

Coral reef ecological pump for gathering and retaining nutrients and exporting carbon: a review and perspectives

Linbin Zhou^{1, 2, 3}, Yehui Tan^{1, 2, 3*}, Liangmin Huang^{1, 3*}

¹ CAS Key Laboratory of Tropical Marine Bio-resources and Ecology/Guangdong Provincial Key Laboratory of Applied Marine Biology, South China Sea Institute of Oceanology, Chinese Academy of Sciences, Guangzhou 510301, China

² Southern Marine Science and Engineering Guangdong Laboratory (Guangzhou), Guangzhou 511458, China

³ University of Chinese Academy of Sciences, Beijing 100049, China

Received 20 August 2022; accepted 21 October 2022

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Abstract

How coral reefs with high productivity and biodiversity can flourish in oligotrophic tropical oceans has inspired substantial research on coral reef ecosystems. Increasing evidence shows that similar to water in an oasis in the desert, there are stable nutrient supplies to coral reefs in oligotrophic oceans. Here, with emphasis on the fluxes of organic matter, we summarize at the ecosystem level (1) the multiple input pathways of external nutrients, (2) the storage of nutrients in reef organisms, (3) the efficient retaining and recycling of dissolved and particulate organic matter within coral reef ecosystems, (4) the distinctly high phytoplankton productivity and biomass inside and near oceanic coral reefs, and (5) the export of reef-related organic carbon to adjacent open oceans. These properties enable coral reefs to function as ecological “pumps” for gathering nutrients across ecosystems and space, retaining and recycling nutrients within the ecosystem, supporting high phytoplankton productivity, and exporting organic carbon to adjacent open oceans. Particularly, the high phytoplankton productivity and biomass make waters around coral reefs potential hotspots of carbon export to ocean depths via the biological pump. We demonstrate that organic carbon influx is vital for coral reef ecosystems’ carbon budget and carbon export. The concept of the coral reef ecological pump provides a framework to improve the understanding of the functioning of the coral reef ecosystem and its responses to disturbance. Prospects of the coral reef ecological pump in coral reef studies are discussed in changing oceans driven by human activities and global change in the Anthropocene.

Key words: Darwin’s Paradox, coral reef, nutrients, coral reef ecological pump, carbon export, ocean carbon cycle

Citation: Zhou Linbin, Tan Yehui, Huang Liangmin. 2023. Coral reef ecological pump for gathering and retaining nutrients and exporting carbon: a review and perspectives. *Acta Oceanologica Sinica*, 42(6): 1–15, doi: 10.1007/s13131-022-2130-1

1 Introduction

On the historic voyage of the *Beagle* from 1832 to 1836, Charles Darwin observed marvelous coral reefs distributed in oligotrophic tropical waters all over the world (Darwin, 1842). The observation inspired the well-known question of how thriving coral reefs can flourish in apparently barren tropical oceans—often termed “Darwin’s Paradox”. It is difficult to imagine that such a species- and biomass-rich community is not highly dependent on nutrients.

Coral reefs’ high productivity and biodiversity are emergent properties only occurring at the ecosystem level (Hatcher, 1997). Increasing knowledge of ecosystem-level nutrient processes underlying the properties is contributing to answering Darwin’s Paradox. Since Darwin attempted to answer this question, much has been known about the nutrient supply to, and nutrient cycling in, coral reef ecosystems (Odum and Odum, 1955; Johannes

et al., 1972; Davis et al., 2009; de Goeij et al., 2013; Gove et al., 2016). A summary work indicates a constantly improving understanding of coral reef nutrient processes (Atkinson, 2011). The main points are as follows: (1) coral reef as a whole can absorb nutrients from the flowing low-nutrient oceanic water by diffusion; (2) many other sources of nutrients, such as submarine groundwater discharge, nitrogen fixation, recycling from sediments, sporadic mixing through internal waves, and local upwelling, are needed to sustain coral reef function; (3) continual nutrient input and tight recycling are important to sustain high productivity; (4) however, knowledge gaps exist both in the importance of fluxes of particulate organic matters to reef function and in the export of reef matters. Ten years after then, many coral reef studies add new data to the knowledge of nutrient supply, recycling, and the influx of particulate organic matter (POM). Nevertheless, the roles of coral reefs in exporting organic matter

Foundation item: The Key Special Project for Introduced Talents Team of Southern Marine Science and Engineering Guangdong Laboratory (Guangzhou) under contract No. GML2019ZD0405; the National Natural Science Foundation of China under contract Nos 41506150 and 41130855; the Guangdong Basic and Applied Basic Research Foundation under contract No. 2019A1515011645; the National Science and Technology Basic Work Program of the Ministry of Science and Technology of China under contract No. 2015FY110600; the Science and Technology Planning Project of Guangdong Province, China under contract No. 2020B1212060058; the Development Fund of South China Sea Institute of Oceanology of the Chinese Academy of Sciences under contract No. SCSIO202204.

*Corresponding author, E-mail: tanyh@scsio.ac.cn; hlm@scsio.ac.cn

to the surrounding oligotrophic open oceans are still less explored.

The water column around the benthic community is a vital pathway and carrier for the exchange of material and energy between a coral reef ecosystem and its outer environment (Ruiz Sebastián and McClanahan, 2013). However, in contrast to the well-known benthic community of coral reef ecosystems, less attention has been paid to the pelagic community in the overlying water column. Based on the investigation in the 1980s and 1990s in the South China Sea, Huang et al. found a widespread phenomenon that phytoplankton productivity and biomass were significantly higher in coral reef waters (especially lagoon waters) than in adjacent open oceans (Huang, 1991, 1997). Increasing evidence of high biological activities in reef waters has been reported around the world (Gove et al., 2016; Lnborg et al., 2017; Huang et al., 2020). Nevertheless, the ecological roles of this phenomenon in carbon export to oligotrophic pelagic ecosystems and ocean depths surrounding coral reefs are still not well understood.

This work attempts to provide an overall picture of the coral reef ecosystem's ability to gather, retain, and recycle nutrients, and the role of coral reefs in the biological pump by forming hot-spots of carbon export. By doing this, a new concept "coral reef ecological pump" was proposed to depict the integral role of coral reefs in gathering and retaining nutrients and exporting carbon.

The prototype of the concept was inspired by the earlier investigations on the high primary productivity in the water column of coral reefs in the 1980s in the South China Sea (Huang, 1991, 1997). At that time, the input of external nutrients and efficient recycling of nutrients were inferred to explain the high phytoplankton productivity (Wu et al., 2001). As an evolution from the prototype, our focus and thinking updated from the water column of coral reefs to the entire coral reef ecosystem. With increasing knowledge of the input, storage, and retention of nutrients and the output of carbon, related to coral reefs, herein we develop a complete description of the coral reef ecological pump.

In this summary, much attention was given to the flux of organic matter, including organic nutrient input from multiple pathways, internal cycling and retaining of dissolved and particulate organic matter, a large amount of animal (e.g., invertebrates and fish) biomass as an organic nutrient pool in the coral reef ecosystem, and the importance of organic carbon input to the coral reef ecosystem. We demonstrated that organic carbon influx should be considered a part of the gross available organic carbon (the sum of gross primary production and organic carbon influx). Otherwise, the net production (the difference between gross available organic carbon and community respiration) and the carbon export to adjacent open oceans could be significantly underestimated. In addition, we summarized the current understanding of the distinctly higher phytoplankton productivity and biomass inside and near coral reefs, especially oceanic coral reefs (including oceanic island and atoll reefs), than in adjacent open oceans (see details in Section 4). By doing this, we discussed the role of coral reefs in exporting organic carbon (including POM, e.g., dying/decaying phytoplankton cells, sinking animal carcasses, feces, and microbial aggregates) to ocean depths.

The definition of "coral reefs" by Crossland et al. (1991) is used here. It defines the outer boundary of reefs as the bottom of the photic zone or transition to <80% reef sediments surrounding structures of a coral framework with living reef organisms. According to this definition, the coral reef ecosystem consists of

not only the whole reef (including reef flats, reef crests, reef slopes, and back reefs) but also lagoons (Atkinson and Falter, 2003) and includes not only benthic communities but also pelagic organisms in the overlying water column.

2 "Pumping" and gathering nutrients from outside

Increasing evidence shows that similar to water in an oasis in the desert, there are stable nutrient supplies to a coral reef in the oligotrophic ocean. Coral reefs, especially oceanic coral reefs, are naturally subsidized solar-powered ecosystems that can function as ecological pumps to gather external nutrients across ecosystems and over long distances. Physical processes (e.g., tides), physical process-mediated input of external nutrients, and nutrient input mediated by reef organisms and visitors (including seabirds, large roving teleosts, elasmobranchs, and cetaceans) are all energy subsidies to coral reef ecosystems. This energy subsidy will help primary producers in a coral reef ecosystem use solar power more efficiently to produce organic matter (i.e., high productivity) (Odum and Barrett, 2005).

The use of external POM as a food and nutrient source is vital to a coral reef ecosystem. A recent study shows that nutrients in oceanic POM are important to maintaining net ecosystem calcification and coral reef health, especially under stressful conditions such as bleaching due to warming (Kealoha et al., 2019). In the following text, we summarize seven main ways by which coral reef ecosystems gather external nutrients (Fig. 1).

2.1 Physical processes increase nutrient supply from both deep and surface oceanic waters

The special topography of a coral reef makes it able to pump nutrients from deep waters. Coral reefs, especially oceanic coral reefs, which are like mountains, rise from the deep ocean, making the local topography and bathymetry around the reef distinguishable from the vast open ocean. Physical processes, such as currents, tides, storms, waves, and internal waves, interact with the local topography and can result in the transport of deep waters rich in nutrients to the upper layers of the water column inside and near coral reefs (Leichter et al., 2003; Gove et al., 2016; Wyatt et al., 2020). This nutrient-rich water could not only contribute to the enhanced near-reef phytoplankton biomass and productivity but also directly support the production of primary producers in the coral reef ecosystem (Green et al., 2019).

Physical processes can also facilitate the uptake of nutrients from surface ocean water flowing over coral reefs. Coral reefs as a whole can continuously obtain nutrients (e.g., phosphate and ammonia) from ocean water flowing over the coral reef (Atkinson, 1987, 1992, 2011; Atkinson and Falter, 2003). However, this kind of nutrient transfer is limited by the diffusion rate of seawater mass. Physical processes such as waves can increase the flow velocity when they come across the shallow waters of coral reefs. The increased flow velocity can increase the diffusion rate of water mass and release the mass transfer limitation on the areal uptake of nutrients by coral reefs (Atkinson, 1987, 1992, 2011).

2.2 Coral reef animals "fetch" nutrients across ecosystems

Coral reef animals such as fish, feed in pelagic waters and other ecosystems away from coral reefs have long been known to be an important pathway of nutrient input to coral reef ecosystems (Geesey et al., 1984; Pinnegar and Polunin, 2006). Many fish (including reef-associated sharks) feed away from and then rest in or over coral reefs, and excretory and fecal products from the fish are a substantial source of nitrogen and phosphorus in coral reef waters (Meyer et al., 1983; Khan et al., 2017; Francis and

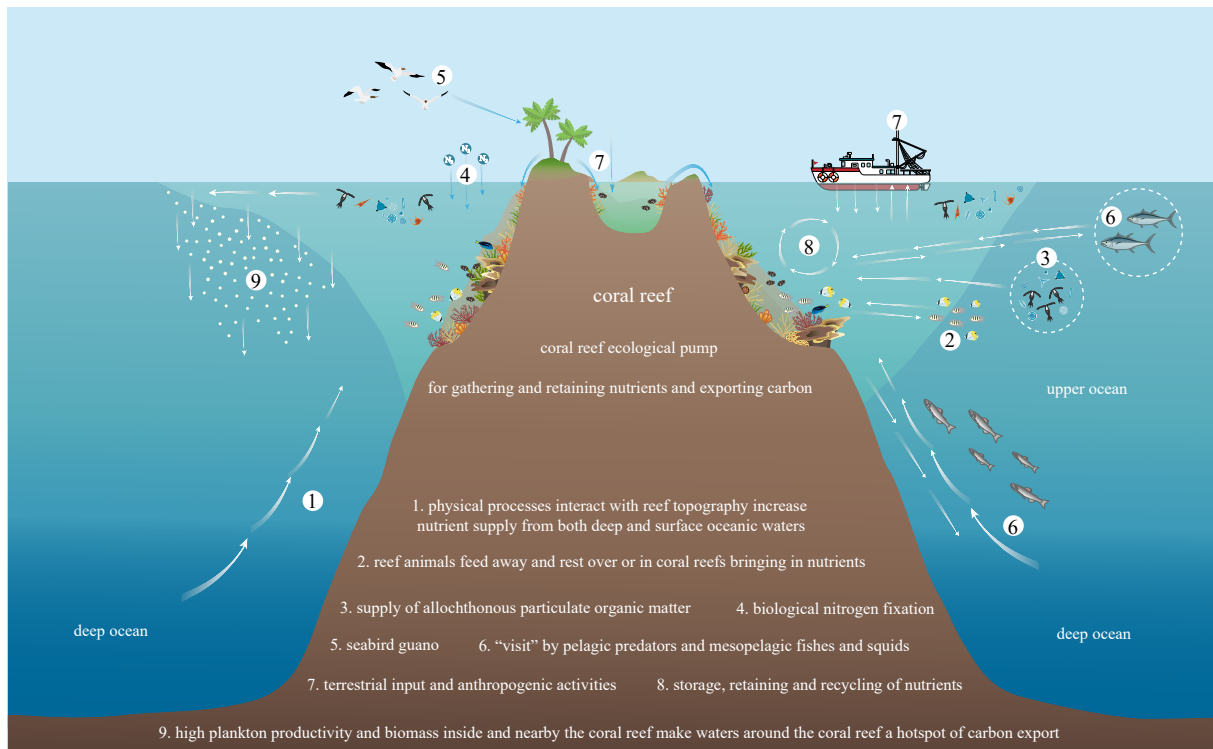


Fig. 1. Schematic map of a coral reef ecological pump for gathering and retaining nutrients and exporting carbon. Numbers ①–⑦ in white circles indicate multiple pathways of nutrient input to the coral reef ecosystem; ③ indicates storage and retention of nutrients within the coral reef ecosystem; and ⑨ indicates waters around the coral reef, especially an oceanic coral reef, a hotspot of carbon export. The colors from green in the reef lagoon, light green near the reef, and light blue off the reef show the decreasing gradient of plankton productivity and biomass from waters inside and near the reef to the open waters off the reef.

Côté, 2018). For example, a study shows that many reef fish species migrate >1 km away from their shelter sites each night (Khan et al., 2017). Some reef fishes can migrate more than 10 km from their nurse and feeding habits (mangroves and seagrass) to coral reefs (Berkström et al., 2020; Sambrook et al., 2020). Some reef fishes (e.g., some groupers, emperors, snappers, and jacks) move even tens to hundreds of kilometers (Green et al., 2015).

Fish-fetched nutrients could be considerable to the coral reef. It has been estimated that the number of nutrients deposited by juvenile French and white grunts could account for 1.0%–1.4% of the nitrogen and 2.6%–4.4% of the phosphorus available to two species of coral heads the fish rest over, and the fish-supplied nitrogen to the coral heads each day was estimated to be approximately 30%–75% of the recorded high nitrogen fixation rate of 179.2 mg/(m²·d) (in terms of N) in coral reef waters (Meyer et al., 1983). Fish-derived nutrients could be much more important for coral reefs. A recent study shows that the delivery of nitrogen and phosphorus to coral heads with aggregations of grunts could be more than 7 times higher than that to similar sites that lack schools of these fishes (Shantz et al., 2015). Nitrogen supply mediated by fish has been reported more than 25 times higher than all other sources combined (Burkpile et al., 2013).

Recent studies show that fish and coral larvae are another important input of organic nutrients to the coral reef ecosystem (Allgeier et al., 2018; Brandl et al., 2019). Most coral reef fishes have planktonic larval stages, especially tiny cryptobenthic reef fishes, which can disperse extremely abundant larvae in the near-reef pelagic waters; the larvae feed and grow in the resource-rich, near-reef environment (Gove et al., 2016); and then, they return to their home reefs to maintain adult population and

form a route of nutrient input to the coral reef ecosystem (Goatley and Bellwood, 2016; Brandl et al., 2019). Due to rapid growth and extreme mortality (on average 30% per day) shortly after settlement, tiny cryptobenthic reef fishes represent almost 60% of the consumed reef fish biomass (Goatley and Bellwood, 2016; Brandl et al., 2019). It has been estimated that fish larvae can replace the nutrients in the entire fish community in Caribbean coral reefs in 28 d and 434 d for nitrogen and phosphorus, respectively (Allgeier et al., 2018).

2.3 Coral reef animals catch nutrients in external POM

POM, including plankton and detritus, is an important nutrient source for many reef animals. External POM can be transported to coral reefs with water movement caused by physical processes (e.g., currents and waves). Currents, tides, and waves can bring POM from various distances to the reef (Costa et al., 2017). It has long been known that plankton is an important source of nutrients for coral reef organisms (Johannes et al., 1970; Sebens et al., 1996; Yahel et al., 1998; Genin et al., 2009; Patten et al., 2011; Wyatt et al., 2013; Xu et al., 2021), and many corals, sponges, almost all clams, and other filter feeders can use POM as a food source (Ribes et al., 2005; Pawlik et al., 2018). Heterotrophic feeding on POM is especially important to many corals for acquiring nitrogen, phosphorus, and other nutrients because photosynthesis by coral's symbiotic algae cannot supply these nutrients (Houlbrèque and Ferrier-Pagès, 2009; Fox et al., 2019).

As a result of the impressive ability of reef organisms to intercept and capture POM, the coral reef margin has been called a "wall of mouths" (Hamner et al., 1988, 2007). A study on the coral reef flat of the north shore of Moorea, French Polynesia, shows

that external POM carried onto the reef flat by currents contributes up to 13% of the net input of organic carbon (including primary production) to the zone nearest the reef crest (Alldredge et al., 2013). Phytoplankton-derived particulate organic nitrogen (28–70 mg/(m²·d), in terms of N) and particulate organic carbon (14–27 mmol/(m²·d), in terms of C) at Ningaloo Reef, western Australia were in the same magnitude as that typical for dissolved nitrogen uptake and net community production, respectively (Wyatt et al., 2010). High rates of net uptake of particulate organic nitrogen (56–420 mg/(m²·d), in terms of N) and carbon (6–130 mmol/(m²·d), in terms of C) by the reef community in the reef crest of a fringing coral reef have also been recorded (Wyatt et al., 2013).

2.4 Biological nitrogen fixation provides new nitrogen

Coral reefs thrive in oligotrophic waters that are often nitrogen-limited. Nitrogen fixation is an important pathway of nitrogen input to coral reef ecosystems. Biological nitrogen fixation, the prokaryote-mediated conversion of atmospheric N₂ to ammonia, provides bioavailable nitrogen to both nitrogen-fixing organisms (diazotrophs) and non-nitrogen-fixing organisms. Diazotrophs are widespread in coral tissues and mucous, crustose coralline algae, many other reef organisms, and habitats, and they bring new nitrogen from the atmosphere for primary production in coral reef ecosystems (Wiebe et al., 1975; Wilkinson and Fay, 1979; Grover et al., 2014; Lesser et al., 2018; Sheng et al., 2023). Nitrogen fixation rates of 9.3 mg/(m²·d) to 18.6 mg/(m²·d) (in terms of N) were observed on reef flats and lagoon patch reefs in the Great Barrier Reef (Larkum et al., 1988), and high nitrogen fixation rates of >160 mg/(m²·d) and 20.3 mg/(m²·d) (in terms of N) were recorded in benthic cyanobacterial mats and algal turfs, respectively, on coral reefs in the southern Caribbean (den Haan et al., 2014; Brocke et al., 2018).

In addition, abundant planktonic diazotrophs, maximum growth rates of the planktonic diazotrophs, and high nitrogen fixation rates have been recorded in coral reef waters (Biegala and Raimbault, 2008; Turk-Kubo et al., 2015; Meunier et al., 2019). Iron and phosphate supplied from land runoff have been reported to enhance nitrogen fixation and maintain abundant *Trichodesmium* spp. around oceanic coral reef islands in the western South Pacific Ocean (Shiozaki et al., 2014). The nitrogen fixation by planktonic diazotrophs can be a significant source of nitrogen to phytoplankton and corals in coral reef waters (Benavides et al., 2016; Tilstra et al., 2018; Pupier et al., 2019). For example, ingestion of planktonic diazotrophs has been reported to provide the tropical coral *Stylophora pistillata* with 182.4 mg/(m²·d) (in terms of N) (Benavides et al., 2016). In fact, nitrogen fixation is considered a major source of new nitrogen in coral reef ecosystems (Fiore et al., 2010). The new nitrogen from nitrogen fixation can support a substantial proportion of the primary production in coral reef ecosystems. For example, up to 20% of net reef primary production is supported by nitrogen fixation during summer in a Red Sea coral reef (Cardini et al., 2016).

2.5 Seabirds provide nutrients by defecating in reef waters or on coral reefs

Coral reefs and islands (cays) are often attracting places for the stay (e.g., for nesting, breeding, and resting) of seabirds. Seabirds can act as carriers to gather nutrients from a large barren area in the open ocean and deposit guano rich in both nitrogen and phosphorus to the small oasis of coral reefs, as they often feed in large areas of the open ocean, and then rest/nest/breed in coral islands or atolls (Staunton Smith and Johnson,

1995; Honig and Mahoney, 2016; Lorrain et al., 2017). Seabirds have been reported providing a large amount of nitrogen (150 mg/(m²·d), in terms of N) and phosphorus (30 mg/(m²·d), in terms of P) on a coral cay, the Heron Island at the southern end of the Great Barrier Reef (Staunton Smith and Johnson, 1995). The nutrients in seabird guano can be transported with submarine groundwater discharge to adjacent coral reef lagoon with a minimum rate of 29.4 mg/(m²·d) (in terms of N) (McMahon and Santos, 2017). A recent study shows that the nutrients in seabird guano enhance the productivity and functioning of coral reefs, and the isotopic signal of the nutrients with seabird guano could be detected in corals, macroalgae, filter-feeding sponges, turf algae, and fish in waters around the coral reefs (Graham et al., 2018; Savage, 2019).

2.6 Highly mobile transient visitors provide nutrients

Highly mobile transient visitors can bring external nutrients from a long distance away to coral reefs. High biodiversity and biomass and special habitats in coral reefs are attractive to many highly mobile transient animals (including sharks, scombrids, cetaceans, and mesopelagic fishes).

Pelagic predators (sharks, scombrids, etc.) and cetaceans are well known to visit or migrate from long distances to coral reefs (Green et al., 2015; Bonnin et al., 2019; Derville et al., 2019; Heupel et al., 2019). Their visits can episodically bring external nutrients to coral reef ecosystems. However, these kinds of nutrient inputs have rarely been quantified. Williams et al. (2018) reported that the egestion of grey reef sharks (*Carcharhinus amblyrhynchos*) could provide allochthonous nitrogen to the Palmyra Atoll (with an area of 12 km²) at a rate of 6.8 mg/(m²·d) (in terms of N).

Mesopelagic fishes, squids, and other organisms can migrate to coral reef waters at night for food and other activities. The excretion and defecation of these foreign organisms and the predation on the mesopelagic organisms by reef predators can bring nutrients to coral reefs (Reid et al., 1991; McManus et al., 2008). A recent study shows that mesopelagic organisms contribute to 17% of the diet of reef manta rays (*Mobula alfredi*) at a remote coral reef in the western Indian Ocean (Peel et al., 2019). This pathway of nutrient input also needs to be quantified.

2.7 Terrestrial and anthropogenic inputs of nutrients

Terrestrial input and anthropogenic activities can also bring nutrients to coral reefs. Terrestrial input of nutrients from surface runoff or/and discharge of submarine groundwater can be an important nutrient source for coral reef ecosystems and adjacent pelagic waters, especially for fringing coral reefs and oceanic coral reefs with outcropping lands (Fabricius, 2005; Cuet et al., 2011; Starke et al., 2020; Jiang et al., 2020). Anthropogenic activities such as domestic sewage and land use can supply nutrients to coral reef ecosystems associated with populated coral atolls and islands (Gove et al., 2016). Nutrients (e.g., nitrogen) originating from the land and human activities can also be transported by the air and supplied to coral reefs through atmospheric deposition and rainfall (Chen et al., 2019). Human activities such as fishing and recreational activities in coral reef waters can also bring nutrients to coral reef ecosystems (Albuquerque et al., 2015; de Paula et al., 2018). Terrestrial and anthropogenic inputs of nutrients may increase with rising anthropogenic activities on coral islands and atolls.

Excess input of anthropogenic nutrients can be a threat to the health of coral reef ecosystems. Increasing evidence shows anthropogenic nutrient enrichment can increase the competitive

advantages of fleshy macroalgae and microorganisms over corals and coralline algae, and increase the prevalence and severity of coral disease and bleaching (Vega Thurber et al., 2014; Haas et al., 2016; Zaneveld et al., 2016). As a result, anthropogenic nutrients cause adverse shifts in benthic and pelagic communities in coral reef ecosystems (Haas et al., 2016; Ford et al., 2017).

3 Storage and retention of nutrients within the coral reef ecosystem

Similar to other tropical ecosystems with barren abiotic environments, coral reef ecosystems can carry out a series of mechanisms for retaining and preserving nutrients to support high system productivity (Hatcher, 1988; Odum and Barrett, 2005). Storage of nutrients in reef biomass, internal nutrient recycling within reef organisms, and efficient recycling of nutrients in dissolved organic matter (DOM) and POM can help retain nutrients within a coral reef ecosystem (Fig. 1).

3.1 Storage of nutrients in reef biomass

Large amounts of biomass, especially those of animals (e.g., corals, sponges, and fish) in coral reef ecosystems, can function as a reservoir pool for nutrient storage and supply. The coral reef ecosystem can not only gather external nutrients through multiple ways (Section 2) but also sequester and preserve the gathered nutrients in reef organisms such as corals and sponges (Zhang et al., 2015; Godinot et al., 2016). Fleshy macroalgae and turf algae can also function in storing nutrients and supplying food for herbivores, especially in degraded reefs (Sandin et al., 2008; Burkepile et al., 2013; Duran et al., 2016; Chen et al., 2019). The important roles of animals have been recognized in the storage and retention of nutrients in their biomass and in the supply of nutrients via excretion and egestion (Allgeier et al., 2017).

Differing from the remarkable dominance of plant biomass in terrestrial ecosystems such as grassland ecosystems and forest ecosystems, animals contribute a conspicuous (even the largest) proportion of the biomass in the coral reef ecosystem (Odum and Odum, 1955; Polovina, 1984; Odum and Barrett, 2005; Allgeier et al., 2017). Corals usually constitute the largest animal biomass in coral reefs (Fitt et al., 2000). For example, the mean colony biomass of the Mediterranean coral *Cladocora caespitosa* has been reported to be 730–990 g ash-free dry weight per square metre (Peirano et al., 2001), and the tissue biomass of several Caribbean coral species ranged from 74–329 g ash-free dry weight per square metre (Thornhill et al., 2011).

Sponges are a ubiquitous and important component of coral reef communities, and their biomass is often second to corals (Richter et al., 2001; Kötter, 2003; Carballo et al., 2019). A sponge biomass of 21.1 g/m² (in terms of C) was reported in a Red Sea coral reef (Richter et al., 2001).

The high abundance and biomass of fish are often present in coral reefs (Edgar and Stuart-Smith, 2014). High fish biomass above 100 g/m² is usually observed in coral reefs (Graham and Nash, 2013). An average reef fish biomass of 40.5 g/m² (8.3–129.6 g/m²) has been reported across the central and western Pacific (Williams et al., 2015). Extremely high fish biomass has been recorded in Caribbean coral reefs (>500 g/m²) (Newman et al., 2006), at the Farquhar Atoll (320 g/m²) (Friedlander et al., 2014), and at the Kingman Atoll (527 g/m²) (Sandin et al., 2008).

Nutrients stored in a large amount of animal biomass can function as a stabilizer for nutrient availability within a coral reef ecosystem. The important roles of reef fish communities in storing and supplying nutrients have been well demonstrated in recent years by Allgeier et al. (2014, 2016). They estimate that glob-

al reef fishes can supply 1 167 Gg of nitrogen to the surrounding waters each year (Allgeier et al., 2017). Importantly, the reef fish-supplied nutrients have proper nitrogen-to-phosphorus ratios that are well suited to the utilization of corals and their symbiotic algae (Allgeier et al., 2014). Therefore, coral reef fish has been proposed as a stabilizing factor for nutrient availability within coral reef ecosystems. As an extension of this idea, we suggest that reef biomass, especially animal biomass, functions as a stabilizer for nutrient availability within coral reef ecosystems.

3.2 Efficient retention and recycling of nutrients

Symbioses and the use of POM and DOM are important mechanisms for coral reef ecosystems to retain and recycle nutrients. Prevailing and diverse symbioses are well known to enable coral reef ecosystems to conserve and recycle nutrients within coral reef communities (Hatcher, 1988; Apprill, 2020). Efficient use of allochthonous and autochthonous POM and DOM, especially those in the pelagic components of coral reef ecosystems, by not only reef organisms but also the “assemblage” of reef organisms with their abiotic environments, is also vital for recycling and retaining nutrients.

Symbioses enable direct recycling and conservation of nutrients within coral reef communities. Symbiosis in coral reefs is not only prevailing but also diverse and complex. Symbioses of autotrophic *Symbiodinium* with heterotrophic hosts occur commonly in corals, sponges, nudibranchs, anemones, clams, hydroids, foraminiferans, and many other invertebrates that make up a large portion of the coral reef community (Venn et al., 2008). The symbioses are usually mutualistic, i.e., beneficial to both the nutrient-limited *Symbiodinium* and the organic carbon-limited heterotrophic hosts. Taking the *Symbiodinium*-coral symbiosis as an example, the endosymbiotic algae provide the coral photosynthetically fixed carbon, while the coral provides the algae metabolites as nutrients. These symbioses enable direct nutrient recycling between primary producers and animal consumers. Symbioses among reef animals and those associated with algae-animal symbioses, such as the well-known relationship of *Symbiodinium*-sea anemone-fish, can also facilitate the conservation and recycling of nutrients in coral reef communities (Hatcher, 1988; Roopin et al., 2008; Apprill, 2020). The formation of a holobiont that comprises an animal host and its endosymbiotic algae and associated microbes (including protozoans, fungi, bacteria, and archaea) further contributes to the efficient recycling and retention of nutrients in coral reef ecosystems (Qiu et al., 2010; Rådecker et al., 2015).

Coral mucus retains and provides POM to the benthic reef community. The reef community releases a large amount of autochthonous POM (such as coral mucus and fish feces) that may be of a similar magnitude to the uptake of allochthonous (external) POM (Wyatt et al., 2013). Endosymbiotic algae can excrete a large proportion (up to >90%) of their photosynthetically fixed carbon to the host coral, and coral exudes up to half of the fixed carbon as mucus (Hata et al., 2002; Wild et al., 2004a). Mucus can function not only directly as an energy and nutrient carrier to the benthic reef community but also as a particle trap to catch and transport both allochthonous and autochthonous POM in reef water to benthic reef communities, reducing the loss of energy and nutrients from coral reef ecosystems (Wild et al., 2004a, 2004b; Hadaidi et al., 2019).

Reef organisms play important roles in recycling and retaining nutrients in sediments. Reef holothurians (sea cucumbers) and other sediment-feeders can ingest sand sediments with organic materials and excrete dissolved inorganic nutrients (Pur-

cell et al., 2016; Lee et al., 2018). Nutrient fluxes mediated by holothurian excretion have been reported to have a similar magnitude as nitrogen fixation rates and nutrient exchange rates between the pore water and the water column (Uthicke, 2001b). The close coupling between nutrient excretion by holothurians and the utilization of nutrients by benthic microalgae is an important mechanism for recycling and retaining nutrients in the benthic community (Uthicke, 2001a). Some reef organisms, such as the jellyfish *Cassiopea* sp., can draw nutrient-rich pore waters from permeable sand sediments, facilitating benthic-pelagic coupling and primary production in oligotrophic coral reefs (Jantzen et al., 2010).

Reef sand sediments function as biocatalytic mineralizing filters. Permeable coral sands, which consist mainly of broken coral skeletons and associated microbes, can function as biocatalytic mineralizing filters to capture, degrade and mineralize coral mucus and other settled POM (Wild et al., 2004b; Schöttner et al., 2011). It has been reported that more than 15.5% of the lagoon water of Heron Island, is filtered through coral sands each day (Wild et al., 2004a). Coral sands with a dense population of benthic bacteria (5.8×10^8 cells/m³ to 6.3×10^9 cells/m³) act as a large filter system that removes coral mucus and other POM from the water column and degrades the organic matter in the upper sediment layers (Wild et al., 2004a). Coral reef sands have also been reported to be able to rapidly process the large episodic load of organic nutrients provided by coral mass spawning (Eyre et al., 2008). The ability to capture and retain POM and release nutrients make reef sediments act as reservoirs of nutrients, which can buffer and mediate the supply of nutrients to coral reefs (Erler et al., 2014; Ning et al., 2019).

The coral reef ecosystem has also special mechanisms for using DOM. As a flourishing aquatic ecosystem with high biomass, high rates of DOM production are expected in coral reef ecosystems. If there is no mechanism for recycling and retaining nutrients and energy within DOM in moving seawater, then there should be a large loss to the coral reef ecosystem. Besides the release of a large amount of POM, corals are known to release large amounts of DOM (Ferrier-Pagès et al., 1998; Tanaka et al., 2008; Wild et al., 2010). A substantial proportion (56%–80%) of the mucus released by corals will dissolve in reef waters (Wild et al., 2004a), and other reef organisms such as fish can also release large amounts of DOM in reef waters (Wild et al., 2010; Ruiz Sebastián and McClanahan, 2013; Liu et al., 2022). In addition, benthic algae (turf algae and macroalgae) and cyanobacterial mats on coral reefs can release large quantities of DOM, too (Brocke et al., 2015; Mueller et al., 2016; Rix et al., 2017; Diaz-Pulido and Barrón, 2020). Coral reef ecosystems carry out several mechanisms to recycle DOM and channel recycled nutrients and energy back to the reef food web.

First, similar to other pelagic ecosystems, through the microbial loop (Azam et al., 1983), planktonic bacteria use DOM in coral reef waters to produce POM and transfer the recycled energy and nutrients back to larger-sized planktonic consumers and/or the benthic reef community (Ferrier-Pagès et al., 2000). Interactions between corals and microorganisms within near-coral seawater microenvironments form a “coral ecosphere”, within which microbial interactions could facilitate the transfer of coral metabolites into the microbial food web (Weber et al., 2019). The rapid uptake of DOM by the unique planktonic bacterial community even can make fringing reefs sinks of oceanic DOM (Nelson et al., 2011). The coupling of phytoplankton production with nutrient recycling by the microbial loop may explain the high phytoplankton biomass and productivity in reef waters (Torréon

et al., 2002) (see discussion in Section 4).

The “sponge loop” is an important mechanism for using DOM and retaining resources within a coral reef ecosystem (de Goeij et al., 2013; Silveira et al., 2015; Rix et al., 2018; Pawlik and McMurray, 2020). In addition to their well-known ability to efficiently capture nutrients and energy from POM, sponges also consume DOM to satisfy a large portion of their respiration, biomass production, and cell replication (Hoer et al., 2018; Pawlik et al., 2018). Sponges can use both the DOM released from corals and macroalgae at different rates (Rix et al., 2017). Sponges are conspicuous and abundant within benthic fauna. Sponges alone have been reported to provide up to 60% of cavity-dwelling cover, outweighing epi-reef filter-feeder biomass by two orders of magnitude in Red Sea coral reefs (Richter et al., 2001). They use flagellated collar cells (choanocytes) to actively filter a volume of water equivalent to many times their body volume each hour (Leys et al., 2011). Sponges can use filtered DOM to produce new flagellated collar cells to replace and shed old cells as detritus or assimilate filtered DOM to build up their biomass; detritus can be used by small detritivores, while sponge biomass could be food to fish, turtles, and other spongivores (McMurray et al., 2018). Through the above two pathways, sponges efficiently transform DOM to POM and make the energy and nutrients stored in the DOM pool available to reef fauna again. The DOM-sponge-fauna pathway is called the sponge loop, which recycles energy and nutrients within DOM and transfers them back into the coral reef ecosystem in a similar way as the microbial loop (de Goeij et al., 2013).

Sediment feeders, sediment-associated bacteria, and DOM compose another pathway for using DOM. As discussed above, coral sands with a high density of benthic bacteria can use the DOM in the reef water filtered through permeable coral sands, and sediment-feeder holothurians can eat bacteria associated with the sands; thus, together, they form a trophic relationship that functions to some degree similar to the microbial loop (Richter et al., 2001; Uthicke, 2001b; Wild et al., 2004a, 2004b).

4 High pelagic primary productivity and phytoplankton biomass in waters related to coral reefs

In contrast to the well-known high benthic primary productivity in coral reefs, far less attention has been paid to the high pelagic primary productivity and plankton biomass nearby and inside the coral reefs. The high phytoplankton productivity and biomass can enable waters around coral reefs to be hotspots of carbon export (Fig. 1).

4.1 High plankton biomass and productivity near coral reefs

Increases in plankton biomass in the vicinity of oceanic islands (Hernández-León, 1991; Palacios, 2002; James et al., 2020), i.e., the island mass effect (Doty and Oguri, 1956), have been shown a near-ubiquitous feature among oceanic coral reefs (Gove et al., 2016). A basin-scale investigation in the tropical Pacific indicated that oceanic coral reefs supported increasingly higher phytoplankton biomass with a decrease in the distance (30 km to 2 km) from shore (Gove et al., 2016). A study on the Ningaloo Reef showed that planktonic productivity, especially in small phytoplankton (<5 µm), increased by an order of magnitude in inshore waters (about 360 m off the reef) compared to offshore waters (~13 km off the reef) (Wyatt et al., 2012). These high levels of plankton biomass and productivity are relevant to coral reef ecosystems, although many of the phenomena occur outside the boundary of coral reef ecosystems. As discussed in Section 2.1, the interaction of currents and other physical processes with the local topography of oceanic coral reefs could

bring nutrients to not only coral reef ecosystems but also nearby pelagic waters. Nitrogen fixation, fish waste products inside reefs, and flushing of lagoon waters can also increase nutrient concentrations and support high phytoplankton biomass near coral reefs (Gove et al., 2016; Shiozaki et al., 2014).

4.2 High phytoplankton productivity and biomass inside coral reef waters

Significant spatial variations in phytoplankton productivity and plankton biomass often occur from inside coral reef waters to the immediate vicinity of coral reefs. In addition to the decreasing gradient of phytoplankton biomass and productivity along with the increasing distance from the shore of oceanic coral reefs (Gove et al., 2016), an even more apparent decreasing gradient occurs from inside coral reef waters (e.g., lagoons) to near off-reef waters. Plankton biomass in terms of chlorophyll *a*, POM, and bacterial abundance could be several-fold or even one order of magnitude higher in lagoon waters than in off-reef ocean waters (Torréon and Dufour, 1996; Charpy et al., 1997; Wu et al., 2001; Hata et al., 2002; Torréron et al., 2002; Ke et al., 2018). A phytoplankton bloom has been documented in coral reef waters after a mass coral spawning event on the Heron Island reef (Eyre et al., 2008). Significantly higher DOM concentrations and biological activities such as phytoplankton productivity, chlorophyll-specific productivity, bacterial productivity, potential exoprotoeolytic activity, nitrogen fixation rates, and bacterial turnover rates in lagoons than in adjacent open oceans have also been reported (Torréron and Dufour, 1996; Wu et al., 2001; Torréron et al., 2002; Biegala and Raimbault, 2008; Lønborg et al., 2017; Ke et al., 2018).

High concentrations of POM (including plankton) and DOM within coral reef ecosystems can directly enrich the waters around coral reefs with POM and DOM, respectively. Flushing of reef lagoon waters with high plankton biomass and detritus can enrich adjacent off-reef waters with POM (Wyatt et al., 2013; Gove et al., 2016). Waves, tides, and currents will drive the exchange of water between a coral reef and the surrounding ocean and help to export reef-derived matter to the adjacent open ocean (Callaghan et al., 2006; Costa et al., 2017). Currents around coral reefs may carry a water plume with high POM and DOM further away from the reef to the open ocean (Fig. 1).

In summary, the coral reef-related waters are distinct from the open ocean in terms of organic carbon availability (including phytoplankton productivity and biomass) (Fig. 1). The high phytoplankton productivity and biomass inside and near coral reefs make the near-reef waters (up to dozens of kilometers off the reef) distinguishable from the vast open ocean. High vertical carbon flux likely occurs in waters around coral reefs and further open oceans because carbon export from the upper layer to ocean depths is proportional to primary productivity and related to available POM (Richardson and Jackson, 2007; Richardson, 2019). Therefore, waters around coral reefs could be hotspots of carbon export. Further attention should be paid to the functioning of coral reef ecosystems in terms of supporting high plankton biomass in waters around coral reefs and the associated export of organic carbon to ocean depths.

5 Re-examination of carbon export by considering the input of external organic matter as available new organic carbon to coral reefs

As discussed above, a large influx of external POM could be an important subsidy of nutrients and energy for coral reef ecosystems. Ignoring the input of external POM may lead to an underestimation of the gross carbon available to coral reef com-

munities, and of the export of organic carbon out of coral reef ecosystems.

The input of organic carbon can account for a substantial proportion of the gross available organic carbon to coral reef ecosystems. Ubiquitous high phytoplankton biomass in near-reef pelagic waters is a steady source of organic nutrients and carbon to coral reef ecosystems. As mentioned above, external POM passively carried by currents accounts for approximately 15% of the gross primary production in a fringing reef (Alldredge et al., 2013). The input of organic carbon mediated by the larval supply of tiny cryptobenthic reef fishes from the pelagic environment and by off-reef feeding fishes could further increase the gross available organic carbon to coral reef ecosystems. The inflow of juvenile cryptobenthic reef fishes accounts for almost 60% of the consumed reef fish biomass on reefs (Goatley and Bellwood, 2016; Brandl et al., 2019). If the annual consumed reef fish biomass equals the annual production of the reef fish and the reef fish production is 8% of the gross primary production (Polovina, 1984), then the organic carbon influx mediated by cryptobenthic reef fishes could be approximately 5% of the gross primary production. Based on the results that off-reef feeding juvenile French and white grunts could account for 1.0%–1.4% of the nitrogen and 2.6%–4.4% of the phosphorus available to the coral heads the fish rest over (Meyer et al., 1983), we could estimate that the off-reef feeding fishes can bring external organic carbon equal to approximately 1.0%–4.4% of the gross primary production. The organic carbon influx mediated by fish could be even higher. Studies show that the delivery of nitrogen and phosphorus to coral heads with aggregations of grunts could be more than 7 times higher than that to similar sites that lack schools of these fishes, and the growth rates of corals with nutrients supplied by fish is about 1.5 times of those of corals with no nutrients supplied by fish (Meyer and Schultz, 1985; Liberman et al., 1995; Shantz et al., 2015). Transient visitors could bring additional organic carbon to coral reef ecosystems. If the mentioned scenarios applied to all coral reef ecosystems, then we could make a first-order estimation that organic carbon influx could account for more than 20% of the gross primary production of global coral reef ecosystems. Therefore, organic carbon influx should not be ignored in the carbon budget of, or in the estimation of carbon export from, coral reef ecosystems.

Without considering the organic carbon influx, the carbon export from coral reefs to the adjacent open ocean could be underestimated. Crossland et al. (1991) made the first estimation of the role of coral reefs in global ocean production, and without considering the influx of external organic carbon, they estimated that most of the gross primary production is respired and recycled in coral reefs, and net community production (gross primary production minus community respiration) and export production (75% of net community production) account for only <3% and approximately 2% of the gross primary production, respectively. Several later studies based on sediment trap reported relatively higher (approximately 4% of the gross primary production) export of particulate organic carbon from reefs (Delesalle et al., 1998; Hata et al., 1998), and the organic carbon export further increased to 6%–7% of the gross primary production if the export of dissolved organic carbon was considered (Hata et al., 2002). As discussed above, many reef organisms including corals, algae (phytoplankton, turf algae, and macroalgae), and fish can release large quantities of DOM in reef waters. Flushing of reef waters by physical processes such as tides and currents can transport DOM to the surrounding open ocean. Coral reefs have been documented as a net source of DOM for the surrounding ocean

(Tanaka et al., 2011a, 2011b). The actual export of organic carbon could be even higher than the estimates because the sediment trap could not account for exported particulate organic carbon in suspension (Bouillon and Connolly, 2009; Gruber et al., 2018). The sediment trap has not been able to account for the carbon export through the active migration of reef animals, by the release of planktonic larvae by reef organisms, and by the removal of reef organisms via fishing (Hamner et al., 2007). In addition, simultaneous uptake and release of allochthonous and autochthonous organic carbon can obscure gross fluxes calculated based on concentration changes (Wyatt et al., 2010, 2012, 2013). If that is true, then the estimation of the export production by Crossland et al. (1991) was severely underestimated, and organic carbon influx should be considered to fill the “gap”.

Organic carbon influx can significantly affect the carbon budget of a coral reef ecosystem and the estimation of carbon export. By considering the input of external POM as part of the organic carbon available to coral reef communities, the gross available organic carbon of a coral reef ecosystem includes not only gross primary production but also organic carbon influx. Net organic carbon is calculated as gross available organic carbon minus community respiration. Carbon export is calculated as net organic carbon minus that buried in reef structure and human harvest. Assuming the estimation of gross primary production and organic carbon allocated to community respiration, burial in reef structure, and sustained human harvest is the same as that reported by Crossland et al. (1991), organic carbon influx at a level of only 10% of the gross primary production will lead to a considerable (fivefold) increase in the estimation of the organic carbon export from coral reefs to off-reef open waters (Fig. 2). As we discussed above, the new estimate of organic carbon export is

closer to field observations by Wyatt et al. (2013), who demonstrated that the release of autochthonous POM by a fringing coral reef may be of similar magnitude to its uptake of allochthonous POM.

In summary, the coral reef ecological pump enables coral reef ecosystems not only to maintain high productivity and biodiversity but also to intensively export organic carbon. Specifically, it functions in gathering external nutrients and organic carbon from outside, and in retaining and recycling nutrients within coral reef ecosystems. The gathered and recycled nutrients can support not only high productivity and biodiversity in the benthic community but also high productivity and plankton biomass in pelagic waters. The enhanced productivity and biomass help maintain high local POM (including phytoplankton) and DOM in reef waters and within the immediate vicinity of coral reefs. Flushing of reef waters by physical processes such as tides and currents can export organic carbon away from the reef and enrich pelagic waters there with POM and DOM. In addition, the active migration of reef animals and transient visitors (e.g., mesopelagic fish), the removal of reef organisms via fishing, and other biological processes (e.g., coral mass spawning) can also export organic carbon from coral reefs. More importantly, the distinctly high particulate organic carbon in pelagic waters inside and around coral reefs could be exported to deep depths in adjacent open oceans via the biological pump (Richardson, 2019). As a result, the coral reef ecological pump functions intensively in exporting organic carbon to ocean depths.

6 Prospects of future work about the coral reef ecological pump

The concept of the coral reef ecological pump provides a theoretical framework to understand the functioning of the coral

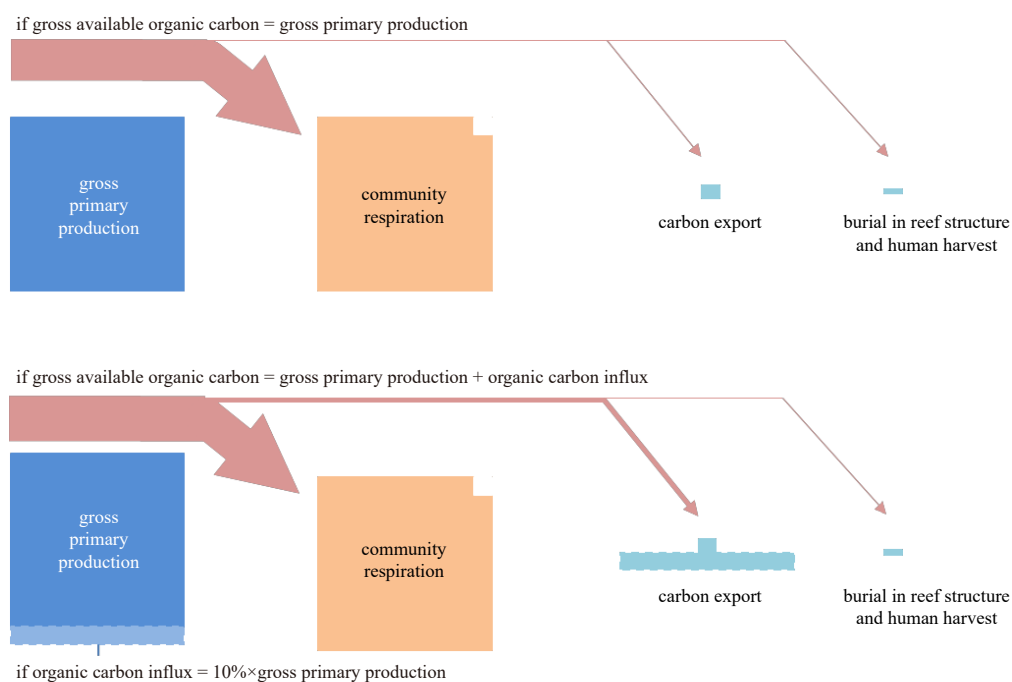


Fig. 2. Schematic map shows the effects of organic carbon influx on the organic carbon budget of the coral reef ecosystem and the estimation of carbon export. Calcification and associated formation and transport of particulate inorganic carbon (i.e., calcium carbonate) are not considered here. The lines with arrows show the flow of the gross available organic carbon to community respiration, carbon export, burial in reef structure, and human harvest. The thickness of the lines varied proportionately with the flux of organic carbon. Different sizes (in surface area) of the rectangles indicate varying amounts of organic carbon. The estimation of gross primary production and organic carbon allocated to community respiration, burial in reef structure, and sustained human harvest were according to Crossland et al. (1991).

reef as a whole at the ecosystem level or the seascape level. It not only helps to answer Darwin's Paradox but also puts forward the functioning of coral reefs in supporting high local phytoplankton productivity and the potentially important roles of coral reefs and adjacent open oceans in exporting carbon to ocean depths. We would like to share some prospects of future work about the coral reef ecological pump, including (1) quantification of the multiple input pathways of external nutrients, the recycled nutrient pool, and the export of organic carbon; (2) understanding the influence of human activities and global change on the coral reef ecological pump; (3) the role of coral reefs in the carbon cycle.

6.1 Quantification of multiple input pathways of external nutrients, the recycled nutrient pool, and the output of organic carbon

Only a few studies quantify the relative contribution of the multiple input-pathways of nutrients to coral reefs in specific sites. [Burkepile et al. \(2013\)](#) reported that fish excretion provided nitrogen to the coral reefs in the Florida Keys at a rate of 35.67 mg/(m²-d) (in terms of N). This rate is more than 25 times higher than the total rate supported by all other sources including nitrogen fixation (0.71 mg/(m²-d), in terms of N), upwelling/internal waves (0.17 mg/(m²-d), in terms of N), Florida Current gyres (0.15 mg/(m²-d), in terms of N), anthropogenic sources (0.13 mg/(m²-d), in terms of N), atmospheric deposition (0.11 mg/(m²-d), in terms of N), sediments (0.11 mg/(m²-d), in terms of N), and Florida Bay waters (0.03 mg/(m²-d), in terms of N). Nitrogen input to the Heron coral island in 1992 from seabirds (9.4 t) was more than 30 times higher than that from humans (0.29 t) ([Staunton Smith and Johnson, 1995](#)). In contrast, upwelling has been reported as the major source of nitrogen for an oceanic atoll system in the Maldives archipelago in the Indian Ocean ([Radice et al., 2019](#)). Submarine groundwater discharge accounts for 81% of dissolved inorganic nitrogen inputs to a tropical reef lagoon (Rarotonga, Cook Islands) ([Tait et al., 2014](#)). [Wyatt et al. \(2012\)](#) reported that the nitrogen input from phytoplankton to Ningaloo reef was significantly higher (10 mmol/(m²-d), in terms of N) during the autumn than that (2 mmol/(m²-d), in terms of N) during the spring, while inputs of allochthonous inorganic nitrogen (NO_x) were similar (12 mmol/(m²-d) (in terms of N) vs. 14 mmol/(m²-d) (in terms of N) between the two seasons. They also estimated that less than 55% of nitrogen may be recycled through reef autotrophs. [Furnas et al. \(1995\)](#) quantified the contribution of river discharge, upwelling, rainfall, and sewage as the main sources of allochthonous nutrients to the central Great Barrier Reef shelf.

These studies indicate that the relative importance of each pathway of nutrients and the recycled nutrient pool varies significantly from site to site. As discussed in Section 5, the inputs of organic carbon via different pathways also vary from place to place, and the organic carbon exported from the coral reef ecosystem is likely underestimated and site-specific. Therefore, more investigation is needed to quantify the relative importance of the nutrient-input pathways, the recycled nutrient pool, and the output of organic carbon from coral reef ecosystems. Categorizing coral reefs into some types (e.g., seabird-impacted type, submarine groundwater-impacted type) based on main nutrient-input pathways to the coral reefs (or other parameters) could be helpful. Closely monitoring the contribution of each pathway can be done in selected typical coral reefs for each type. After that, it may be feasible to estimate at regional and global scales of the relative importance of the nutrient-input pathways, the recycled nutrient pool, and the output of organic carbon from coral reef ecosystems.

6.2 The influence of human activities and global change on the coral reef ecological pump in the Anthropocene

The degradation of coral reefs is receiving increasing attention in the Anthropocene, a term that denotes the current geological age, during which human activity has been the dominant influence on climate and the environment ([Andradi-Brown et al., 2020](#)). Just 3% of the world's coral reefs remain in near-pristine condition ([Borsa et al., 2018](#)). Anthropogenic stressors (e.g., nutrient loading, sewage pollution, fishing, and tourism) and global stressors (e.g., warming and acidification) are leading to a worldwide decline of corals ([Rice et al., 2019](#)). How will coral reef ecosystems respond and feedback to these stressors has become an increasing concern throughout the world. The concept of the coral reef ecological pump will help to answer this question by examining the abilities of the coral reef ecosystem as a whole in gathering and retaining nutrients and exporting organic carbon under the influence of human activities and global stressors. We will briefly discuss this in the following paragraphs.

Human activities such as sewage discharge, agriculture, and aquaculture will increase nutrient input to coral reef ecosystems. However, the anthropogenically derived nutrients are often rich in nitrogen; excess loading of such nutrients, as well as sewage itself, can cause the degradation of coral reefs and drive benthic community shifts by increasing the prevalence and severity of coral disease and bleaching and promoting the advantages of fleshy macroalgae, turf algae and microorganisms ([Vega Thurber et al., 2014](#); [Haas et al., 2016](#); [Ford et al., 2017](#); [Karcher et al., 2020](#)). As a result of the decrease in corals and fishes on coral reefs, the shift from coral to algae dominance may decrease the input of nutrients and organic carbon mediated by the feeding of external POM by reef organisms (see Section 2.3) ([Silveira et al., 2015](#)). However, sponges and DOM cycling via the sponge loop may benefit from this shift, because sponge holobionts can withstand eutrophication pressure and use the algal-derived DOM more efficiently than the coral-derived DOM ([Rix et al., 2017](#); [Baquiran and Conaco, 2018](#)). Therefore, the shift may enhance the recycling and retaining of nutrients in DOM and decrease the export of DOM from coral reef ecosystems.

Other human activities such as fishing and tourism can also influence nutrient availability on coral reefs. For example, fishing can not only directly remove nutrients stored in fish, but also reduce nutrient input mediated by the active migration of fish ([Allgeier et al., 2016](#)). Recreational activities can disrupt nutrient subsidies from seabirds to coral reefs because many human visitors can disturb breeding seabirds by scaring away nesting adults and bringing in rats to deplete seabird populations on coral reefs ([Borsa et al., 2018](#); [Benkwitt et al., 2020](#)).

Global changes such as warming and acidification can affect nutrient availability on coral reefs. Warming-induced thermal stress has caused massive coral bleaching worldwide. In the short term, the loss of endosymbiotic algae could decrease nutrient acquisition capacity in corals ([Ferrier-Pagès et al., 2018](#)). In the long term, acidification and warming can be in favor of the competitive advantage of macroalgae over corals ([Diaz-Pulido and Barrón, 2020](#); [Dudgeon and Kübler, 2020](#)). As discussed above, the shift from coral to algae dominance will influence coral reefs' capability for recycling nutrients in DOM and the export of DOM from coral reefs. There is still lacking data to estimate the effects of warming and acidification on nutrient input, nutrient recycling, and organic carbon export of coral reefs at the ecosystem level.

Changes in physical processes with global warming may also affect nutrient inputs to coral reefs. Tropical cyclones, vertical

stratification, upwelling, mesoscale eddies, and ocean currents are changing along with global warming (Elsner et al., 2008; Karnauskas and Cohen, 2012; Yamaguchi and Suga, 2019; Kossin et al., 2020; Martínez-Moreno et al., 2021). Changes in the physical processes may influence the nutrient supply to coral reefs from deep waters and the dispersal of corals (Kumagai et al., 2018).

6.3 The role of coral reefs in the carbon cycle

The coral reef ecological pump provides a new angle of view to examine the role of coral reefs, and the association of coral reefs with adjacent ecosystems (i.e., the adjacent open ocean pelagic ecosystem, mangroves, and seagrass) as a whole seascape (Nagelkerken, 2009; Du et al., 2020), in the atmospheric carbon budget. There is a long debate about the role (source or sink) of coral reefs in atmospheric CO₂ (Ware et al., 1992; Kayanne et al., 1995; Gattuso et al., 1999). Photosynthesis fixes CO₂ to produce organic carbon, while the formation of calcium carbonate releases CO₂ into seawater. The net balance of the two processes and multiple other factors (e.g., local climatic forcing) determine coral reefs' role as a source or sink to atmospheric CO₂ (Bates, 2002; Massaro et al., 2012).

More and more investigation data about the differences between the partial pressure of CO₂ (*p*CO₂) in coral reef seawater and that in the atmosphere indicate that coral reefs generally act as sources of atmospheric CO₂ (Suzuki and Kawahata, 2003; Yan et al., 2016; Lønborg et al., 2019). Production of calcium carbonate and remineralization of organic carbon derived from land or other ecosystems support the role of coral reefs as sources of CO₂ in the atmosphere (Kinsey and Hopley, 1991; Suzuki et al., 2001; Gray et al., 2012). Upwelling can enhance coral reefs' role as a source of CO₂ to the atmosphere because the upwelled deep water usually has high *p*CO₂ and will outgas CO₂ to the atmosphere (Ikawa et al., 2013; González-Dávila et al., 2017). With the rapid increase of CO₂ concentrations in the atmosphere, coral reefs' role may shift from a net source to a net sink.

However, the present study suggests that coral reefs can also function in supporting high local phytoplankton productivity and in intensively exporting organic (in particulate and dissolved forms) to adjacent open oceans and ocean depths. Coral reefs may play as both sources of CO₂ to the atmosphere and hotspots of organic carbon export to ocean depths. This indicates that measuring only the *p*CO₂ in seawater overlying coral reefs is not enough to evaluate the intact role of coral reefs in the carbon cycle. We suggest taking coral reefs and adjacent open oceans as whole seascapes, and examining coral reefs' functioning in importing and exporting organic carbon at both the ecosystem level and seascape level. The coral reefs' functioning of exporting organic carbon to deep ocean depths could be important for the understanding of coral reefs' responses and feedback to further global warming.

In summary, further work is needed to explore both the coral reef ecological pump and its application to the coral reef ecology.

Acknowledgements

We thank Xinming Lei for the helpful discussion, and Xiaodong Xu for preparing Fig. 1.

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