28), facilitated by benthic space competition between corals, macroalgae, and sponges, may contribute to stabilizing reef dynamics under a runoff scenario. However, the presence of many positive loops (6 of 9 loops) may lead to destabilization of the reef system, for example, through the feedback in which sponge populations increase the production of detritus, in turn, increasing turbidity, leading to declining populations of macroalgae, which reduces benthic space competition with sponges, leading to further turbidity (via links 28, 29, and 33).

Overall, we find a possible tradeoff between food-producing anthropogenic activities such as agriculture and aquaculture and reef benthic state. Runoff from these and other anthropogenic activities may increase the supply of nutrients to reefs and adjacent waters, leading to potential declines in coral populations and increasing water turbidity.

Scenario 3: Land use change and coastal development

Land use change has a primarily negative impact on benthic state (13 of 17 pathways, Fig. 4). Under a land use change scenario, sediments, particulate nutrients, and dissolved organic carbon increase in coastal waters (Fig. 4, links 49–51). Abrasion from sediments is expected to negatively affect all benthic organisms, including macroalgae, corals, and sponges (links 37, 38, 40). The turbidity generated by increased sediments in the water column (link 39) also negatively affects photosynthesizing organisms, including corals and macroalgae (links 31 and 32).

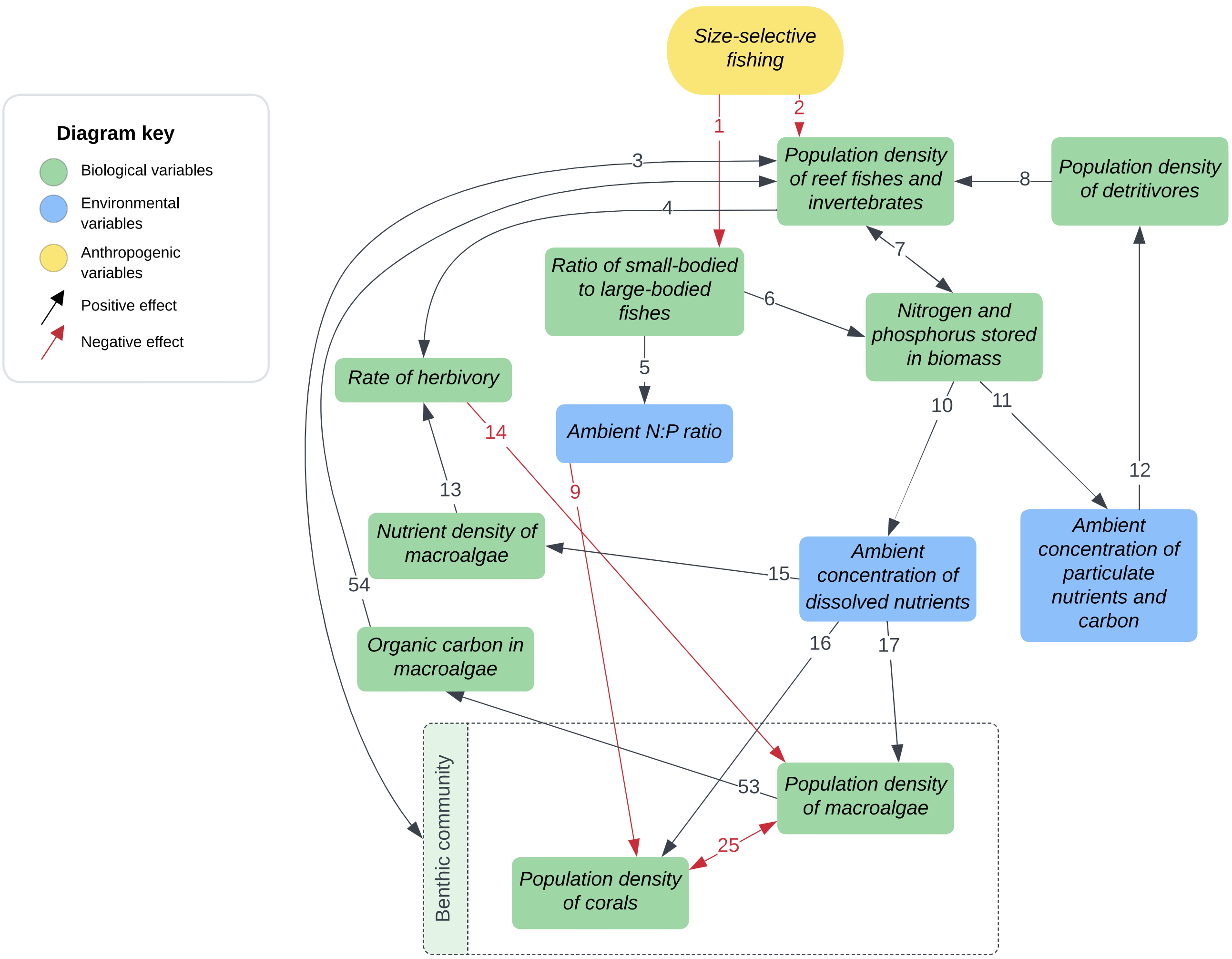

Figure 2. Scenario 1: Fishing effort selectively removes large-bodied individuals from reef systems. Causal loop diagram shown with selected variables and links from Fig. 1. A positive (negative) direct link from variable A to variable B means that an increase in the first variable will cause an increase (decrease) in the second variable, in the absence of effects from other links. A double-headed arrow indicates that interactions of the same sign flow in both directions between the two variables. Each link has a unique number identifier. Where arrows flow into the dashed rectangle (benthic community), this indicates that the link exists for all benthic community variables.

An increase in particulate nutrients and dissolved organic carbon, however, which result from land use change (links 49 and 50), provides a competitive advantage to sponges as they are the only benthic organisms to benefit from this resource (links 43 and 45; 2 positive pathways). As they cycle dissolved organic carbon (link 45), the reef biome changes, becoming less hospitable to corals and allowing sponges to win out in benthic space competition. Macroalgae and corals, damaged by sedimentation and photosynthetically hindered by turbidity, are less able to compete for space, and as they die, they increase dissolved organic carbon in the water column (links 24, 26), furthering the 'sponge loop'.

Sponges are the likely winners in this scenario, given that direct pathways from land use change to their benthic competitors (i.e. macroalgae and corals) are negative (Table 4). Positive feedback loops (8 of 11 feedback loops) involving dissolved organic carbon cycling (e.g. via links 22, 28, and 26) reinforce sponges' dominance over the other benthics, leading to a potential stable state of sponge dominance. The presence of several negative loops (e.g. between links 25, 28, and 27 and between links 22, 27, 25, and 26), facilitated by benthic space competition, stabilizes the reef system and provides nuance to reef dynamics under a land use change scenario. Based on our analysis, we conclude that land use change associated with coastal development may result in tradeoffs with the dominant benthic state of the reef, including possible shifts to a sponge-dominated reef state.

Discussion

Nutrient and carbon cycling in reefs

We find that there are multiple interacting variables and mechanisms involved in nutrient and carbon cycling in reef systems. Our study of nutrient cycling focuses on nitrogen and phosphorus, as they are the two most widely studied nutrients and play a key role in reefs (Schiettekatte et al. 2022). Reefs are typically limited by these two nutrients, and their health is strongly affected by the ambient nitrogen-to-phosphorus ratio in the water column (Wiedenmann et al. 2013). We also restrict our analysis to the organic carbon cycle. While inorganic carbon cycling is also crucial in reef functioning, it involves different processes than the organic carbon cycle, which is closely linked to the nutrient cycles (Matear et al. 2010). Anthropogenic activities interact directly with the nu-

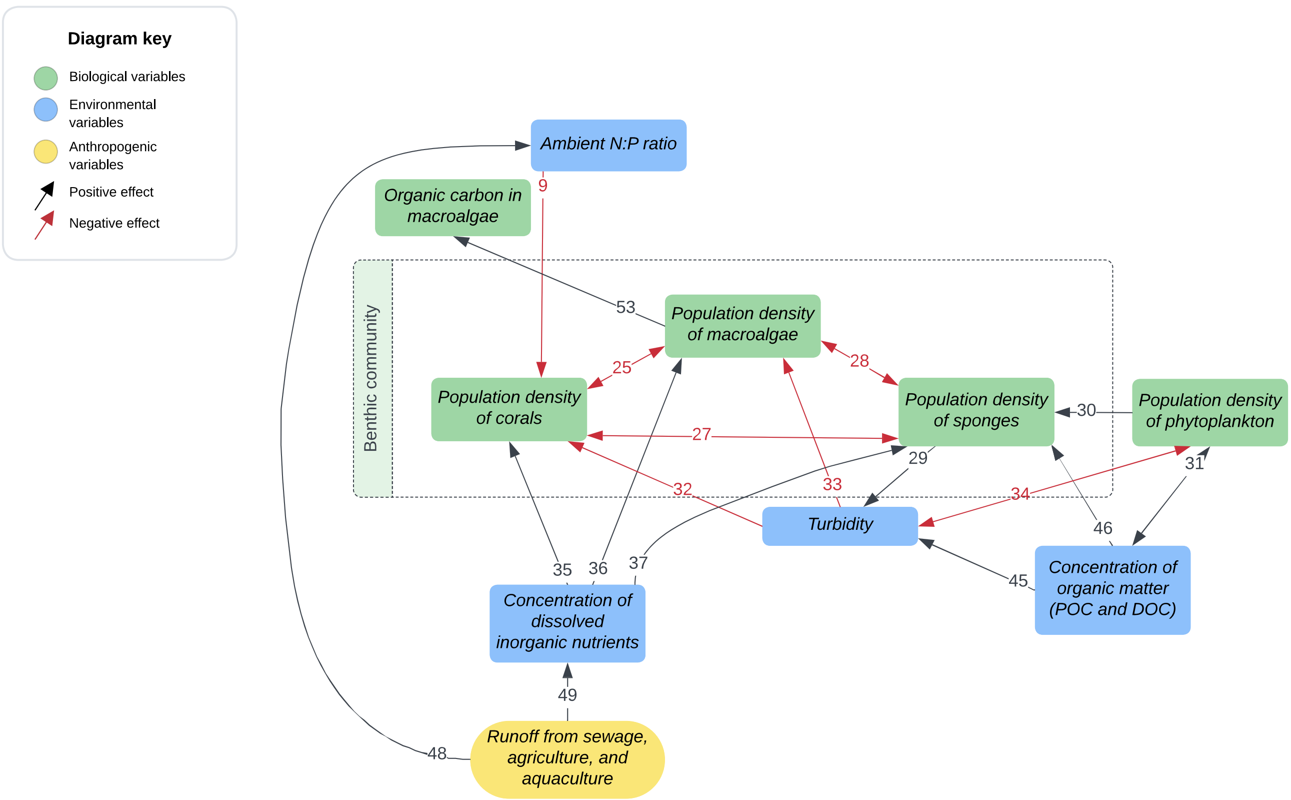

Figure 3. Scenario 2: Runoff from sewage, agriculture, or aquaculture introduces dissolved inorganic nutrients into the reef system. Causal loop diagram shown with selected variables and links from Fig. 1. A positive (negative) direct link from variable A to variable B means that an increase in the first variable will cause an increase (decrease) in the second variable, in the absence of effects from other links. A double-headed arrow indicates that interactions of the same sign flow in both directions between the two variables. Each link has a unique number identifier.

trient and organic carbon cycles by changing ecological dynamics and through the introduction of nutrients in multiple chemical forms and in proportions that differ from that which is naturally occurring. The impact of anthropogenic activities on reefs and, in particular, on populations of coral, has been well established (Bellwood et al. 2004, Fabricius 2005, Cinner et al. 2009, Zaneveld et al. 2016). Our study provides a new lens through which to understand the mechanisms by which anthropogenic activities impact reefs, by focusing on processes occurring within the nutrient and carbon cycles.

Nutrient and carbon cycling are just two of the many ecosystem services produced via ecological processes occurring within reef systems. Nutrient and carbon cycling are supporting services that are necessary for many other ecological processes (IPBES 2022) and that are foundational for many other ecosystem services reefs generate (Eddy et al. 2021). In ecosystem service assessments, it is common practice to identify metrics of the magnitude of delivery of various services (IPBES 2022). However, because nutrient and carbon cycling are complex processes involving many components within CRSES, quantifying the total cycling performed may provide only a partial view of reef health and the overall contribution of reefs to ecosystem services. The difficulty of measuring services that result from interactions among many ecosystem components, such as nutrient and carbon cycling, is part of a broader challenge of integrating such ecosystem services into policy and practice for marine and coastal systems (Drakou et al. 2017). In light of these limitations, we acknowledge the importance of considering multiple ecosystem services together, rather than individual services. The complexity of processes underlying nutrient and carbon cycling within reef systems, and the fact that rates of cycling are highly context dependent, imply that multiple ecosystem services may need to be considered together (e.g. ecosystem service bundles) to better account for trade-offs and synergies in reef management (Pellowe et al. 2023).

Anthropogenic activities trigger cascading effects through the nutrient and carbon cycles

In our causal loop model, we find a prevalence of positive feedback loops that destabilize the CRSES (Table 1). Anthropogenic activities interact with the nutrient and carbon cycles in multiple ways, with the potential to alter the dominant reef benthic state. The anthropogenic impact scenarios we highlight have primarily negative consequences for corals via direct pathways through the nutrient and carbon cycles. The size-selective fishing scenario, through changes in fish community structure and abundance, shifts nutrient concentrations on the reef, affecting both corals and macroalgae. Fisheries can alter fish community size-structure (Graham et al. 2005, Bosch et al. 2022) and composition (D'agata et al. 2016, Loiseau et al. 2021) since they are often both species- and size-selective. By targeting species at higher trophic levels or large herbivorous fishes (Graham et al. 2017, Edgar et al. 2018), size-selective fisheries shift fish populations towards smaller species and individuals, which generally have higher N:P ratio excretions due to their higher metabolic rates (Moody et

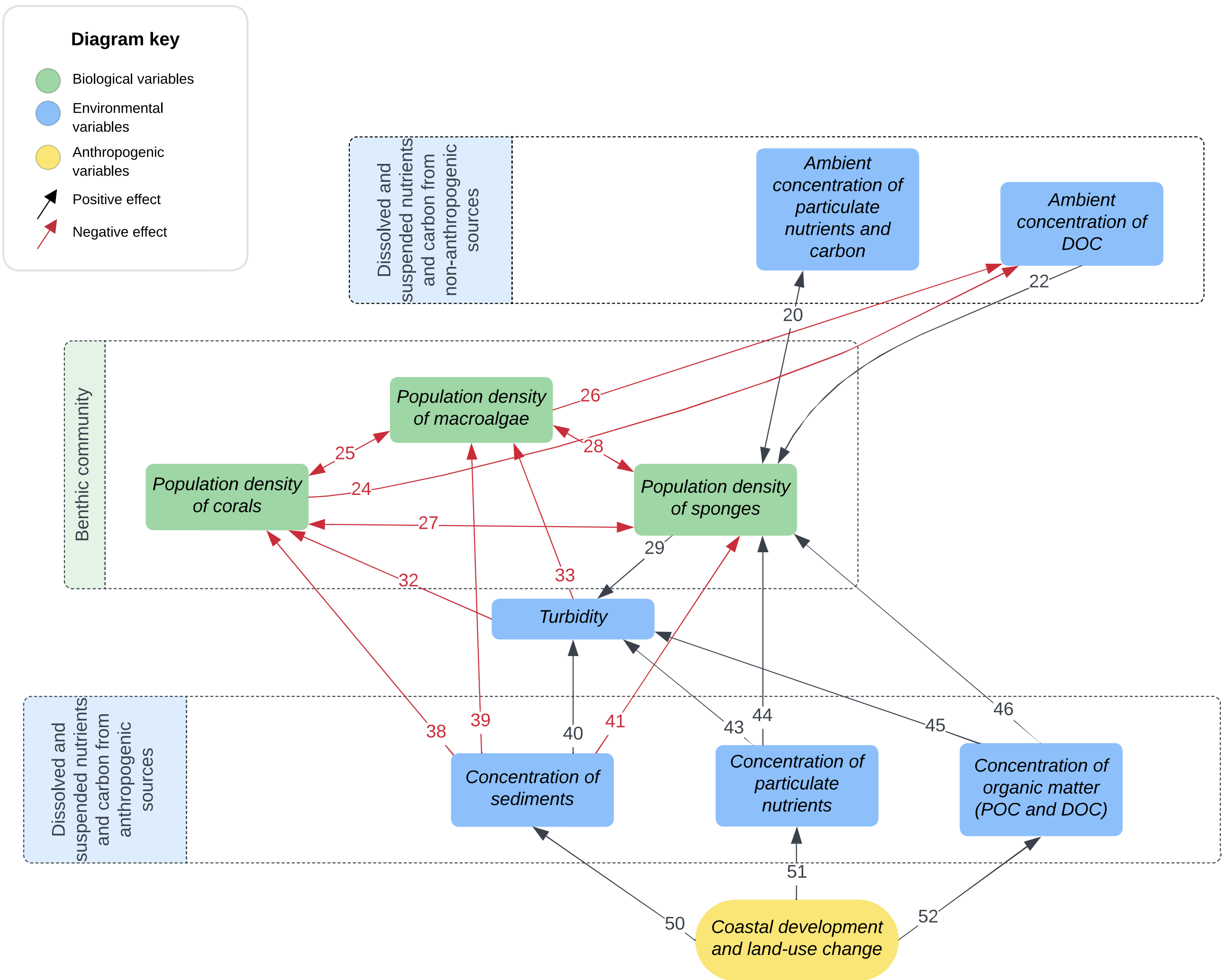

Figure 4. Scenario 3: Coastal development and land use change introduce sediments and particulates into reef systems. Causal loop diagram shown with selected variables and links from Fig. 1. A positive (negative) direct link from variable A to variable B means that an increase in the first variable will cause an increase (decrease) in the second variable, in the absence of effects from other links. A double-headed arrow indicates that interactions of the same sign flow in both directions between the two variables. Each link has a unique number identifier.

al. 2015). Shifting N:P ratio away from the optimum value (around 20:1) may be deleterious to corals (Allgeier et al. 2014). Similarly, our causal loop analysis finds more pathways that benefit macroalgae than corals (Fig. 2), introducing the possibility of a macroalgae-dominated state. A positive feedback loop via benthic space competition may make it difficult to revert to a coral-dominated state once macroalgal dominance is reached.

The terrestrial runoff scenario also contains both pathways and loops that reinforce macroalgal dominance (Fig. 3). The input of nutrients is a major anthropogenic pressure on reefs (den Haan et al. 2016), affecting reef nutrient cycles and, in some cases, leading to ecosystem degradation (Herbert 1999). While reef species such as corals need nutrients to survive, nutrients supplied by fish contribute to coral growth, while nutrients from human sources do not have the same effect (Allgeier et al. 2020). Corals have a competitive advantage in nutrient-poor environments (Muscatine and Porter 1977), but may lose this competitive advantage under high nutrient-concentration conditions (D'Angelo and Wiedenmann 2014), in which macroalgae may outcompete corals for space and increase in abundance (Burkepile et al. 2013, Faizal et al. 2020).

The land use change scenario, on the other hand, contains 14 pathways (12 through benthic space competition) and seven feedback loops that lead to a sponge-dominated state (Fig. 4). Indeed, transitions to sponge-dominated states are predicted in response to increasing anthropogenic stress (Bell et al. 2013, 2018). Land-use changes such as deforestation and the expansion of agriculture can decrease the retention of organic matter in soils, causing it to runoff into rivers, which eventually empty into the ocean. 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). 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).

We found a prevalence of positive over negative feedback loops in all anthropogenic impact scenarios, pointing to a destabilization of the CRSES. However, the presence of multiple negative feedback loops in all scenarios introduces possibilities for maintaining coral dominance despite anthropogenic pressures. The dynamics of SESs are the products of multiple interactions and feedbacks between system components (Levin et al. 2013). As such, the explicit consideration of feedback loops is necessary in SES modelling to capture the complexity of such systems and aid in the prediction of outcomes (Schlüter et al. 2012). In reefs *in situ* it is likely that feedback loops will have different strengths and that the strength of loops will change in response to shifting conditions. The eventual state of a given reef will depend on the balance of multiple feedback loops and pathways; feedback loops determine the stability of the current state, while pathways affect the direction of change. Predicting dominant benthic state will require site-specific information on the relative strength of each loop.

Implications for policy

Understanding how human activities impact natural biogeochemical cycles is a fundamental step towards management that accounts for the complexity of marine SESs and mitigates the effects of anthropogenic activities on reefs. By revealing how anthropogenic activities interact with nutrient and carbon cycling to influence reef system outcomes, this study reveals several possible avenues to reduce anthropogenic stressors on reefs.

Fishing activities can shift the amounts of nitrogen to phosphorus stored in biomass and the ratio of nitrogen to phosphorus excreted by fishes. The primary avenue identified in this study whereby fishing activities influence reef benthic state is through changes in the amount of nitrogen and phosphorus stored in biomass and the ratio of nitrogen to phosphorus, triggered by shifts in reef fish population density and size structure. Fisheries management plans that consider the nutrient storage and cycling capacities of different fish species (Allgeier et al. 2015), and aim to maintain the ratio of nitrogen to phosphorus may help ensure that fisheries do not disrupt the environmental conditions necessary for corals to thrive. Anthropogenic activities such as coastal development and agriculture, as well as inputs such as sewage, result in an increased load of dissolved and particulate nutrients in coastal waters, which we find have negative effects on corals through the nutrient and carbon cycles. However, mangroves and wetlands can act as buffers by providing places where nutrients can be cycled and sediments can settle before they reach reefs (Wickramasinghe et al. 2009). The restoration of these coastal zones can help mitigate anthropogenic effects and contribute to reef conservation (Wickramasinghe et al. 2009).

Human pressures are increasing in reefs around the world (Hughes et al. 2017), and it is likely that reefs will experience an increase in all three anthropogenic scenarios explored here, compounding the number and magnitude of interactions and loops affecting benthic community composition. Increasing concentrations of dissolved inorganic nutrients from runoff, coupled with the addition of sediments, particulate nutrients, and organic matter from land-use change are likely to reinforce the so-called 'sponge loop' (de Goeij et al. 2013), wherein sponges utilize excess nutrients and organic matter to the ultimate benefit of sponges over other benthic organisms. Benthic space competition loops between corals, macroalgae, and sponges occur in all anthropogenic impact scenarios. Size-selective fishing impacts benthic organisms via pathways distinct from those of runoff and land-use change but, through space competition loops among benthic organisms, may further destabilize a reef that is already in transition from other stressors.

Future research directions

We aimed to represent a simplified and generalized picture of common variables and interactions related to nutrient and carbon cycling across diverse reef systems, however, the causal loop diagram we developed is not exhaustive of all variables and interactions that exist within CRSES. We focus primarily on benthic organism cover and local-scale interactions; however, we acknowledge the importance of regional and broader-scale movement and transport of nutrients and carbon within ocean ecosystems (Cyronak et al. 2018, Saba et al. 2021). We encourage future work on how local-to-regional scale mechanisms influence nutrient and carbon cycling on reefs, reef health, and ecosystem service outcomes. Microbes in the water column and ocean sediments also play a critical role in ocean nutrient and carbon cycles (Glaze et al. 2022). They play a regulating role through their interactions with sponges (Freeman et al. 2021) and macroalgae (Wegley Kelly et al. 2022), which contributes to the functioning and resilience of coral reefs (Nelson et al. 2023). Future work to include microbial cycling in social-ecological models of coral reefs will improve understanding of how microbes contribute to reef health and reef-associated ecosystem services.

Most previous work on nutrient and carbon cycling performed by specific types of organisms has focused on reef fishes (Allgeier et al. 2016). Our literature search revealed few studies on the relative contributions of other taxa, including invertebrates, marine mammals, fishes, sharks, and birds, to reef nutrient cycles. Historically, large animals, including sharks, whales, and birds played a major role in the transport of nutrients, both within oceans and across the land-sea barrier (Doughty et al. 2016). However, with declining populations and extinctions, animals' role in the global and vertical transport of nutrients has decreased (Doughty et al. 2016). Further research is needed about the magnitude and spatial distribution of the role of marine macrofauna in the translocation of nutrients to and from reefs. This information would enhance our understanding of the variables and mechanisms of nutrient and carbon cycling in CRSES, and better guide policy that accounts for their complexity.

In addition to the three anthropogenic impact scenarios we explore, which interact with the nutrient and inorganic carbon cycles, reefs experience numerous other stressors, including impacts of climate change, rising ocean temperature, changing pH, and increasing fishing pressure (Hughes et al. 2017), all of which may interact with and influence the strength of the feedback loops we identify. Considering how these feedback loops are impacted by multiple interacting stressors is an important direction for future work. The maintenance of reef biological functions is a key objective of reef management in the Anthropocene (Hughes et al. 2017), and social-ecological modelling of coral reefs is one approach to identify leverage points within CRSES towards this aim.

Conclusions

(1) Within reef SESs, the variables and mechanisms involved in nutrient and carbon cycling create complex dynamics, interacting pathways, and both positive and negative feedback loops. Qualitative causal loop analysis is useful for summarizing the feedback loops and pathways that contribute to dynamical processes in reefs, and identifying possible strategies to mitigate the impact of anthropogenic activities on reef health.

(2) Anthropogenic activities interact directly with the nutrient and organic carbon cycles, e.g. by changing reef fish size structure and composition and through the introduction of dissolved and particulate nutrients and carbon. Our analysis reveals multiple mechanisms whereby anthropogenic activities affect the dominant benthic state of reefs.

(3) Multiple feedback loops introduce avenues whereby coral reef dominance can be maintained. Specific and detailed information about the social-ecological context of individual reefs will be necessary to predict their future state.

Author contributions

K.E.P.: Conceptualization, design & methodology, formal analysis, funding acquisition, investigation, visualization, writing—original draft, writing—review & editing. A.D.: Conceptualization, formal analysis, investigation, visualization, writing—original draft, writing—review & editing. D.E.B.: funding acquisition, validation, writing—review & editing. D.M.: funding acquisition, validation, writing—review & editing. S.J.L.: Conceptualization, design & methodology, formal analysis, funding acquisition, supervision, writing—original draft, writing—review & editing.

Conflict of interest

The authors declare that they have no known conflicting financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary data

Supplementary data is available at *ICES Journal of Marine Science* online.

Data availability

The data underlying this article are available in the article and in its online supplementary material.

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