Bulletin of Chinese Academy of Sciences 中国科学院院刊

Volume 36 | Issue 3 Article 5

3-20-2021

Coral Reefs: Potential Blue Carbon Sinks for Climate Change Mitigation

Tuo SHI
Institute of Marine Science and Technology, Shandong University, Qingdao 266237, China, tuoshi@sdu.edu.cn

See next page for additional authors

Coral Reefs: Potential Blue Carbon Sinks for Climate Change Mitigation

Abstract

Coral reefs are one of the most productive, and yet most vulnerable marine ecosystems. The global decline of coral reefs induced by climate change and human activities has already affected the processes of coral calcification and carbon cycling in the reef ecosystem, intensifying the long-standing CO2 "source-sink" debate over coral reefs. Despite the fact that coral calcification is accompanied by the release of CO2 to the atmosphere, the significance of coral reefs as a carbon sink cannot be ignored, given the complex biogeochemical processes in the reef ecosystem and the characteristic mixotrophic lifestyle of the reef-building corals. From the perspective of increasing coral resilience to climate change, this study attempts to clarify the controversy over the coral reef CO2 "source-sink" debate, explore the possible ecological regulations and pathways to transform coral reefs from a carbon source to a carbon sink, and provide theoretical framework and technical support for the deployment of ocean negative carbon emissions and the implementation of the national carbon neutrality strategy

Keywords

coral reefs, carbon neutrality, negative emissions, resilience, ecological restoration

Authors

Tuo SHI, Xinqing ZHENG, Han ZHANG, Qifang WANG, and Xin ZHONG

Corresponding Author(s)

ZHENG Xinqing[2,3*]

2 Fujian Provincial Key Laboratory of Marine Ecological Conservation and Restoration, Third Institute of Oceanography, Ministry of Natural Resources, Xiamen 361005, China;

3 Observation and Research Station of Island and Coastal Ecosystems in the Western Taiwan Strait, Ministry of Natural Resources, Xiamen 361005, China

This technical roadmap and strategic thinking of ocean negative emissions aiming carbon neutrality is available in Bulletin of Chinese Academy of Sciences (Chinese Version): https://bulletinofcas.researchcommons.org/journal/vol36/iss3/5

Citation: SHI Tuo, ZHENG Xinqing, ZHANG Han, WANG Qifang, ZHONG Xin. Coral Reefs: Potential Blue Carbon Sinks for Climate Change Mitigation [J]. Bulletin of Chinese Academy of Sciences, 2021 (3): 270–278.

Coral Reefs: Potential Blue Carbon Sinks for Climate Change Mitigation

SHI Tuo[1], ZHENG Xinqing[2,3], ZHANG Han[1,2], WANG Qifang[2], ZHONG Xin[1]

1. Institute of Marine Science and Technology, Shandong University, Qingdao 266237, China;
2. Fujian Provincial Key Laboratory of Marine Ecological Conservation and Restoration, Third Institute of Oceanography, Ministry of Natural Resources, Xiamen 361005, China;
3. Observation and Research Station of Island and Coastal Ecosystems in the Western Taiwan Strait, Ministry of Natural Resources, Xiamen 361005, China

Abstract: Coral reefs are one of the most productive, and yet most vulnerable marine ecosystems. The global decline of coral reefs induced by climate change and human activities has already affected the coral calcification and carbon cycling in the reef ecosystem, intensifying the long-standing CO_2 source-sink debate over coral reefs. Despite the fact that coral calcification is accompanied by the release of CO_2 to the atmosphere, the significance of coral reefs as a carbon sink cannot be ignored, given the complex biogeochemical processes in the reef ecosystem and the characteristic mixotrophic lifestyle of the reef-building corals. From the perspective of increasing coral resilience to climate change, this study attempts to clarify the coral reef CO_2 source-sink debate, explore the possible ecological regulations and pathways to transform coral reefs from a carbon source to a carbon sink, and provide theoretical framework and technical support for the deployment of ocean negative carbon emissions and the implementation of the national carbon neutrality strategy. **DOI:** 10.16418/j.issn.1000-3045.20210217102-en

Keywords: coral reefs; carbon neutrality; negative emissions; resilience; ecological restoration

The increased emissions of greenhouse gases such as carbon dioxide (CO_2) since the industrial revolution has led to a warmer climate and more frequent natural disasters [1]. As a party to the Paris Agreement, China has always been the backbone of global climate governance. In 2020, Chinese President Xi Jinping announced to the world that China will make efforts to achieve maximum CO_2 emission before 2030 and carbon neutrality before 2060. In the same year, the Fifth Plenary Session of the 19th Communist Party of China (CPC) Central Committee further proposed the new requirement of guarding the boundary of natural and ecological security and the new deployment of improving the quality and stability of ecosystems, reflecting China's determination to actively combat global climate change and its role as a responsible great power. Emission reduction (reducing CO_2 emissions to the atmosphere) and sink enhancement (increasing absorption of atmospheric CO_2) are equally important to carbon neutrality. However, compared with emission reduction, sink enhancement has not received much attention. The traditional sink enhancement measures mainly focused on terrestrial ecosystems (e.g., afforestation). As the conflict between population growth and land/food shortage intensifies, the negative emissions of oceans, which store 93% of the total carbon on Earth, have been revisited [2].

Coral reef is the most biologically diverse marine ecosystem, with an estimated annual sequestration of 900 million tons of carbon on a global scale [3]. The primary productivity of coral reefs is up to 300–5 000 g $C \cdot m^{-2} \cdot a^{-1}$, while that of non-coral reef systems only accounts for 50–600 g $C \cdot m^{-2} \cdot a^{-1}$ [4]. Although the role as a potential carbon sink has long been recognized [5,6], coral reefs have been defined as a carbon source due to CO_2 release during calcification [7]. Currently, the carbon source/sink properties of coral reefs are still controversial and coral reefs have not been included in the blue carbon budget of coastal zone represented by coastal wetland ecosystems (e.g., mangroves, salt marshes, seagrass beds) [8]. Therefore, clarifying the source-sink debate over coral reef ecosystems and exploring the ecological approaches to transform coral reefs from a carbon source to a carbon sink are urgent tasks for the ecological restoration of coral reefs and will serve the national goal of carbon neutrality and green development strategy.

1 Impact of global change on coral reef ecosystem

Coral reefs, known as the "rainforests in the ocean", represent the marine ecosystem with the highest productivity (i.e., organic matter production via CO_2 fixation) and play an

Received: 2021-3-2
Supported by: National Key R&D Program of China (2020YFA0607602, 2016YFA0601203); National Natural Science Foundation of China (41876119, 41976127); Open Project of Southern Marine Science and Engineering Guangdong Laboratory (Zhuhai) (SML2020SP004)

important role in the global carbon cycle. The high productivity of coral reef ecosystems relies mainly on photosynthetic dinoflagellates in the family Symbiodiniaceae (collectively called zooxanthellae) that are symbiotic with corals [9,10]. Zooxanthellae provide 95% of photosynthates (sugars, amino acids, oxygen) to corals for their growth and calcification, while corals provide zooxanthellae with metabolic wastes (CO_2, nitrogen, and phosphorus) as nutrients [11].

Coral reefs are yet the most vulnerable marine ecosystems sensitive to environmental changes. Since the industrial revolution, massive emissions of greenhouse gases, rapid development of economy in coastal areas, continuous land reclamation, and excessive exploitation of resources have led to a series of ecological problems such as global warming, ocean acidification, and sea level rise. These problems have put nearly 1/3 of global reef-building corals on the verge of extinction, caused continuous degradation of coral reef ecosystems, and increased the frequency and severity of coral bleaching events [12]. Coral bleaching is a status of response to environmental stress, making the corals become pale or even completely transparent as a result of a large number of symbiotic zooxanthellae expelled from the coral tissue. If not relieved promptly, bleaching will eventually cause massive mortality or even extinction of corals. Global warming and increased seawater temperature have caused three ultra-large-scale bleaching events in the famous Australian Great Barrier Reef since 1980 when observational data were available [13]. The triangle area of coral reefs located at the confluence of the Indian Ocean and the Pacific Ocean has also experienced a severe recession. For example, the coverage of reef-building corals in the Philippines has declined by nearly 1/3 in the past decade [14]. The scale and severity of coral bleaching in the northwestern part of Hainan Island and Weizhou Island in Guangxi of China in 2020 were described as “historically rare,” and the coral mortality was estimated to be more than 86%, with less than 20% of the corals still retaining intact polyps [15]. The increasing environmental stress not only threatens the survival of coral reefs, but also increases the difficulty of judging their carbon source/sink properties. Therefore, there is a pressing need to address the scientific challenges of strengthening ecological restoration of coral reefs, improving their resilience to environmental stress, and maintaining their potential carbon sink function.

2 Debate on carbon source/sink properties of coral reefs

The sea-air CO_2 partial pressure difference is the key factor in determining whether a sea area is the source or sink of atmospheric CO_2 [16]. It has been long in debate on whether coral reefs are net source [17–19], net sink [5,6,20], or shifting between source and sink [21,22]. The complex physical, chemical, and biological processes in different coral reef areas make it difficult to achieve consistent calculation of carbon flux and carbon budget [6,7]. The carbon flux in coral reef areas is mainly regulated by organic carbon metabolism (photosynthesis versus respiration) and inorganic carbon mineralization (precipitation versus dissolution of $CaCO_3$) (Figure 1). The efficiency of organic carbon metabolism is extremely high in coral reefs, with the net productivity of $(0 \pm 0.7)\ g \cdot C \cdot m^{-2} \cdot d^{-1}$ [23]. That means almost all the CO_2 fixed by photosynthesis is utilized. Therefore, the CO_2 flux in coral reefs may be mainly regulated by inorganic carbon mineralization, i.e., net CO_2 release during coral calcification and dissolution [24]. It is estimated that precipitation of 1 mol $CaCO_3$, even buffered by seawater, releases 0.6 mol CO_2 to the atmosphere [7]. However, tracing the source and transport of inorganic carbon using $H^{14}CO_3^-$ and ^{45}Ca dual-isotope labeling showed that 70%–75% of the dissolved inorganic carbon utilized by reef-building coral calcification was derived from metabolism of the coral holobionts [25]. This is consistent with the hypothesis that not all the CO_2 released by respiration is emitted to the atmosphere, but some was used for the formation of $CaCO_3$ skeleton [26], suggesting that organic carbon metabolism can also be a net sink. In addition, the primary productivity of coral symbionts may be limited by CO_2 [27]. Therefore, the relative contributions of net organic carbon metabolism and net inorganic carbon mineralization in the coral holobionts should be considered in the evaluation of the net CO_2 flux of coral reef community [28].

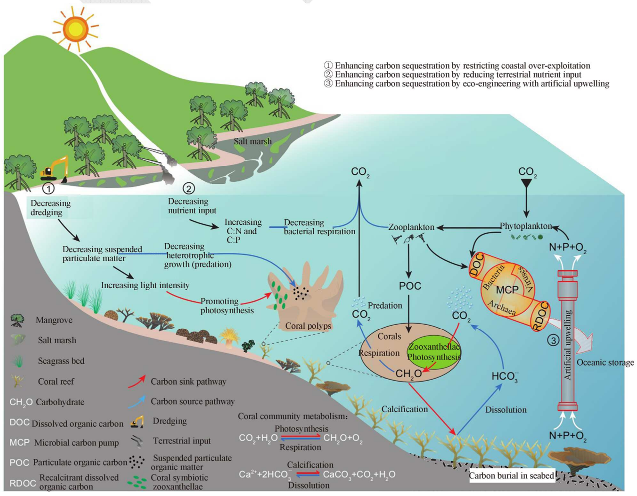

Figure 1 Schematic illustration of modes and pathways of enhancing carbon sequestration in coral reef ecosystems

It is worth noting that the source/sink properties of coral reef ecosystems are not necessarily the same as the carbon source or sink functions of reef-building corals. (1) From the perspective of reef-building corals, elevated atmospheric CO_2 concentration may effectively relieve the carbon limitation on the symbiotic zooxanthellae and enhance their photosynthesis and primary productivity. However, ocean acidification caused by elevated CO_2 inhibits the calcification of reef-building corals, resulting in lower carbon sink activity. Models have predicted the uncertainty in the source/sink properties of multiple reef ecosystems in the Indo-Pacific

Ocean on the seasonal scale when excluding the effects of other biological factors [29]. (2) Ecosystems are not isolated, and carbon exchange exists between coral reefs and other blue carbon ecosystems, which is often ignored in the source-sink calculations. In the mangrove–seagrass–coral reef continuum, zooxanthellae can fix large amounts of dissolved inorganic carbon from mangroves and seagrass beds. The CO_2 released by corals into seawater can be reused by primary producers such as macroalgae, seagrasses, and calcifying algae, and the continuum as a whole thus demonstrates high carbon sink activity [30]. In addition to zooxanthellae, corals also associate with bacteria, archaea, fungi, and viruses. The concept of microbial carbon pump (MCP) proposed by Chinese scientists has confirmed that microbial communities can convert organic carbon into recalcitrant dissolved organic carbon (RDOC) through a series of metabolic processes for millennial-scale storage, and this mechanism of carbon storage has become an important driving force of blue carbon [31]. Despite a lack of estimated contribution of symbiotic microorganisms to coral reef carbon cycle, this MCP-driven RDOC storage process, which can occur simultaneously inside and outside the coral holobionts, has a significant effect on the carbon sequestration of coral reefs (Figure 1).

At present, the research on carbon source-sink of coral reef ecosystems has been rather limited. In particular, the processes and mechanisms underpinning carbon cycling at cellular, organismal, and community levels may be much more complicated than previously thought [17], and the role of coral reef ecosystems as a blue carbon reservoir has not been clarified. The tackling of this issue necessitates a global study on the contribution of coral reefs to sea-air CO_2 exchange.

3 Coral reef ecological health and its source-sink effect

As a typical mixotroph, the flexibility of reef-building corals to shift between autotrophic and heterotrophic lifestyles, will affect or even determine the carbon source/sink properties of coral reef ecosystems [32]. Theoretically, when the holobiont is dominated by autotrophic growth, the amount of CO_2 fixed by the photosynthesis of zooxanthellae is higher than that released by coral respiration, and the coral reef area would act as a carbon sink. When the holobiont is dominated by heterotrophic growth, corals will obtain additional energy by feeding on zooplankton and suspended particulate organic matter through polyp tentacles. In such case, the amount of CO_2 released by respiration exceeds that fixed by zooxanthellae, and the reef area generally serves as a carbon source. With intensified external stress, corals expel a large number of symbiotic zooxanthellae (i.e., bleaching), resulting in the shortage of autotrophic energy mainly produced by zooxanthellae to maintain the basic metabolism of corals, and the holobiont passively undergoes the source-sink inversion from autotrophic to heterotrophic growth. Although heterotrophic predation to some degree can alleviate the stress on corals, coral reef ecosystems are highly likely to collapse and disintegrate when corals overly depend on heterotrophic growth and abandon the efficient, self-sufficient carbon cycle within the holobionts. Due to environmental disturbance and prolonged stresses of nutrients, suspended solids, and sediments caused by excessive anthropogenic activities (reclamation, dredging, terrestrial input), coral reefs in China are experiencing severe degradation [33], and reef-building corals are dominated by stress-tolerant species [34]. Enhanced heterotrophic metabolism may be a contingent adaptation of stress-tolerant corals [35], and the ecological consequence would be a shift from a carbon sink system dominated by healthy reefs to a carbon source system dominated by degraded reefs.

During reef formation, a large amount of carbonate is deposited, and the annual deposition of $CaCO_3$ in coral reef areas is estimated to be 0.084 Pg C (1 Pg = 10^{15} g), accounting for 23%–26% of the annual $CaCO_3$ deposition globally [24]. It is conceivable that CO_3^{2-} concentration, carbonate saturation, and coral calcification will decrease with the increase in seawater CO_2 concentration (ocean acidification). Meanwhile, coral skeletons become brittle and fragile, and show slower growth and weaker resistance to wind and waves. As a direct consequence of ocean acidification, $CaCO_3$ skeleton is dissolved to release large amounts of CO_2 into the ocean, causing irreversible effects on the carbonate system. In addition, the degradation of coral reef ecosystems may have significant cascading effects, leading to a decline in spatial structural diversity, a decrease in biodiversity, simplification of food web structure, and a decrease in trophic levels. Consequently, this “phase transition” leads to the release of organic carbon originally fixed in organisms at various trophic levels and reduces the total carbon storage of coral reef ecosystems. Thus, healthy coral reef ecosystem can be a net sink of atmospheric CO_2 while the degraded one becomes a net source of atmospheric CO_2.

The rapid development of science and technology facilitates the research on the ecological health of coral reefs and their carbon “source-sink” effects. For example, the $\delta^{13}C$ stable isotope technique based on specific compounds (e.g., amino acids and lipids) can quantitatively evaluate the share of energy obtained at different trophic levels by tracing the transport and partitioning of organic carbon in food webs. This technique is expected to solve the problem of carbon partitioning and energy traceability in coral reef ecosystems, and clarify the flexible nutritional modes of corals, especially the energy transfer and carbon partitioning in coral reefs at different health states [36]. In addition, nanoscale secondary ion mass spectroscopy (NanoSIMS) emerged in recent years can be used to trace and quantify the fingerprints of organic carbon transport in coral holobionts *in situ* at the subcellular ultra-microscale, and delineate in greater detail the processes and mechanisms of nutrient interaction, element cycling, and energy transfer among corals, zooxanthellae, and microorganisms, especially the relative contribution of different biological processes (e.g., coral calcification, zooxanthellae carbon fixation, and microbial metabolism) to carbon source/sink [37]. These techniques help reveal the mechanisms of carbon fixation and storage and the dynamics of carbon flux in coral reef ecosystems in a comprehensive and multi-faceted manner, providing theoretical framework for the establishment of modes and pathways of enhancing carbon sequestration in coral reefs.

4 Modes and pathways of enhancing carbon sequestration in coral reef ecosystems

The following four measures should be considered to clarify the carbon "source-sink" debate and enhance the carbon sink function of coral reefs.

(1) Conduct systematic research on carbon flux and budget to clarify the long-standing "source-sink" debate on coral reefs. On the ecosystem scale, efforts should be made to reveal the mechanisms of energy transfer between coral reefs and adjacent blue carbon ecosystems (e.g., seagrass beds), establish the energy transfer models for specific sea areas, and explore the feasibility of increasing the overall carbon storage benefits of blue carbon ecosystems from the perspective of improving energy transfer efficiency [30]. Meanwhile, comparative analysis of the carbon cycle and carbon flux in selected coral reef areas on the regional scale is needed to identify the potential factors affecting the carbon source/sink of coral reefs, the spatial and temporal differences, and the coral reef responses to climate change and human activities. On the ultramicroscopic subcellular scale, monitoring organic carbon transport *in situ* within the coral holobionts using high-precision, high-resolution isotope tracing techniques (e.g., amino acid $\delta^{13}C$) is highly recommended, which facilitates the reconstruction of energy transfer model involving zooxanthellae, corals, and microorganisms [38].

(2) Strengthen the practice of protection and restoration towards healthy coral reefs as a potential carbon sink. Improving coral survival and coral reef coverage is a prerequisite to enhance the carbon sequestration of coral reef ecosystems. In the context of climate change, asexual propagation-based restoration approaches, such as coral nursery, transplantation of coral colonies or fragments, and artificial reefs [39], can no longer meet the need to improve coral genetic diversity and ecosystem stability [40,41]. Modern restoration techniques developed on the basis of coral sexual reproduction, such as trans-latitude transplantation [42], gamete hybridization [43], heritable breeding based on the screening of stress resistance genes [44], and probiotic therapy [45], provide insights into the screening and breeding of super corals with strong environmental adaptability, stress resistance, and resilience. On one hand, these genetically modified super corals are resilient to climate change, which facilitates the maintenance of biological hotspots in coral reef areas and the storage of organic carbon within the system. On the other hand, persistent and stable symbiotic relationships can be maintained between corals and zooxanthellae, which would enhance carbon burial in coral reef ecosystems by improving algal photosynthetic carbon fixation and coral calcification.

(3) Restrict terrestrial nutrient loads and anthropogenic activities for coordinated land and ocean carbon sinks. Strengthening land–ocean coordination and reducing terrestrial nutrient input can alleviate eutrophication in coastal waters, reduce respiratory consumption of organic carbon, and improve conversion of recalcitrant carbon, effectively promoting the ability of MCP to sequester, store and transport carbon to the deep sea [46,47]. In densely populated coastal areas, proper treatment of domestic sewage and aquaculture wastewater as well as intensive monitoring and early warning can be employed to maintain nutrient hemostasis for a healthy, autotrophic lifestyle of the coral reef ecosystem [48]. Avoiding strong disturbance from human activities (especially excessive coastal zone development, reclamation, and dredging) can reduce the concentration and turbidity of suspended particulate particles in coral reef areas, thus increasing light penetration and improving the zooxanthellae photosynthesis while reducing the heterotrophic feeding of the corals. Therefore, the coordinated land–and ocean development not only regulates the trophic lifestyle of corals, but also enhances the potential carbon sink capacity of coral reef areas (Figure 1).

(4) Apply artificial upwelling to improve nutrient cycling and carbon sinks in coral reefs. Artificial upwelling is an emerging marine eco-engineering technology that has been incorporated into the Special Report on the Oceans and Cryosphere in a Changing Climate (SROCCC) of the Intergovernmental Panel on Climate Change (IPCC). This technology has great potentials in carbon sequestration enhancement applications in coastal wetlands, mangroves, and fish farms [49]. Upwelling brings up low-temperature and nutrient-rich seawater from deep-ocean to shallow reefs, enhancing the coral health and coral reef carbon sink capacity by improving water quality and zooxanthellae photosynthesis [50]. Upwelling also facilitates the transport of organic matter by water currents to the open ocean and increases the RDOC generated by MCP while mitigating the coastal lagoon eutrophication caused by human activities and terrestrial input (Figure 1). Continued observations also suggest that corals in the reef areas with upwelling exhibit lower probability of bleaching and stronger resilience, which showcases the potential application of artificial upwelling in ecosystem protection and carbon sequestration enhancement [51].

5 Conclusions

At present, climate change undoubtedly represents the greatest threat to global coral reefs. Carbon neutrality is a key factor in mitigating climate change, which can only be achieved by increasing sink while reducing emissions. Therefore, reasonable and effective approaches should be developed to protect coral reefs against stresses caused by climate change and human activities and to increase their function as carbon sinks, which will contribute to future coral reef conservation and restoration. In this article we propose a scheme for coral reef restoration based on carbon sequestration enhancement. We suggest to increase the resilience of coral reefs to climate change while enhancing their carbon sink capacity through stepping up land–ocean coordination, reducing terrestrial pollution, and planning rational coastal zone construction. These draft plans need to be refined and optimized in the future. By linking science to policy, we hope to promote demonstrative research and development in qualified sea areas to better serve the implementation of the national strategy of carbon neutrality.

Acknowledgements

We would like to express our sincere appreciation to Niu Gaofeng (Institute of Marine Science and Technology, Shandong University) for assistance in figure drawing and Liu Yina (Third Institute of Oceanography, Ministry of Natural Resources of China) for help in materials collection during preparation of this manuscript.

References

1 Morais R A, Connolly S R, Bellwood D R. Human exploitation shapes productivity-biomass relationships on coral reefs. Global Change Biology, 2020, 26 (3): 1295–1305.

2 Jiao N Z. Developing ocean negative carbon emission technology to support national carbon neutralization. Bulletin of Chinese Academy of Sciences, 2021, 36 (2): 179–187.

3 Kinsey D W, Hopley D. The significance of coral reefs as global carbon sinks–Response to Greenhouse. Global and Planetary Change, 1991, 3 (4): 363–377.

4 Hatcher B G. Coral reef primary productivity: A beggar's banquet. Trends in Ecology & Evolution, 1988, 3 (5): 106–111.

5 Kayanne H, Suzuki A, Saito H. Diurnal changes in the partial pressure of carbon dioxide in coral reef water. Science, 1995, 269: 214–216.

6 Chisholm J R M, Barnes D J. Anomalies in coral reef community metabolism and their potential importance in the reef CO_2 source-sink debate. PNAS, 1998, 95 (11): 6566–6569.

7 Ware J R, Smith S V, Reaka-Kudla M L. Coral reefs: Sources or sinks of atmospheric CO_2?. Coral Reefs, 1992, 11 (3): 127–130.

8 Macreadie P I, Anton A, Raven J A, et al. The future of Blue Carbon science. Nature Communications, 2019, 10 (1): 1–13.

9 Shi T, Niu G F, Kvitt H, et al. Untangling ITS2 genotypes of algal symbionts in zooxanthellate corals. Molecular Ecology Resources, 2021, 21(1): 137–152.

10 LaJeunesse T C, Parkinson J E, Gabrielson P W, et al. Systematic revision of Symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. Current Biology, 2018, 28 (16): 2570–2580.

11 Muscatine L. The role of symbiotic algae in carbon and energy flux in reef corals//Dubinsky Z, ed. Ecosystems of the World vol. 25: Coral Reefs. New York: Elsevier, 1990: 75–87.

12 Putnam H M, Barott K L, Ainsworth T D, et al. The vulnerability and resilience of reef-building corals. Current Biology, 2017, 27 (11): 528–540.

13 Hughes T P, Kerry J T, Álvarez-Noriega M, et al. Global warming and recurrent mass bleaching of corals. Nature, 2017, 543: 373–377.

14 Licuanan W Y, Robles R, Reyes M. Status and recent trends in coral reefs of the Philippines. Marine Pollution Bulletin, 2019, 142: 544–550.

15 Huang J Z, Wang F X, Zhao H W, et al. Reef benthic composition and coral communities at the Wuzhizhou Island in the South China Sea: The impacts of anthropogenic disturbance. Estuarine, Coastal and Shelf Science, 2020, 243: 106863.

16 Fagan K E, MacKenzie F T. Air-sea CO_2 exchange in a subtropical estuarine-coral reef system, Kaneohe Bay, Oahu, Hawaii. Marine Chemistry, 2007, 106(1–2): 174–191.

17 Gattuso J P, Allemand D, Frankignoulle M. Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: A review on interactions and control by carbonate chemistry. Integrative and Comparative Biology, 1999, 39 (1): 160–183.

18 Lønborg C, Calleja M L, Fabricius K E, et al. The Great Barrier Reef: A source of CO_2 to the atmosphere. Marine Chemistry, 2019, 210: 24–33.

19 Cotovicz L C Jr, Chielle R, Marins R V. Air-sea CO_2 flux in an equatorial continental shelf dominated by coral reefs (Southwestern Atlantic Ocean). Continental Shelf Research, 2020, 204: 104175.

20 Yan H Q, Yu K F, Shi Q, et al. Air-sea CO_2 fluxes and spatial distribution of seawater pCO_2 in Yongle Atoll, northern-central South China Sea. Continental Shelf Research, 2018, 165: 71–77.

21 de Goeij J M, van Duyl F C. Coral cavities are sinks of dissolved organic carbon (DOC). Limnology and Oceanography, 2007, 52 (6): 2608–2617.

22 Wimart-Rousseau C, Lajaunie-Salla K, Marrec P, et al. Temporal variability of the carbonate system and air-sea CO_2 exchanges in a Mediterranean human-impacted coastal site. Estuarine, Coastal and Shelf Science, 2020, 236: 106641.

23 Crossland C J, Hatcher B G, Smith S V. Role of coral reefs in global ocean production. Coral Reefs, 1991, 10 (2): 55–64.

24 Yan H Q, Yu K F, Tan Y H. Recent development in the research of carbon cycle in coral reef ecosystem. Acta Ecologica Sinica, 2009, 29 (11): 6207–6215.

25 Furla P, Galgani I, Durand I, et al. Sources and mechanisms of inorganic carbon transport for coral calcification and photosynthesis. The Journal of Experimental Biology, 2000, 203 (22): 3445–3457.

26 Rinkevich B, Loya Y. Does light enhance calcification in hermatypic corals?. Marine Biology, 1984, 80 (1): 1–6.

27 Rädecker N, Pogoreutz C, Wild C, et al. Stimulated respiration and net photosynthesis in *Cassiopeia* sp. during glucose enrichment suggests in hospite CO_2 limitation of algal endosymbionts. Frontiers in Marine Science, 2017, 4: 267.

28 Suzuki A, Kawahata H. Carbon budget of coral reef systems: An overview of observations in fringing reefs, barrier reefs and atolls in the Indo-Pacific regions. Tellus B: Chemical and Physical Meteorology, 2003, 55 (2): 428–444.

29 Mayer B, Rixen T, Pohlmann T. The spatial and temporal variability of air-sea CO_2 fluxes and the effect of net coral reef calcification in the Indonesian Seas: A numerical sensitivity study. Frontiers in Marine Science, 2018, 5: 116.

30 Akhand A, Watanabe K, Chanda A, et al. Lateral carbon fluxes and CO_2 evasion from a subtropical mangrove-seagrass-coral continuum. Science of the Total Environment, 2021, 752: 142190.

31 Jiao N Z, Herndl G J, Hansell D A, et al. Microbial production of recalcitrant dissolved organic matter: Long-term carbon storage in the global ocean. Nature Reviews Microbiology, 2010, 8 (8): 593–599.

32 Conti-Jerpe I E, Thompson P D, Wong C W M, et al. Trophic strategy and bleaching resistance in reef-building corals. Science Advances, 2020, 6 (15): eaaz5443.

33 Hughes T P, Huang H, Young M A L. The wicked problem of China's disappearing coral reefs. Conservation Biology, 2013, 27 (2): 261–269.

34 Darling E S, Alvarez-Filip L, Oliver T A, et al. Evaluating life-history strategies of reef corals from species traits. Ecology Letters, 2012, 15 (12): 1378–1386.

35 Burmester E M, Breef-Pilz A, Lawrence N F, et al. The impact of autotrophic versus heterotrophic nutritional pathways on colony health and wound recovery in corals. Ecology and Evolution, 2018, 8 (22): 10805–10816.

36 Ferrier-Pagès C, Leal M C. Stable isotopes as tracers of trophic interactions in marine mutualistic symbioses. Ecology and Evolution, 2019, 9 (1): 723–740.

37 Loussert-Fonta C, Toullec G, Paraecattil A A, et al. Correlation of fluorescence microscopy, electron microscopy, and NanoSIMS stable isotope imaging on a single tissue section. Communications Biology, 2020, 3: 362.

38 Tanaka Y, Suzuki A, Sakai K. The stoichiometry of coral-dinoflagellate symbiosis: Carbon and nitrogen cycles are balanced in the recycling and double translocation system. The ISME Journal, 2018, 12 (3): 860–868.

39 Zheng X Q, Li Y C, Liang J L, et al. Performance of ecological restoration in an impaired coral reef in the Wuzhizhou Island, Sanya, China. Journal of Oceanology and Limnology, 2021, 39 (1): 135–147.
40 van Oppen M J H, Gates R D, Blackall L L, et al. Shifting paradigms in restoration of the world's coral reefs. Global Change Biology, 2017, 23 (9): 3437–3448.
41 Omori M. Coralrestoration research and technical developments: What we have learned so far. Marine Biology Research, 2019, 15 (7): 377–409.
42 Thomas C D. Translocation of species, climate change, and the end of trying to recreate past ecological communities. Trends in Ecology & Evolution, 2011, 26 (5): 216–221.
43 Suzuki G, Okada W, Yasutake Y, et al. Enhancing coral larval supply and seedling production using a special bundle collection system "coral larval cradle" for large-scale coral restoration. Restoration Ecology, 2020, 28 (5): 1172–1182.
44 Barshis D J, Ladner J T, Oliver T A, et al. Genomic basis for coral resilience to climate change. PNAS, 2013, 110 (4): 1387–1392.
45 Peixoto R S, Rosado P M, Leite D C D, et al. Beneficial microorganisms for corals (BMC): Proposed mechanisms for coral health and resilience. Frontiers in Microbiology, 2017, 8: 341.
46 Jiao N, Robinson C, Azam F, et al. Mechanisms of microbial carbon sequestration in the ocean—future research directions. Biogeosciences, 2014, 11 (19): 5285–5306.
47 Zhao H, Yuan M, Strokal M, et al. Impacts of nitrogen pollution on corals in the context of global climate change and potential strategies to conserve coral reefs. Science of the Total Environment, 2021, 774: 145017.
48 Morris L A, Voolstra C R, Quigley K M, et al. Nutrient availability and metabolism affect the stability of coral-Symbiodiniaceae symbioses. Trends in Microbiology, 2019, 27 (8): 678–689.
49 Liu C C K, Jin Q. Artificial upwelling in regular and random waves. Ocean Engineering, 1995, 22 (4): 337–350.
50 Radice V Z, Hoegh-Guldberg O, Fry B, et al. Upwelling as the major source of nitrogen for shallow and deep reef-building corals across an oceanic atoll system. Functional Ecology, 2019, 33 (6): 1120–1134.
51 Bayraktarov E, Pizarro V, Eidens C, et al. Bleaching susceptibility and recovery of Colombian Caribbean corals in response to water current exposure and seasonal upwelling. PLoS One, 2013, 8 (11): e80536.

(Translated by ZHAO B)

SHI Tuo, Professor at the Institute of Marine Science and Technology, Shandong University, with a PhD in Biological Oceanography. Prof. Shi has long been devoted to the study of microbially-mediated marine biogeochemical cycles and their responses to global change. In the past 5 years, he has been a Principal Investigator in a dozen projects focusing on coral reefs global change biology, with a special reference to the marine carbon and nitrogen cycling, sponsored by the National Key Research and Development Program of China, the National Natural Science Foundation of China, and so on. He has also been involved in the drafting, formulation, and evaluation of a number of national policies on science and technology. E-mail: tuoshi@sdu.edu.cn

ZHENG Xinqing, PhD, Professor of the Third Institute of Oceanography, Ministry of Natural Resources of the People's Republic of China. Prof. Zheng is Youth Top-notch Talent of Fujian Province. His research mainly focuses on global change biology and restoration ecology of coral reefs. In recent years, he has undertaken more than 20 major projects, mainly sponsored by National Natural Science Foundation of China, National Key Research and Development Program of China, and China-ASEAN Maritime Cooperation Fund. He established the first indoor hatchery for large-scale live coral breeding in China. His work has revealed the physiological and molecular mechanisms of reef-building corals in response to changing climate, as well as the resilience mechanisms of coastal food web to the eutrophication in a typical marine ecosystem. E-mail: zhengxinqing@tio.org.cn

