Coral Reefs of the World 14

Jing Zhang · Thamasak Yeemin
R. John Morrison · Gi Hoon Hong
Editors

Coral Reefs of the Western Pacific Ocean in a Changing Anthropocene

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Coral Reefs of the World

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Cover Image: The highly urbanised Dalap-Uliga-Darrit (DUD) area, Majuro Atoll, Marshall Islands.
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1 Introduction and Background

R. John Morrison, Jing Zhang, Gi Hoon Hong, and Thamasak Yeemin

Abstract

Coral reefs are important ecosystems, especially in regions like the Western and South-Western Pacific, where they play vital roles in food provision, resource production and coastal protection. They are, however, under severe pressure from human and climate change. The importance of reefs is recognised globally, and substantial research efforts are being made to improve our understanding of the chemical, ecological, geological and physical processes occurring in and around reefs. This research will, in turn, provide information essential for the improved and more sustainable management of reefs. Success in such research often requires multidisciplinary/multinational teams. One such grouping was the Coral Reefs under Climate and Anthropogenic Perturbations (CorReCAP) Project established through the UNESCO-IOC-WESTPAC office in 2008. This monograph presents the outcomes of the CorReCAP Project, and this chapter outlines the aims, objectives and activities of the project.

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Keywords

Coral reefs · Western Pacific · Climate change · Human impacts, CorReCAP Project · Aims · Background

Coral reefs are one of the most important ecosystems found on the Earth's surface. They are found in tropical and subtropical oceanic waters, and have evolved to form structures that are home to an enormous number of organisms. Coral reefs facilitate the very efficient production of organic matter, particularly notable as they operate in waters that would otherwise be considered relatively infertile. Surrounding communities use coral reef areas as a major source of foodstuffs, pharmaceuticals and building materials, as well as coastal protection sites. If the resource use activities are well managed, the coral reef can be a major community asset for many years. The balance is a delicate one and can be disturbed by population increase (locally driven by improved living conditions, e.g. better health standards, or by migration, or internal drift of people from inland to the coast).

The importance of reefs as resource providers has been known to humans for a long time, but as they became more of a focus for global exploration and inquisitive scientists, interest in understanding and managing reefs expanded. This is especially true in the twentieth century, when it was observed that reefs were an important contributor to ocean-atmosphere interactions and the global carbon budgets. Thus, coral reefs, being dominated by carbon, are being impacted by human activities altering oceanic processes, and also by human actions changing atmospheric conditions. As one of these atmospheric changes is carbon dioxide concentration, a significant contributor to global climate change, it can be considered that coral reefs are clearly impacted by both anthropogenic and climate forcings.

The tropical and subtropical Western Pacific Ocean Region (see Fig. 1.1) possesses an enormous marine biodiversity but suffers impacts from a combination of high population density and rapid economic development that result in

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high material inputs from land-based sources (i.e. rivers). Furthermore, this region is exposed to frequent climatic and oceanic perturbations, e.g. monsoons with episodic typhoons—ca. 10–20 events or even more frequent in a year. This region is, therefore, particularly vulnerable to the combined effects of land-based human activities and ocean-/atmosphere-based climate events.

In the Western Pacific Region, humans are critically dependent on the coral reefs and related food webs because of the goods and services they provide, such as fishery resources and tourism. The region is well recognised for its biodiversity richness in both the terrestrial and marine zones (the Wallace and Huxley lines discussion in the nineteenth century), and considered to contain "hot spots" for biogeochemical and ecosystem studies, such as in the connecting area between the Indian and Pacific Oceans at low latitudes. Despite their recognition of the vital role of reefs, humans have significantly damaged coral reef systems through overfishing and destructive fishing practices (e.g. dynamite and cyanide fishing), coastal engineering, land-source pollutant discharge and marine aquaculture which have considerably changed the structure and function of fringing coral reefs, to such an extent that they have caused the extinction of important marine species (Huang et al. 2000). As a result, increased knowledge of the status and functions of coral reefs, as well as better understanding of the connectivity between individual coastal habitats, is required for sustainable management of these ecosystems. Climate change and natural disasters (e.g. typhoons, high tectonic activity and tsunamis) are other threats to coastal ecosystems with the potential to cause severe damage (Burke et al. 2011).

Anthropogenic perturbations both from terrestrial and from marine sources impact the functioning of reef ecosystems; this, in turn, regulates the nature of the sustainability of the ecosystems and thus affects the services that can be provided to reef users (see Fig. 1.2). Freshwater, sediment and nutrient inputs from land-based sources have changed and are continuing to change, often with adverse consequences for the technical, social and economic functions of the coral reef ecosystems, including tourism, sewage disposal, illegal fisheries and direct exploitation of resource materials from coral reefs (Brodie and Fabricius 2019).

The global changes outlined above also affect physical, biogeochemical and ecological processes in coastal coral reef ecosystems; these can be considered as added stresses on an already over-stressed environment. These will further reduce the ability of coral reef systems to provide goods and services. Some of the impacts that have been noted include loss of habitat and shifts in community structure, which have consequences for food web dynamics. These changes can be severe, particularly in areas of rapid economic development and population growth, such as in the Western Pacific Region (Holbrook et al. 2015).

The obvious need for increased/improved understanding of coral reef systems has led to the initiation by many agencies of numerous research and training activities to further investigate the complex reef biogeochemistry and ecosystem behaviour. One such international collaborative research group was established in 2008, by the IOC/WESTPAC Sub-Commission when a new initiative study of "Coral Reefs under Climate and Anthropogenic Perturbations" (i.e. IOC/WESTPAC-CorReCAP Project) was adopted.

The terms of the reference (TORs) of the IOC/WESTPAC-CorReCAP Project were as follows:

- To understand the biogeochemical and ecological nature of coral reefs in WESTPAC (i.e. the Western Pacific Ocean) in different geographic, physical and environmental settings, as well as different types of human interventions;
- To evaluate the consequences of impacts of climate change and other human activities on the health of coral reefs and their sustainable use; and
- To promote capacity building in areas related to research on coral reefs through sharing scientific knowledge and training activities, as well as collaboration within research networks in WESTPAC.

These TORs were in accordance with the IOC Medium-Term Strategy (2008–2013), which has highlighted the prevention and reduction of harm from natural hazards to coral reef ecosystems as a matter of urgency. In addition, the mitigation of impacts from climate variability and human impacts is a major challenge for the IOC/WESTPAC Sub-Commission, given that coral reefs form substantial but sensitive ecosystems for most of its member countries in the region. Linkage to the IOC/WESTPAC Sub-Commission would also facilitate meetings with other marine environmental research groups to compare results for tropical and subtropical zones of the region.

The project had initially a steering group of regional researchers; more than 15 researchers (from the nine IOC/WESTPAC countries) contributed to the project planning. After the launch of the IOC/WESTPAC-CorReCAP Project in May 2008, the following activities were organised to facilitate greater regional cooperation among research programmes, training of young marine researchers and international workshops.

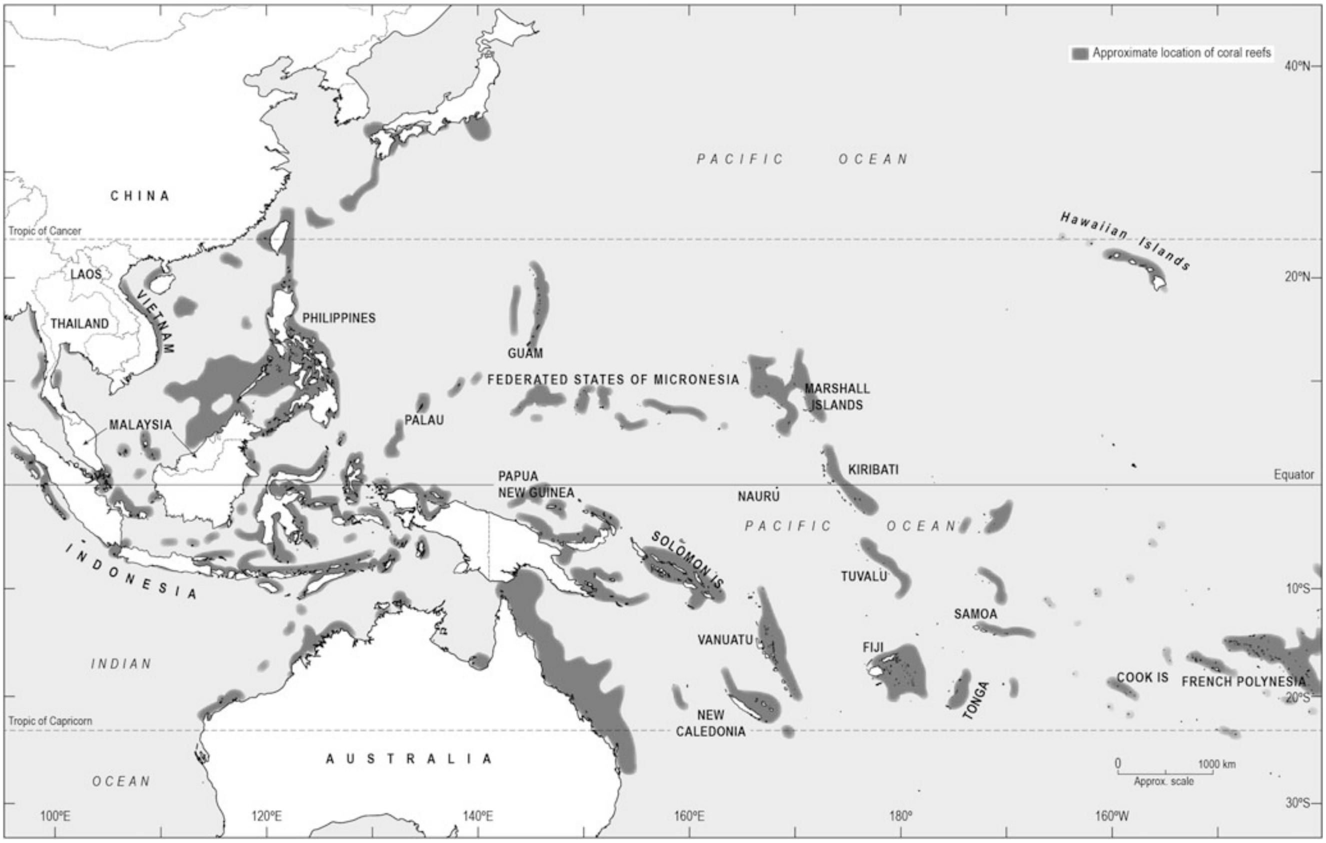

Fig. 1.1 The tropical and subtropical Western Pacific Region—the geographic focus of the IOC/WESTPAC-CorReCAP Project. Note the extensive distribution of coral reefs in the tropical and subtropical latitudes. In the figure, shadow areas represent coral reef locations. The Western Pacific Region is the largest area of coral reefs with biodiversity richness on this planet. In this region, major external forcings and feedback loops are illustrated in Fig. 1.2

1.1 International Workshops

- Shanghai, China (26–29 May, 2009): meeting of about 25 researchers to establish a work programme, determine priorities, discuss paper writing and identify support funding options.
- Phuket, Thailand (22–24 June, 2010): meeting of about 12 scientists to receive progress reports, identify common issues and provide advice as required to various research projects.
- Busan, Republic of Korea (28–31 March, 2011): meeting of about 35 researchers with ten CorReCAP collaborators. Meeting was in three parts: first, some presentations; second, discussion of writing papers; and third, drafting some short items for implementation.
- Shanghai, China (31 July–4 August, 2012): co-funded by the Asia-Pacific Network *(APN); Capacity Building in Marine Research*—this meeting was attended by 20 researchers, government officials and representatives from international funding agencies.

The outputs of this workshop included an Asia-Pacific Network Report:

Fang Luo, Liuming Hu and Jing Zhang (2014) Capacity building assessment for integrated marine biogeochemistry and ecosystem research in the Asia-Pacific region. APN Science Bulletin, 4(1) 35–39.

A refereed international research journal paper from the Shanghai workshop (31 July–4 August, 2012) as below:

R.J. Morrison, et al. (2013). Developing human capital for successful implementation of international marine scientific research projects. *Marine Pollution Bulletin*, **77**, 11–22.

It was also agreed that attempts would be made to publish a special volume of an international and peer-reviewed journal in 2013, focusing on the IOC/WESTPAC-CorReCAP Project.

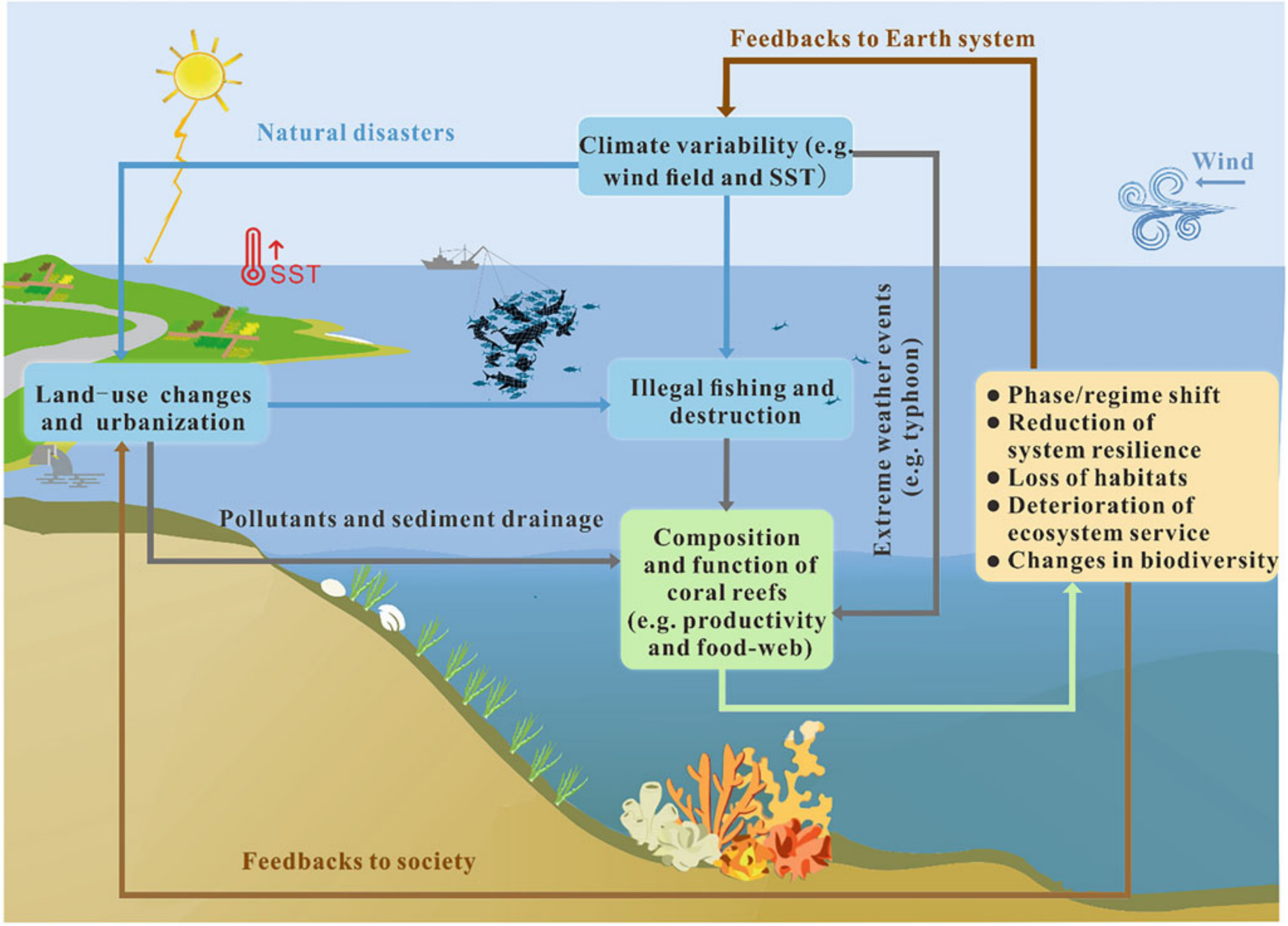

Fig. 1.2 Illustration of external forcings and feedback loops of coral reefs under the impacts of climate variability and anthropogenic activities for the Western Pacific Ocean. The light blue boxes indicate external forcings, the green box denotes the ecosystem response, the yellow box shows the consequences to the marine ecosystem (i.e. coral reefs) in terms of sustainability, while the illustration next to the coloured line with arrow highlights the example of known mechanisms through which the impacts can produce a result

Deep Sea Research II agreed to publish such an issue; *Volume 96 (2013)* contained 11 research articles from scientists in the IOC/WESTPAC Region. The papers, in a collective way, give snapshots of various aspects of the biogeochemistry, ecology and environmental sciences of coral reefs of the Western Pacific Ocean, and examine the response of coral reef ecosystems to the external driving forces from change in climate and anthropogenic activities in various hydrodynamic as well as geographic situations.

1.2 IOC/WESTPAC Summer Training Courses Were Organised

- Koh Samui, Thailand (15–18 June, 2010) on the "Impact of Sedimentary Dynamics and Biogeochemistry on Coral Reefs"
- Sanya, Hainan, China (8–12 June, 2011) on the "Water Quality and Its Impact on Coral Reefs"
- Nha Trang, Vietnam (18–21 April, 2015) "Resilience of Coral Reefs to Climate Change and Anthropogenic Disturbances"

Each of the above-mentioned training activities had 25–30 participants who were postgraduate students (e.g. Ph.D. candidates) and young scientists from IOC/WESTPAC countries. Mentors at the courses were experts or senior scientists from IOC/WESTPAC countries.

A workshop on "IOC/WESTPAC-CorReCAP" outreaches was convened in Shanghai, March 2016, with participants from China, Australia, Korea, the Philippines and Thailand, to review the project. During the meeting, participants noted that some completed work had been published independently, while outputs from other completed projects had not been published. It was proposed that a synthesis be prepared by IOC/WESTPAC-CorReCAP collaborators focussing on the research progress of this project with consensus on publication of a monograph on coral reefs of the Western Pacific Region. The book has several advantages and could be used for follow-up training activities of the IOC/WESTPAC-CorReCAP Project for young scientists and graduate students. Suggested chapter titles at the time were ambitious and composed of various aspects of coral reefs for the Western Pacific Region, which were as follows: hydrodynamics in coral reef ecosystems, anthropogenic environmental impacts on coral reefs in the Western Pacific Region, advances in coral biology, reef ecology in the Western Pacific Ocean for adaptation to global change, biogeochemical cycles of coral reef ecosystems, climate change and records from coral reefs, environmental and climate proxies embedded in coral skeletons, social and economic dimensions of coral reefs as well as change of coral communities and implications. Leading scientists, co-authors, potential additional contributors and reviewers were assigned and invited at that meeting.

1.3 This Monograph Is an Output from These Activities!

In conclusion, the IOC/WESTPAC-CorReCAP Project has implemented a well-coordinated and multidisciplinary range of activities contributing to a better understanding of the evolution of coral reefs under the external forcings from the climate change and anthropogenic activities. The critical importance of strong partnerships within the research network at the regional scale to guide the joint research activities has been noted, and the implementation of the IOC/WESTPAC-CorReCAP Project has provided a platform on which people from different countries and backgrounds can share knowledge and research techniques, and contribute to the development of the capacity to sustainably manage the coral reefs in the Western Pacific Region.

In this monograph, Chap. 2 provides information about the current environmental conditions of the Western Pacific Ocean, with focus on the climate and anthropogenic issues that are impacting coral reefs in terms of sustainability. Chapter 3 provides an up-to-date summary of the knowledge on coral biology, from genetics to life cycles, with an emphasis on the situation in the West Pacific Region. In Chap. 4, reef ecology is examined in light of the current view of ecosystem sustainability, from individual organisms to the system behaviour. In Chap. 5, the recent progress on the biogeochemical studies for coral reefs is summarised, with focus on carbon and nutrient cycling. In Chap. 6, a critical review of the application of proxies, such as radioisotopes and other tracers, is elaborated based on the recent findings. In Chap. 7, we review the achievements and success of coral reef studies and synthesise major knowledge in this Western Pacific Region, and then provide thoughts for the research in the near future. Finally, in the postscript, the chronology and major activities of the IOC/WESTPAC-CorReCAP Project are listed for a better understanding of the scientific research and capacity development activities needed in this region in the next decade or so.

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Anthropogenic Environmental Impacts on Coral Reefs in the Western and South-Western Pacific Ocean

2

R. John Morrison and W. G. L. Aalbersberg

Abstract

Coral reefs are amongst the most important ecosystems globally. They provide food and construction materials for millions of people living in the tropics, but this use of the reefs by humans comes at a cost. This chapter provides an overview of the many anthropogenic impacts on the coral reef environments in the SE Asia and Pacific Island region. The issues covered include population increase, migration of people to coastal areas and issues relating to subsistence and low-income community's response to the global economic situation through their changing use of reef resources, e.g. increased reef gleaning. Pollution from small-scale developments, e.g. tourism, and industry, as well as impacts from large industry including agriculture, tourism (resorts, diving), mining, commercial fishing including marine and coastal mariculture and issues like land use change, sedimentation and eutrophication are highlighted. Related impacts caused by coastal city expansion (e.g. building of ports, roads, industrial areas, waste management—including location of 'landfills' and sewage treatment facilities) are examined. The significant impacts of shipping activities, oil spills, reef collisions, waste disposal and antifouling materials are also considered. A comprehensive listing of the activities impacting on coral reefs, together with a review of the impacts from each type of anthropogenic activity, has been developed. This is complemented by commentary on the effects of climate change that are superimposed on the direct anthropogenic impacts (temperature, rainfall, acidification, sea level rise, storms). Some introductory/general remarks on hydrodynamics relating to coral reefs are included, as these will also be altered by anthropogenic activities. The driving forces based on the impact types (e.g. hydrodynamic changes, sediment fluxes, nutrient flows, contaminant mobilisation/transport/transformation) are presented, and the consequences for coral reefs of changes in these driving forces are discussed.

Keywords

Western Pacific · Coral reefs · Anthropogenic impacts · Subsistence activities · Major industries · Responses

2.1 Introduction

2.1.1 The Western and South-Western Pacific Region and the Coral Reefs

The region of interest in this chapter stretches from the Bay of Bengal in the west (longitude approximately 95°E) to French Polynesia in the east (longitude approximately 130°W), and from Midway Island in the north (latitude approximately 28°N) to Oeno Atoll (latitude approximately 24°S) (Fig. 2.1). Coral reefs are a dominant feature of the countries in this zone, including atolls (essentially reefs of variable thickness built up by corals (and other organisms) resting on a volcanic base), barrier and fringing reefs (limestone platforms having an elevation generally less than 5 m above mean sea level). Reefs are unique to tropical and certain subtropical oceans since the reef-building organisms require water temperatures in excess of 22 °C. In the central and south Pacific, some countries consist entirely of low elevation coral structures, e.g. Tuvalu; others contain atoll groups, e.g. the Cook Islands; and some countries consist of mainly volcanic islands with a few isolated atolls, e.g. Ontong Java in the Solomon Islands (Cumberland 1956). Atolls also commonly occur in the western Pacific (e.g. in the Philippines and

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W. G .L. Aalbersberg—deceased February 2018, four weeks after making his final contribution to Chapter.

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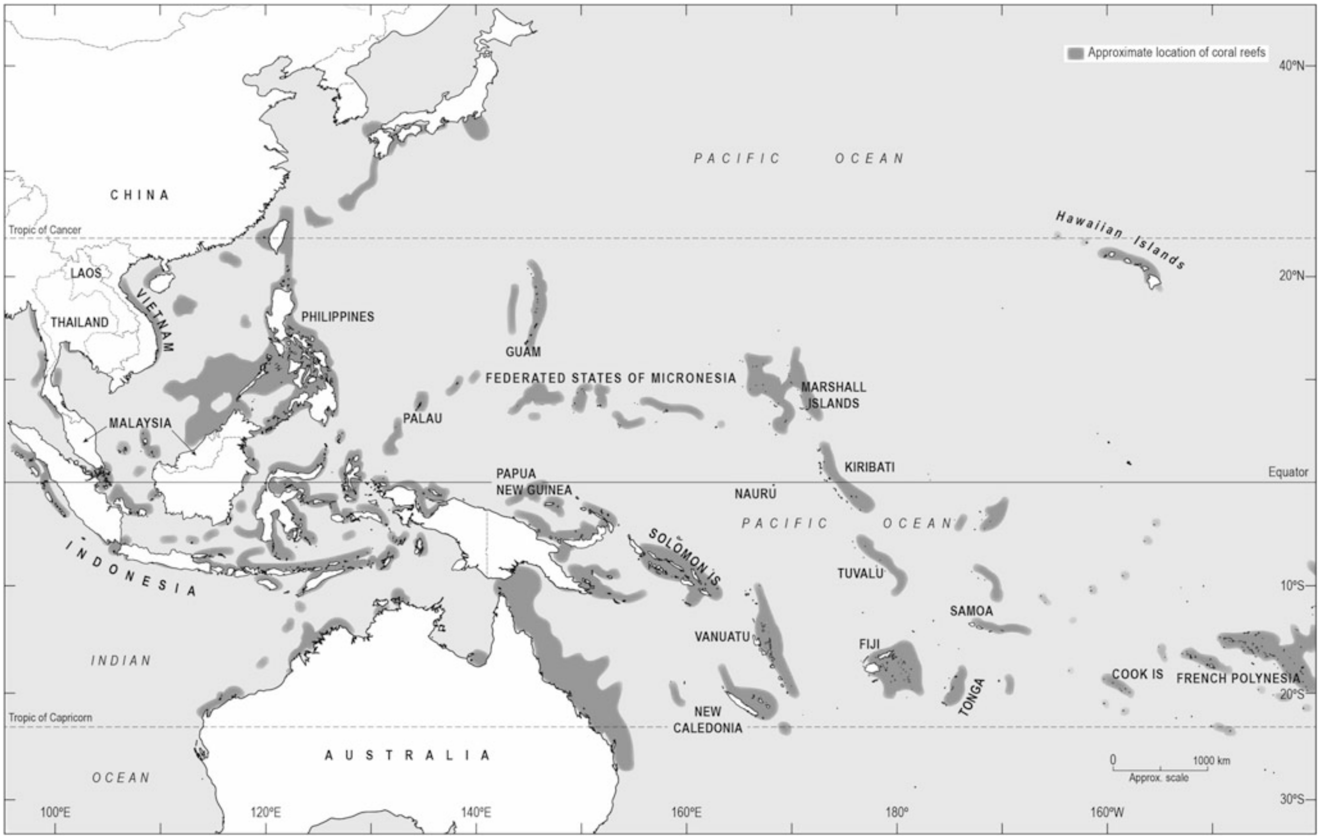


Fig. 2.1 Geographic region covered by this paper with distribution of coral reefs in grey

Indonesia), while fringing and barrier reefs are found in coastal areas of almost all countries in the region, dominating the coast in places like the east coast of Hainan Island (China), Apo Island (Philippines) and Kepulauan Seribu (Indonesia). Many major population centres in the region (e.g. Sanya and Wenchang on Hainan Island, Apia, Suva) evolved in coastal locations that afforded some protection against storms in an era when shipping was the main mode of transport. Many of these centres are located in bays protected by barrier reefs, by islands or by riverine deltas. It should be noted, however, that these barriers also have the effect of limiting mixing of near-shore and open ocean waters (Viles and Spenser 1995), and this may facilitate contaminant accumulation in the near-shore waters most often utilised by local residents.

Anthropogenic impacts on coral reef environments can take many forms and vary from devastating to relatively minor, be direct and indirect, accidental or deliberate. Many of the impacts, types and their causes are summarised in Table 2.1.

2.1.2 Population Change and Migration of People to Coastal Areas

The total population of SE Asia and the Pacific Islands (excluding China) is currently about 650 million, with China having about 1376 million inhabitants (United Nations Population Division 2015). This is an increase from about 165 million in 1950 (China 550 million). Given that on average about 50% of the population lives in the coastal zone (within 200 km of the coast) (Neumann et al. 2015), this indicates a coastal population of the region of interest of over 1 billion people. Coastal populations are increasing faster than in non-coastal areas (Creel 2003) with over 1000 people per day arriving in each of the large urban centres in China, Vietnam, the Philippines and Indonesia giving rise to urbanisation levels of on average about 45% in 2015 compared to 15% in 1950 (United Nations Population Program 2015). The average population density in coastal areas is about twice the world's average population density (Creel

Table 2.1 Anthropogenic impacts on coral reefs

Anthropogenic activity	Impact on reef	Ecological consequences	Locations where impact identified
Dynamiting/blasting reef passage for small boats	• Direct mortality of corals, invertebrates and fish • Sedimentation • Hydrodynamic changes	Reef decline, loss of marine biodiversity Burial and death of corals, invertebrates Change in coral diversity decline in reef stability in some areas	Kiribati, Tuvalu, Tonga, Marshalls, Palau, Indonesia, Malaysia All countries All countries
Groyne emplacement	• Reef hydrodynamic change	Change in coral diversity decline in reef stability in some areas	All countries
Dredging for ship passages or coral sand extraction	• Sedimentation • Hydrodynamics • Contaminant mobilisation	Burial and death of corals, invertebrates Change in coral diversity decline in reef stability in some areas Fish kills, shellfish contamination, biodiversity change	All countries All countries Fiji, Guam, China, Indonesia, Philippines, Vietnam, Thailand
Reef gleaning for subsistence food supply	• Biodiversity change • Mechanical damage	Loss of key species Death of some corals, sediment mobilisation	All countries Most countries
Small-scale (eco-)tourism developments and operations	• Pollution by sewage • Sedimentation from construction	Algal blooms, water deoxygenation, fish kills Burial and death of corals, invertebrates	All countries Most countries
Construction of ports, resorts, roads	• Direct damage and death of corals, invertebrates and fish • Sedimentation • Hydrodynamic changes • Chemical discharge • Poor waste management • Possible eutrophication	Burial and death of corals, invertebrates Burial and death of corals, invertebrates Change in coral diversity decline in reef stability in some areas Poisoning of corals, fish and shellfish Clogging of fish gills, interference with reproductive systems, burial of sedentary organisms Algal blooms, water deoxygenation, fish kills	All countries All countries All countries Most countries Most countries All countries
'Coastal' agriculture Land use change involving soil and sediment mobilisation	• Sedimentation • Eutrophication • Possible hydrodynamic changes	Change in coral diversity, decline in reef stability in some areas Algal blooms, water deoxygenation, fish kills Change in coral diversity decline in reef stability in some areas	All countries except atoll-dominated ones As above As above
Tourism activities Boat anchoring Reef walking Diving	• Boating impacts including anchor chain damage and fuel spills • Walking—damage and death of corals • SCUBA diving • Eutrophication	Direct death of corals, loss of structure, some sediment mobilisation Change in reef biodiversity Physical damage to reef structures, damage by mooring/anchoring boats Algal blooms, water deoxygenation, fish kills	Most countries Most countries Most countries except small atolls As above
Commercial fishing	• Use of poisons • Anchoring of boats—damage and death of reef organisms • Biodiversity changes • Disposal of damaged nets	Poisoning of corals, fish and shellfish Direct death of corals, loss of structure, some sediment mobilisation Decline in reef zone quality Long-term cause of fish and seabird death	Most countries All countries All countries Most countries
Coastal aquaculture and mariculture	• Biodiversity loss • Pollution • Sedimentation	Decline in reef zone quality Possible death of a range of organisms, biodiversity change, algal blooms, water deoxygenation, fish kills Burial and death of corals, invertebrates	All countries except the very smallest As above As above
Poorly managed waste disposal including location of landfills	• Sedimentation • Hazardous substances (including plastics) into reef system • Toxic leachate	Burial and death of corals, invertebrates Possible death of a range of organisms, biodiversity change, algal blooms, water deoxygenation, fish kills Death of organisms, long-term biodiversity change	All countries All countries except the very smallest As above
Coastal shipping	• Oil spills • Reef collision damage—loss of habitat, death of organisms, spills • Antifouling chemicals • Waste dumping	Coating of corals, fish and shellfish, death and diversity loss Direct death of corals, loss of structure, some sediment mobilisation Possible death of a range of organisms, biodiversity change	All countries All countries Most countries Most countries

(continued)

Table 2.1 (continued)

Anthropogenic activity	Impact on reef	Ecological consequences	Locations where impact identified
		Burial of organisms, poisoning of organisms, reef death, loss of biodiversity	
Climate change	• Temperature increase • Acidification • Rainfall-related salinity change • Storm activity increased	Reef bleaching, death of corals Weakening of coral structures, reef decline Death of corals, loss of reef diversity Damage to corals, reef death, sedimentation	All countries All countries All countries except the very smallest All countries
Mining	• Sedimentation • Contaminant mobilisation • Toxic chemical use • Live corals removal • Bulk coral removal damage	Burial and death of corals and invertebrates Fish kills, shellfish contamination, biodiversity change Death of organisms, long-tern biodiversity change Reef damage—death of organisms, diversity change Reef structure weakening, hydrodynamic change	Many larger countries Many larger countries Many larger countries All countries All countries
Military activities	• Sedimentation • Hazardous substance and toxic use • Blast damage in limited areas	Burial and death of corals and invertebrates Fish kills, death of invertebrates, diversity change Death of organisms, short-term diversity change	Many larger countries Many larger countries Many larger countries

2003) giving an average value for the coastal zones in the region of about 260 persons/km^2 with a range from about 50 to 7500 persons/km^2.

Neumann et al. (2015) reviewed population predictions for the low elevation coastal zone (LECZ) regions and found that China, Indonesia and Vietnam were three of the five countries worldwide with the largest share of population in the LECZ. This represents more than 150 million people. All three countries were characterised by extensive non-urban settlements in the LECZ (>70%). Since coral reefs are a significant part of the coastal environment in most regional countries, the impacts of population increase and coastal drift/migration will be substantial and likely to increase.

2.1.3 Subsistence Living and Impacts of the Global Economic Situation on Reef Resources

Coral reefs have provided a subsistence living for millions of people in coastal areas of SE Asia and the Pacific. Reefs have provided, through fish and shellfish, much of the protein utilised by these communities for thousands of years (Birkeland 2015). Traditionally, access to the reef resources was by foot, by swimming or via canoes (single hull or outrigger) and such mechanisms enabled a sustainable livelihood to be maintained (Salvat 1992).

Traditionally, people lived in coastal villages with small populations and subsistence culture. Over the last century, as noted above, people have moved to these coastal communities in significant numbers, leading to increases in village populations with more intensive fishing and reef gleaning and more intensive food production in many areas including cereal and root crop farming, chicken and pig production. These changes have contributed to dramatic changes including extensive damage to reef structures, damage to adjacent seagrass beds and mangrove communities, overfishing and increased water column nutrient concentrations derived from sewage and animal sources particularly during wet weather. Overfishing also contributes to diversity changes, such as decreases in herbivore populations that have resulted in extensive growth of algal species (e.g. *Sargassum*) and other flora, leading to corals in many parts of reef systems being overwhelmed (e.g. Morrison et al. 2013).

Many subsistence communities have gradually moved towards involvement in the global economic cycle by, for example, selling surplus produce in urban markets, developing small tourism facilities (including eco-tourism) and entering into fish supply agreements with larger tourism resorts. When a global economic downturn occurs, market prices for commodities often decrease, tourism numbers decline and the cash income to the small coastal communities also falls. These communities often respond to this by increasing their ‘subsistence’ activities, including greater removal of local reef resources; if the local population has increased because of the successful move towards wider economic development, there are more people to feed and the extraction of reef resources is substantial (Cinner and McClanahan 2006; Cinner 2014).

Responses to these changes have been many and varied. Successful responses have usually involved a cooperative effort from the whole community. An example from Fiji illustrates what can be achieved. Alarmed by the changes in their reef systems (resulting from greater economic activity) in terms of food supply and tourism, local communities in the Coral Coast of south Viti Levu solicited assistance from local scientists. The scientists carried out investigations, including grazing exclusion trials that clearly revealed the impact of herbivory (reduction due to overfishing of herbivores) in *Sargassum* control. This finding led to the establishment of locally managed marine areas (LMMAs) under local community control with *tabu* (bans) on fishing, in certain areas, especially for herbivorous species. Community members monitored fisheries stocks through catch per unit effort (CPUE) information recording; the results have been passed on to the scientists for analysis. The findings are discussed with the community to assess the effectiveness of the management actions. Local strategies for improved management of nutrient sources have been developed, including improved solid waste management practices, replanting of buffer strips of vegetation along adjacent river banks, relocating intensive animal husbandry facilities away from river banks and the construction of wetlands for treatment of wastewater. Community-coordinated reafforestation of catchment areas and mangrove replanting along the coastline have also emerged along the Coral Coast. In these initiatives, scientists play a facilitation and advisory role to the communities (Tamata 2007). This approach is also being carried out under the LMMA Network in the Federated States of Micronesia, Indonesia, the Philippines, Palau, Papua New Guinea and the Solomon Islands.

2.1.4 Pollution from Small-Scale Developments

Pollution usually conveys an image of large industrial complexes belching out smoke from stacks; dark coloured and often oily water through drains into rivers, lakes or the ocean; and smelly contaminated solid waste that is left in the landscape unmanaged. What is less appreciated is that small economic activities such as laundries, food packaging facilities, print shops, clothing manufacturers, electroplating works and garages, employing less than 30 people, can also be significant polluters, depending on the location and effectiveness of local regulation. Depending on their size, breweries, tanneries and fish canneries could also be included in this consideration. Small industry zones, being a home to up to 50 small enterprises, located close to a coastal water body can create similar impacts to a single large industry (Clark 1992).

Typical pollutants from these small operations are high biochemical demand (BOD) water/suspensions, water with high (>8.5) or low (<4.5) pH, metals (e.g. Cd, Cr, Cu, Ni), solvents (e.g. carbon tetrachloride, dichloromethane), particulates in air and water and organic-rich solid wastes. The extent of pollution depends on the regulations controlling industry establishment and the degree of enforcement of discharge regulations. Some of these small industrial zones have centralised waste disposal management systems that collect the wastes from the various operations and treat them before appropriate final disposal. In other locations, each individual operation is responsible for managing its own wastes. No matter which type of operation is in place, the enforcement of appropriate environmental protection measures is critical.

Small tourism facilities are not often thought of as pollution sources, but poor management and regulations can lead to discharge of sewage (raw or partly treated) into coastal waters, bilge discharges (if boats are used), along with plastics and toxic materials such as batteries, oils and cleaning chemicals. Again a single unit may cause limited problems leading to algal blooms, fish death and limited local deoxygenation of waters, but in many locations with attractive coastal scenery including reefs, several operations may be located close together, each contributing to a larger problem in the adjacent environment.

Planning is important—which industries (number and type) should be allowed to operate where and what degree of control is necessary. Should each industry be allowed to operate its own water management system or should a centralised system be put in place funded communally (all companies contributing to the cost)? Should small industries be required to self-monitor and what action will be taken if no control is in place? Consultation and interaction between operators and regulators is critical so that both sides are aware of each other's requirements and limitations, especially when assessment of cumulative impacts is required; in this way, targeted action strategies for protection of key resources, such as coral reefs, can be developed and implemented.

2.1.5 Shipping Impacts

The wide range of boats and ships that move into and through coral reef zones leads to an extremely diverse set of impacts. The vessels can vary from 5 m local fishing and dive support boats to ocean going cruise ships, container ships, bulk carriers to oil supertankers that are now up to 400 m in length and carry a load exceeding 400,000 t. In addition to the impacts of the vessels directly on reefs, shipping also leads to impacts from the development and maintenance of ship handling facilities onshore. These onshore construction and related activities are discussed below (see coastal cities expansion), and this section will consider the impacts of the boats and ships themselves.

The impacts of boats and ships include those caused by maritime transport in general (not related to specific uses) and

Fig. 2.2 Ship groundings occur regularly on reefs in this region a—wreck on a reef in the Marshall Islands (photograph by J. Morrison)

those related to specific boating/shipping activities. These general reef impacts include poor waste disposal (plastics, chemicals, organic matter), fuel spillages and leakages, damage from the wash created by fast-moving vessels, anchor and anchor chain impairment and damage created by collisions with reefs. Boats and ships generate a wide range of wastes including oily wastes, garbage, sewage, grey water and hazardous materials such as battery components and solvents. Discharge into a coral reef zone of such materials, along with fuel spillages and leakages, can cause direct toxic effects on some organisms, and impact others as a result of smearing over gas exchange organs and interference with reproduction.

Wash created by fast-moving vessels can impact reefs directly at low tide when the waves thus generated can strike and damage exposed surficial structures. While such structures are well conditioned to dealing with waves, the effects of boat waves can be important if they cause the waves to hit the reef from angles different from tidal influence as resistance may be lower in those directions.

The impact of anchors and anchor chains on coastal marine environments is well known (Dinsdale and Harriott 2004). In coral reef zones, this has been identified as a significant cause of direct death of organisms and indirect impairment through fragmentation and sedimentation. While detailed studies in the SE Asia/Pacific region are sparse, impacts on reefs in other regions have been reported (Kitching 2015).

Ship collisions, sunken ships and groundings on coral reefs (see Fig. 2.2) can lead to a range of impacts. These include:

- Collision impact, physical damage and direct death of organisms due to pressure impact (Riegl 2001);
- Sediment (suspended solids) plumes released from collisions smothering nearby organisms, and impacting on larval recruitment and development (Dollar and Grigg 1981);
- Fuel oil leakage with direct toxicity to some organisms and possible smearing of surficial organisms;
- Cargo spillage (oils, solids such as iron ore, coal (impacts of fine materials), toxic chemicals (cyanide, arsenic, acids, etc.), impacts of containers and drums (more physical impact outcomes)) (Jones 2007);
- Release of biofouling anti-barnacle chemicals (e.g. Cu-based) (Negri et al. 2002);
- Release of ballast water with exotic organisms (Coles and Eldredge 2002); and,
- Long-term impacts if vessel is not removed—slow release of toxic materials plus ongoing mechanical impacts.

One particular group of vessels requires special mention—those linked to reef tourism (Smith 1988). These create many of the impacts listed above (anchoring and chain damage, fuel spillage, waste discharge), but in addition bring tourists

Fig. 2.3 Dynamite fishing is still a common technique used in the region with significant damage to coral reefs (photograph courtesy of T. Heeger)

in close proximity to reefs through SCUBA diving and reef walking activities.

SCUBA diving was, for a long time, thought to have minimal impact on reefs, but evidence of broken coral fragments, reattached corals, abraded corals and dead organisms has been commonly found at heavily used sites globally (Barker and Roberts 2004), with the extent of damage linked to the types of corals present. Although many divers touch the reef during dives, a minority cause most of the damage with inexperienced divers thought to create many problems. Most damage is caused by flippers (direct damage to substrate and mobilisation of sediment), followed by hands, knees and equipment collisions, and even camera users have been observed to create reef damage. Reef walking also causes significant mechanical damage, along with removal of materials (Woodland and Hooper 1977; Williamson et al. 2017). The extent of damage depends on the amount of activity and also the coral species impacted. Recovery rates also depend on species impacted and length of time between walking groups.

Another group of vessels that merit special comment are those involved in fishing. In addition to fuel spillage and waste disposal problems, fishing vessels often leave behind pieces of fishing tackle and broken nets that create problems for fish, turtles and seabirds. Fishers may also use dynamite (see Fig. 2.3) leading to severe mechanical impact on the surrounding system (Riegl 2001), including the death of many non-target species, and the use of cyanide and natural toxins (e.g. *Barringtonia acutangula* (L.) Gaertn) in both the catch and live fish trade has caused significant reef system damage (Johannes and Riepen 1995). Recovery from blasts and toxins use varies depending on amount of initial impact (Fox and Caldwell 2006).

The surfaces of various marine vehicles and almost all marine infrastructure in contact with seawater are armoured by protective coatings against corrosion and fouling. Antifouling agents (e.g. copper, zinc, tin and synthetic organic compounds) are designed to be toxic to a range of marine organisms, inhibiting photosynthesis and growth of bacteria, algae, barnacles, etc.; they are designed to be released slowly (1–3 μg cm^{-2} day^{-1}, Takahashi 2009) into the ambient environment and persist in seawater. Ports, harbours, marinas and tourist spots are locations of high densities of marine vessels, and adjacent coral reefs and mangroves may become vulnerable to these toxic chemicals when released from the original treatment site.

One final impact related to marine/coastal transport is the use of blasting to create channels through reefs to facilitate movement (of usually small vessels). This has been carried out in many atolls and also in areas with barrier reefs and obviously has similar impacts to reef fishing, plus in many cases will also alter local hydrodynamics with subsequent additional ecological consequences. Reef blasting has been outlawed in various countries, but enforcing the regulations is difficult especially in more isolated localities where reporting

Fig. 2.4 Coastal urban expansion causes dramatic impacts on reefs—the south-east section of Majuro Atoll is covered with the highly developed Dalap-Uliga-Darrit (DLD) area (photograph by J. Morrison)

is minimal and enforcement staff are not permanently located.

2.1.6 Coastal City Expansion

Coastal cities are an extremely important component of human habitation on Earth, especially in the South East Asia region, where such centres occur in most countries and are often significant commercial and administrative locations. In addition to the established coastal centres, such as Manila, Jakarta, Singapore and Hong Kong, rapid expansion is quickly enhancing the populations of cities like Da Nang, Nha Trang, George Town (Penang), Phuket City, Surabaya, Macassar, Port Moresby and Sanya. In all these locations, significant infrastructure is being developed to support the expanding populations in terms of housing, transport, jobs (industry and tourism), waste management and recreation (see Fig. 2.4).

The new infrastructure establishment involves the building of roads, bridges, residential accommodation, commercial non-manufacturing buildings, industrial/manufacturing premises, power plants, landfills, sewage treatment plants, port facilities and recreational sites. These activities do not require any unique operations; rather, they involve:

- Substantial earthworks possibly with underground tunnels and car parks;
- Demolition of older buildings (possibly with contaminated materials therein);
- Dredging;
- Dust generation;
- Rerouting of surface waters;
- Groundwater extraction;
- Power transmission facilities (overhead or underground cables); and,
- Movement of hazardous materials, such as paints, solvents, petroleum products, sealants, pesticides and cleaning products.

All these operations will have impacts on coral reefs in the area, especially fringing reefs including possibly, the complete loss of reefs. Mobilisation of sediments, spillages of hazardous materials and rerouting of surface waters could also lead to impacts on barrier reefs. In many locations, damage done during earlier developments almost certainly will have impacted on local reef systems, and the effects of expansion will depend to some extent on the degree of reef recovery from the previous impacts. In addition, having larger numbers of people in the vicinity will also create issues resulting from more reef gleaning and greater recreational use damage.

As expected, extensive construction activities have major impacts on the surrounding environment and the reef systems are no exception. Lai et al. (2015), examining impacts around Singapore, found a nearly 50% decline in the total cover of intertidal coral reef flats between 1993 and 2011, and a similar decline was estimated for the period 1922 to 1993. Similar reductions were found by Valadez-Rocha and Ortiz-Lozano (2013) for port development, with three types of impacts: (a) direct reef loss caused by landfills and coastal structures, (b) fragmentation in short and medium scales of the fringing reef and (c) long-term modification of coastal dynamics leading to sedimentation and loss of a complete reef area.

Small island situations can provide an encapsulation of such impacts and the island of Guam (13°28′N, 144°45′E) is a good example. Guam, having a land area of only 544 km^2, has been the major shipping centre in Micronesia for about 400 years and has undergone considerable economic growth and urban expansion over the last 75 years to accommodate military and tourism operations (tourism attracts over 1 million visitors annually). Guam's current environmental problems are largely associated with solid and hazardous waste disposal, storm water runoff and the treatment and disposal of domestic and industrial wastewaters (Morrison et al. 2013). The island has some 5000 species of marine organisms, many of which rely on healthy coral reefs; the combined area of coral reef and lagoon is approximately 69 km^2.

Construction of a new airport (in 1982 with a second terminal in 1998), major tourism facilities along the west coast (Agana and Tumon Bay) and port facilities over the past 50 years have had significant impacts on the reef systems. Issues have included the damage to or complete loss of fringing reefs resulting from military operations; port, hotel and road construction (Prouty et al. 2014); serious algal blooms arising from poor sewage management causing reef impacts (Denton and Sian-Denton 2007); and pollution from heavy metals, PAHs and organochlorines (Denton et al. 2005, 2006a, b).

Although not an issue specifically related to coastal city expansion, the situation with regard to plastics impacts on reefs deserves a separate mention. This topic has become of much greater global interest recently with the widespread use of (and subsequent pollution caused by) microplastics (i.e. plastic particles <5 mm in diameter). Lamb et al. (2018) assessed 159 coral reefs in the region covered by this paper and estimated that about 11 billion plastic items were entangled on reefs in the region. Of greater concern was their discovery that the likelihood of disease increases from 45% to 89% when corals are in contact with plastic. Another study found that scleractinian corals ingest microplastics (at up to 50 μg plastic/cm^2/h), suggesting that these microplastics could potentially impair coral health (Hall et al. 2015).

2.1.7 Large Industry Impacts

2.1.7.1 Agriculture and Forestry

Although agriculture and forestry are different in many ways, the impacts on coral reefs have many similarities, so they will be discussed together. The main issues relate to land use change, vegetation disturbance, sediment mobilisation and transport, changes to hydrology as a consequence of land and vegetation changes (mainly enhanced flows of freshwater) and the use of chemicals including insecticides, herbicides and fertilisers (Morrison et al. 2013).

Changes in land use are particularly important in the west and south-west Pacific region as there is a significant proportion of relatively steep land near the coasts (Sidle et al. 2006), the soils are relatively erodible (Chappell et al. 2007) and the rainfall in many areas is dominated by heavy downpours causing runoff and the associated movement of unconsolidated materials (Manton et al. 2001). Land disturbance can occur during initial clearing of land for agriculture or forestry, during ploughing in agriculture and during harvesting of both crops and trees.

Mobilised sediment carried by runoff during wet periods is transported initially into river systems and eventually will be carried out to sea where the freshwater can reduce salinity with dramatic impacts on coral reef organisms, and the sediment, especially the finer fraction is transported quite long distances where it settles on the sea bottom (on top of sedentary reef organisms) leading to burial, light limitation and general interference with organism life cycles (Fabricus 2005). This is evidenced by the fact that many rivers have no reefs near their mouths, but in coastal embayments where barrier reefs may occur, sediment can be transported out as far as the offshore reefs leading to serious problems.

Chemicals used in agriculture and forestry operations include a wide range of biocides, almost all of which are toxic to coral reef organisms. The impact on reef organisms depends on the concentrations that reach the reef system through either wind or water transport and the (biochemical) activity in that environment. Transport depends on the quantities used in the land-based activities, the timing of application and the prevailing climatic conditions. If the chemicals are used as intended, the concentrations that can be transported by wind should be minimal; in addition, application should render the chemicals less active as any excess is adsorbed on soil particles and many of these chemicals have a relatively short (<1 year) high activity life.

Fertilisers are commonly used in agriculture in coastal areas as the soils there are commonly alluvial and, thus, relatively productive, so the application of chemicals is often economic. The main agricultural chemicals used are compounds of nitrogen (N), phosphorus (P) and potassium (K). Two of these elements (N and P) are recognised as being two of the major limiting components for algal growth in coastal areas (Howarth 1988). As a result, runoff containing N and P materials, moving into coastal areas, can lead to significant enhancement of algal growth with a range of impacts on adjacent reef ecosystems. The main impact is eutrophication and the enhanced growth of algae which can outcompete corals for living space (leading to changes in species abundance), develop algal blooms of some species that can lead to shading and reduce dissolved oxygen in the water column and in extreme cases to hypoxia (Middelburg and Levin 2009).

2.1.8 Tourism

Issues relating to small tourism operations were briefly discussed above. The tourism industry is booming worldwide

Fig. 2.5 Tourism development causes extensive impacts on coral reefs—Tumon area in Guam (photograph by W. Aalbersberg)

and many large facilities are now located on or close to coral reef systems. Modern large tourism resorts cover extensive areas, and often incorporate a number of hotels, other accommodation units, restaurants, shopping arcades, swimming pools, tennis courts, golf courses and other outdoor recreation facilities, harbours, marinas for yachts and other small craft, car parks, sewage and other waste handling facilities (see Fig. 2.5). Large tourism operations, thus, have the potential to create a wide range of serious environmental problems; Hall (2001) summarised these into five categories:

- Environmental degradation and pollution;
- Destruction of habitats and damage to ecosystems;
- Loss of coastal and marine resources;
- Coastal pollution; and,
- Surface and groundwater diversion.

All of these issues apply in coral reef zones. Some impacts are encountered mainly during the establishment of the tourism facilities, e.g. destruction of high environmental quality situations either by direct mechanical (bulldozer) excavation or by reef blasting, runoff and dredging impacts and diversion of streams and water courses, while others are mainly encountered during the operation of the facilities, e.g. damage of reefs by poorly managed direct human contact (walking and diving), introduced exotic species and coastal oil pollution due to motorised vehicles, boats and ships.

The impacts of siltation, freshwater flows and chemicals such as those in golf course runoff, sewage effluent and overflows have been described earlier; in large resort locations, the large numbers of people and buildings means that an integrated management system is required to achieve good management outcomes. Different resorts handle this better than others with a range of impacts on the surrounding environment and the tourists themselves. Tourists often get minor complaints (diarrhoea, skin rashes, headaches) and put this down to something eaten or poor hygiene, when, in fact, they may be a result of contact with contaminated coastal water (Morrison, unpublished personal observations) resulting from poorly designed or managed resort facilities.

Many countries have legislation that requires environmental impact assessment (EIA) of such large facilities, and these often identify the issues described above along with mitigation steps and control procedures. There is significant evidence to indicate that even when good EIAs have been completed, many of the recommendations to minimise impacts are ignored or are implemented in a slapdash manner resulting from lack of awareness, inadequate enforcement of the regulations (lack of staff or funding) or lack of political will (Harvey and Clarke 2012).

2.1.9 Commercial Fishing Including Marine and Coastal Mariculture

Commercial fishing is hard to define other than saying it is the non-subsistence component of the sector. Small-scale commercial (artisanal) activity aimed at supplying local markets and limited export opportunities is important, while larger-scale activities usually utilising more sophisticated equipment (e.g. seine nets, sonar, GPS), often involving multiple vessels, and utilising constructed growing sites have become of greater significance in the last 20 years. The harvests include a wide range of finfish, as well as items like algae, pearls, shrimp and oysters. In addition to harvesting 'wild' populations, extensive effort is being expended on aquaculture and mariculture. Since much of the aquaculture is land-based, this will not be discussed further as the impacts are similar to those discussed under coastal city expansion.

Commercial fishing is a key industry in almost all countries in the Asia-Pacific region where coral reefs occur. Apart from the economic benefits of the industry, protein sourced from commercial fishing is an essential requirement of the local populations. Wild fish catches in the region have risen from about 2 million tonnes in 1950 to about 20 million tonnes by 2010 (FAO 2010).

Mariculture is widely practiced in tropical coastal areas of the region covered by this manuscript and is the human managed production of algae (red and green), molluscs (cockles, mussels and oysters), crustaceans (prawns and shrimp), giant clams and ocean finfish (e.g. sea bass, sea mullet, milkfish, barramundi). Only a limited diversity of the relevant species is cultivated (de Silva 1998).

While some commercial finfish operations target particular species, others take what they can get (multispecies fisheries). In coral reef areas, this can often lead to removals from a given area of large numbers of fish (usually larger ones) first impacting stock size (growth overfishing) and eventually leading to the loss of so many mature fish that reproduction is affected (recruitment overfishing). This can also lead to a reduction in the diversity of fish. Similar issues can arise with invertebrate populations. It is not uncommon for a commercial operation to fish out a given area, and then move to a new area where repeated large removals occur. Over time, in the absence of any regulatory controls aimed at recovering the stock and improving productivity by reducing fishing effort, such removal can have a devastating impact on fish populations. While it is also recognised that high numbers of artisanal fishers can have a similar impact, the time required for unrecoverable impact may be shorter with many commercial fishing operations (Pauly et al. 2003; Froese et al. 2016).

The range of impacts of commercial fishing on coral reefs is extensive, including ecological impacts on finfish and invertebrate populations and diversity, unwanted by-catch, physical damage to reefs resulting from boat impacts, anchoring, trawls, the direct and indirect effects of fishery industry wastes (such as plastics, damaged nets), oils/fuels, unused mariculture food materials (often high in nutrients), ammonia excreted by various organisms when found in large numbers (= high ammonia concentrations) and sediments suspended and mobilised during mechanical operations.

Direct effects of fishing on reefs are determined over the longer term by the influence on the rates of reef accretion and damage/erosion. These rates are influenced by the types and intensity of the activity. Trawling and dredging impact on infauna and epifauna, the extent often determined by the gear type. Some changes are relatively easy to detect and assess, but this is more difficult with smaller fauna. Trawls and dredges damage the substrate, and remove some biogenic species and the associated fauna. This biogenic material removal can influence predation patterns and thus biodiversity (Jennings and Kaiser 1998).

Static fishing methods such as small nets, traps and pots, often targeting specific species, can also impact reefs. The setting of nets/traps and the collection of catch can physically damage the reef, especially if the density of traps is high. Nets and traps can be lost in bad weather or through dredging activity, but still continue to trap biota (ghost fishing) for significant time periods after loss.

Seagrass communities adjacent to coral reefs are also likely to be affected by fishing, especially when dredges and trawls are utilised. The direct effects on the plants (e.g. uprooting, shredding of leaves, rhizome exposure, resuspended sediment shading) reduce the food source and protective capacity for juvenile fish (Saenger et al. 2013).

2.1.10 Mining

Although considered here as a major industry, mining, like fishing and tourism, is carried out over a wide range of scales in the region where reefs occur, from family operations to small companies (<25 staff), to substantial operations involving hundreds of people. Mining in the region could involve removing live corals for the aquarium trade, or extraction of bulk dead coral as a building material or for use in cement manufacture, or extensive land-based soil moving activities for extraction of ores, or drilling for and exploitation of petroleum resources.

All of these activities have, to a varying extent, impacts on adjacent coral reef communities. Impacts are often difficult to assess accurately because they are complex and the outcomes may be the combination of recent and older activities, plus the concurrent impact of natural processes (storms, floods, bleaching) (Guzman et al. 2005). A recent review of the impact of petroleum compounds on corals (Turner and Renegar 2017) highlights many of the issues in assessing such pollutant impacts on reefs.

The taking of live corals for the aquarium trade obviously has a direct impact on the reef system, particularly when a limited number of species are targeted. Apart from the items removed, the collection (walking on reef, boat collision with reef) will also impact on adjacent areas. Removal of live corals and collateral damage will also lead to reduced coral cover and facilitate increases in algae affecting coral growth and recruitment. Removal of bulk samples of dead coral could lead to damage to the overall reef and subsequent increased coastal erosion. Reef damage will also contribute to reduction in fish abundance and diversity (Dulvy et al. 1995).

The impacts of nearby onshore mining will depend on the type and scale of the mining; the most notable impacts are usually associated with sediment and suspended solid increases, but transport of toxic chemicals can also occur leading to death and impairment of fish, invertebrates and even corals (Ellis 1989).

Specific examples from the region include the reduction in density, extension and calcification rates of *Porites* adjacent to gold mining at Misima Island, Papua New Guinea (Barnes and Lough 1999). Extensive nickel mining in New Caledonia has been shown to impact on adjacent reef systems in New Caledonia, mainly arising from relatively uncontrolled sediment transport away from the mine sites onto the coastal reef systems. Once again, separating the effects of natural and anthropogenic runoff is an issue, but sediment damage and coral diseases have been observed (Carey 1982; Fernandez et al. 2006; Heintz et al. 2015). Growth anomalies and white syndrome were identified, but the most obvious impacts were algal overgrowth and sediment impairment, with the Poritidae dominated west coast sites being more extensively damaged than the Acroporidae dominated east coastal locations investigated (Heintz et al. 2015).

Tin mining on Phuket Island, Thailand, has been observed to have impacted on reefs there, but again separating natural and anthropogenic impacts was problematic. Sediment impacts, as observed elsewhere, and enhanced concentrations in metals were found in oysters, bivalves and algae (Brown and Holley 1982). The extent of sediment impacts on *Porites* and *Acropora* was similar, so specific effects of mining at impacted sites and control sites could not be discerned by Chansang et al. (1982). Coral mining at the Wakatobi Marine Park, south-east Sulawesi, Indonesia, was shown by Caras and Pasternak (2009) to have produced greater percentages of dead coral (and obviously less live coral), plus reduced species richness and abundance. For non-coral species, differences between impacted and control sites were less significant.

2.1.11 Military Activities and Atomic Bomb Testing

While military activities in wars are unlikely to target coral reefs, incidental damage may occur due to, for example, the use of explosive devices during coastal bombardments, landing craft being beached on reefs and human and vehicle traffic moving over reefs. An example can be found in Chuuk Lagoon, Federated States of Micronesia, a scallop-shaped lagoon about 60 × 60 km in area with water 30–40 m deep. This was given as a Mandate to Japan in 1919 and became the Imperial Japanese Navy's Fourth Fleet Base that was destroyed by warfare in 1944. Twelve warships, 32 merchant ships and 249 aircraft were sunk in the lagoon, with fuel oil, other oils and explosives' electrical components on board that gradually leak out or corrode releasing a wide range of chemicals (including trace metals and PCBs) into the lagoon waters (Monfils et al. 2006).

Even peacetime activities can create problems as noted in Pago Bay, Guam, where the fringing reef showed contamination from lead resulting from the area being used as a rifle range for training (Denton and Morrison 2009).

As a result of their isolation, a number of Pacific Islands (especially atolls) have been used for nuclear experimentation with impacts on adjacent coral reefs (Hamilton et al. 1996). Testing of weapons in the atmosphere occurred in the Marshall Islands in the late 1940s and 1950s, in Kiritimati (Christmas Island) in the 1950s and early 1960s and in French Polynesia from 1966 to 1975. The resulting contamination of the coral reef islands close to the test sites has been of considerable interest to residents because of the potential health impacts.

In the northern Marshall Islands, atmospheric nuclear testing began in 1946 on Bikini Atoll, and expanded to Enewetak in 1947. The local inhabitants were relocated prior to the tests being carried out. In 1954, the BRAVO test on Bikini exploded with about three times the predicted intensity, and the fallout travelled eastwards and seriously contaminated Rongelap and Utirik atolls, including the resident populations. These residents were evacuated a few days later, but not until they had been subjected to substantial internal and external exposure to radionuclides (National Research Council 1994). Sites in the Marshall Islands have been monitored for over 50 years and represent the most detailed field investigations of the impact of radioactivity on tropical coastal ecosystems (Robison et al. 1994).

Initially, the problems were related to short-lived and intermediate life isotopes (e.g. ^{55}Fe, ^{60}Co), but the contaminants of present concern in the northern Marshalls are ^{137}Cs (half-life 30.2 years) and ^{90}Sr (half-life 28.1 years), with Cs being the major source (>90%) of activity, and Sr 2–5%. Plutonium and americium, both present 'forever' in very small amounts (<2% each of activity), are not considered as serious problems for humans apart from one or two sites on Rongelap. There are variations in the distribution of isotopes due to differences in the design of the devices tested.

In undisturbed areas, the highest activities are in the surface materials, with activity decreasing exponentially with depth, except in places where significant disturbance has occurred. In addition to radioactive decay, there is evidence that caesium is being lost to groundwater through leaching. The terrestrial food chain is still the most significant potential exposure pathway. While a number of 'hotspots' have been located, the relative uniformity in distribution of radioactivity indicates that there is little chance of finding many others, except where burial of contaminated material occurred or there was other major disturbance of the surface materials. It would be interesting to determine the impact of the continuing radiation on the reef microbial ecology, given the interest in the use of radiation in food treatment. While many artificial radionuclides have decayed to negligible, long-lived isotopes, ^{239}Pu ($t_{1/2} = 24{,}100$ year) and ^{240}Pu ($t_{1/2} = 6563$ year) will persist for many millennia. It is estimated that about 90TGq of $^{239\ +\ 240}$Pu remains in the lagoon sediment of Enewetak and Bikini Atoll and that about 0.2 TBq is released into the ocean each year (Hamilton et al. 1996) and transported westwards. Even though the Pu isotope concentrations are far below levels of health concern, Pu laden water flows into the Indian Ocean largely via Indonesian Throughflow. Deterioration of the Runit Dome constructed in 1979 to contain radioactive wastes in Enewetak Atoll has raised concerns about sea-level rise. As corals incorporate Pu isotopes from ambient seawater as they accumulate calcium carbonate, the Pu isotopes may be proxy indications of the ambient water environment at the time of coral growth (Hong et al. 2011; also see Hong et al., Chap. 6).

The British and USA governments carried out atmospheric nuclear tests on Kiritimati in 1957, 1958 and 1962. Investigations of the impacts have been undertaken since 1964, with the most authoritative being that by the New Zealand Radiation Laboratory in 1981 (McEwan et al. 1981). This study concluded that no site on the island presented a risk to the health of the resident population; no specific impact on the reefs was identified.

In French Polynesia, a small number of official investigations of the impacts of nuclear underground testing have been permitted on Mururoa, but these have been limited in extent (Atkinson et al. 1983; Martin et al. 1990). There is no doubt that the atmospheric testing did lead to significant contamination. Sediment analyses have identified ^{60}Co, ^{155}Eu, ^{54}Mn, ^{137}Cs and various Pu isotopes; the quantities are small. As the atoll is under French military control with imported food and restricted use of local resources, the direct impact of these contaminants is limited. The impact on surrounding islands which are occupied by Polynesians living a more traditional lifestyle is expected to be small, but in the absence of detailed investigations, this cannot be confirmed.

Despite large publicity on the artificial radionuclide contamination over the Pacific Ocean, exposure to them is much less than the naturally occurring alpha emitting ^{210}Po and ^{210}Pb. The activity concentrations of ^{210}Po and ^{210}Pb in the diet of Marshall Islanders were investigated by Noshkin et al. (1994). They found that local foods contribute 87% of the ^{210}Po and 47% of the ^{210}Pb associated with the diet. The items contributing the majority of the activity to the diet were derived from the marine environment. The presence of ^{137}Cs and its movement through the food chain, e.g. incorporation into coconuts, has been a major concern for the health of people returning to the contaminated islands.

2.1.12 Dredging and Dumping of Dredge Materials (Spoils)

Dredging keeps rivers, harbours and other waterways at a required depth by removing deposited sediments. These deposited sediments bring about environmental issues, and they increase in importance when the material is contaminated (Bray 2009). The main reason for dredging is usually to achieve one, or a combination, of the following:

- To excavate material from underwater, thereby creating a greater depth in a river, lake or sea;
- To fill a void, either underwater or on land, with material excavated from underwater;
- To replace material underwater (to substitute poor quality material with good quality);
- To win material for construction; and,
- To improve the environment.

The potential adverse and beneficial effects of dredging and related operations (transport of dredged material, relocation of dredged materials onshore or offshore) are categorised according to the nature of the activity (Bray et al. 2001). Impacts can be short term, lasting only for the duration of the dredging works, and those which are medium to long term or permanent. Direct impacts of dredging are the destruction of benthic habitats, resuspended sediment issues (turbidity, smothering, nutrient release), underwater noise and the possibility of hydrodynamic effects on tidal and current flows. A wide range of physical, chemical and biological impacts may come from dredged-spoil disposal (Bray 2009). Most sediments found in highly populated and industrial countries are contaminated. Thus, the disposal of these sediments with minimum impact on the quality of the environment is a significant problem. Thus, there are impacts from deposited and suspended sediments as outlined above, plus the toxic effects arising from any contained contaminants.

The major problems of disposal of dredged material on coral reef zones are the detrimental impact on existing floral and faunal communities, restricting light penetration and increasing the quantity of nutrients in the water column, leading potentially to the occurrence of large algal blooms (McGinn 2001) and thus anoxic conditions as well as smothering or burying existing benthic plants and animals by placing large amounts of sediment. International conventions ban disposal of contaminated sediments in the open sea (e.g. the London Convention), but dumping does occur in coastal areas including close to reef ecosystems. The elevated pollutant levels cause direct toxic effects on biota. The severity of the impacts depends on the extractability of the contaminants in the spoil. pH is an important factor in bioavailability of trace metals, with reef zones having a pH around 8, which can lead to significant releases of iron and manganese, but minimal release of zinc and lead (Atkinson et al. 2007). Dredged materials with high sulfide contents may turn acid during changing of the wet sediment from anaerobic to aerobic conditions; the impact of this in reef areas is limited by carbonate neutralisation and so the impacts are usually only noticed close to the source of acid generation.

2.2 Hydrodynamic Impacts of Anthropogenic Activities on Coral Reefs

The complex coral reef ecosystems require clean, warm, well-aerated, nutrient-limited waters for maintenance of healthy conditions. These requirements must be produced by hydrodynamic processes (water movements) that occur at a wide range of scales from major ocean currents (e.g. Kuroshio, East Australian) to vertical and horizontal tidal movements, to longshore flows, to eddies within reef segments/components and even around individual corals. Understanding these flows and the interactions between flows at different scales is important for managing the impacts of anthropogenic activities on coral reefs. Reef structures are complex at either the whole reef or individual coral scale and the movement of waters will vary greatly because of the wide diversity in shapes of corals and combinations of shapes. The flowing waters have to carry nutrients, carbon species and oxygen, transport particulates into and out of reefs and facilitate reproduction by larval dispersal. Hydrodynamics is therefore a very significant component of coral reef ecosystems, and impacts on the water movements by human activities can be substantial.

It is important to note that while reefs are influenced by water movements, the reef structures themselves have a marked influence on hydrodynamics by providing barriers to currents, their complex mix of individual coral structures creating unpredictable local current patterns, and through variable roughness in bottom materials (Wolanski 1991). Some corals appear to prefer ‘turbulent’ locations (reef crests), while others are normally located in lower water motion locations. In areas of high wave energy and current velocities, massive (Porities type) corals are dominant but some strong branching structures can be found. In deeper waters where currents are generally less strong, delicate branching corals take over.

Jokiel (1978) suggested that water motion influences corals by controlling the rate of exchange of material across the interface between the water and the coral surface. Hearn et al. (2001) commented that ‘reefs grow best at their margins’—possibly because the turbulent flows there encourage maximum transfer of materials including nutrients. The interactions are complicated by the observation that in many cases, unsteady flows due to surface waves behave very differently from steady flows for which the coral structures appear to have quite high resistance to any flow (Monismith 2007).

The corals living inside a lagoon protected by barrier reefs are of great interest in this regard. As they are subject to the increase in CO_2 concentration at the surface layer and the CO_2 generation from calcification of corals, respiration of corals and decomposition of organic matter produced in situ. If wind or wave conditions change, lagoon water can become isolated from offshore waters outside the lagoon, and the lagoon can become stagnant and start to become stratified with solar heating at the sea surface; CO_2 then starts to accumulate in the water column and the lagoon water becomes more acidic. Such increased acidity in water is very corrosive to corals and may also bleach them. Frequent exchange of lagoon and offshore waters is essential for lagoon corals to remain healthy (Ko et al. 2016).

Human activities that are likely to impact on the hydrodynamics of nearby reefs include construction of harbours, jetties, groynes and causeways, channel bridging (between reef islets) and also reef blasting, dredging and anchoring changing roughness. Coral reef organisms and ecosystems are shaped by flow; at the smallest scales, flow hydrodynamics of water movement across complex structures determines local mass transfer and morphology of the coral skeleton (Monismith 2007). Anthropogenic changes can be brought about by modifying current direction and velocity (remembering that currents are primarily due to tides, wind and oceanic forcing) at small and medium scales through the construction or removal of barriers to water movement, by density change effects when freshwater movements are altered, or by thermal effects caused by addition or removal of heat. These effects are exaggerated in reef systems as they have an unrivalled natural roughness amongst benthic communities (Hearn et al. 2001; Madin and Connolly 2006). It should also be noted that coral structures' resistance to water flows (especially strong ones) is determined more by the weaker strength of the reef substrate to which they are attached than by the strength of the coral itself (Madin 2005).

Changes in flows, especially of current velocity, can play a very important role in temperature regulation for upper reef structures. This will be very important with increasing sea surface temperatures and the known effects of higher temperatures on corals. Slowing of flows will reduce mixing adjacent to coral surfaces leading to the opportunity for heat to accumulate and temperatures to rise, potentially contributing to a greater bleaching threat. This has to be considered in comparison with the impacts of flows on settling and particle capture, where slow flows favour these processes.

2.3 Climate Change

Superimposed on many of the impacts discussed above is the influence of anthropogenic-induced climate change. In this context, the major concerns relate to:

- The increase in greenhouse gas (carbon dioxide, methane and nitrous oxide) concentrations in the atmosphere and the associated increase in atmospheric and oceanic temperatures;
- The increase in dissolved carbon dioxide in the oceans and its contribution to increased acidification therein;
- Changes in local climate variability especially rainfall quantity and intensity which will affect sediment mobilisation and freshwater runoff; and,
- Sea-level change.

Some impacts are predictable, while some still need more information to evaluate.

The direct effect of increased carbon dioxide in the atmosphere results in increased concentrations of carbon dioxide in surface seawater (a result of Henry's law), and thus higher levels of carbonic acid (H_2CO_3); this in turn, because of the carbonate equilibrium system in water, leads to production of more H^+ and hence surface ocean acidification (Royal Society 2005). Surface oceans are slowly getting more acidic with average pH having dropped by 0.1 units to 8.1 since the beginning of the Industrial Revolution, and it is predicted the value will drop from pre-industrial levels by 0.5 units by the year 2100 (Linares et al. 2015). This may not seem large but the pH scale is logarithmic and so this change is quite dramatic. Higher acid levels also contribute to a lowering of carbonate ion concentrations in the ocean. The surface waters are supersaturated with carbonate, and this facilitates the deposition of carbonate minerals by organisms, and also ensures stability of these mineral (mainly calcite and aragonite) structures. Increased acidity interferes with the processes of carbonate deposition and weakens the basic carbonate structure of corals. Unless there is an as-yet unknown feedback mechanism to counter this change, there will be increased weakening of coral reefs.

Higher ocean temperatures are associated with more incidences and intensity of coral bleaching in which coral polyps temporarily express their coloured zooxanthellae. Depending on the duration of and time between bleaching events, coral reefs can recover. Since 1979, there have been nine major coral bleaching events. In the greatest one of 1997–1998, it is estimated that 16% of the corals did not recover. A major bleaching event that rivalled 1997–1998 occurred in late 2016. The trend is towards greater incidence area and duration of coral bleaching (Baker et al. 2008).

Sea-level rise poses an added threat to coral reefs. Corals need exposure to sunlight and so if sea-level rises faster than corals grow, this will be a threat to coral reefs as they slowly sink below the surface. Early evidence is that fast-growing corals may 'keep pace' with change in seal level, while slow-growing massive corals will not. Thus, the most likely scenario is changed, more fragile coral reef ecosystems (Peevor and Carey 2009).

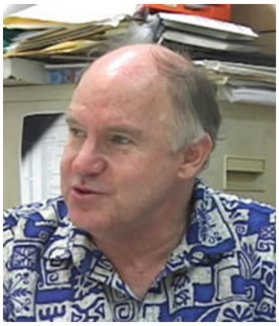
A final outcome relevant to the SE Asia/Pacific region is more intense rainfall events, including stronger cyclones/hurricanes. Two Category 5 hurricanes hit the Philippines and Fiji in 2015 and 2016, respectively, the first on record in the Pacific. These cause massive damage to coral reefs. Heavy rainfall events increase sedimentation and nutrient pollution, the negative effects of which are likely to outweigh possible benefits of bleaching mitigation due to the cooler water of the run-off.

Although ocean warming is seen as the main cause of coral bleaching, acidification, pollution and other stresses are also likely to contribute. It is the combined stresses of these climate change-associated changes that are especially worrying for SE Asia/Pacific coral reefs. In the Caribbean, it was coral diseases that wiped out 80% of the coral reefs, reefs that were made more susceptible to these diseases by their weakened state due to numerous threats. Many Asia/Pacific reefs are relatively healthy and many efforts at community and national level are being made to make them more resilient and lessen non-climate change anthropogenic threats. Whether these efforts, as well as global efforts to cap global warming at 2 °C, will succeed remains to be seen.

2.4 Conclusions

The studies described above illustrate that anthropogenic impacts on reef in western and south-western Pacific region are significant, but most of the problems occur near major population centres or industrial zones. While a large amount of information is available about these anthropogenic impacts, many incidents are not widely reported, so the problems are probably greater than indicated in this report. Although there is now a body of well-trained local scientists to work on this issue, many of these professionals remain limited in their opportunities to tackle the situation by inadequacies of funding and facilities. The development of sound coastal management and resource protection policies lags behind the more developed countries of the world despite improved interactions between scientists and community leaders, regulators and environmental managers.

Appendix: Tribute to Dr. William G. L. (Bill) AALBERSBERG (1949–2018)



William (Bill) Aalbersberg was born in Riverside, CA, in 1949. He passed away on February 8, 2018, in Kula, Hawaii. His extreme intelligence, humanitarian ways and thoughtful wisdom, interspersed with his quick wit and humour, made him unique. He graduated from San Clemente High School in CA, as the class Valedictorian, when he was only 16 years old. Then, on a full scholarship, he completed a BSc in Chemistry with Honours from Cornell University, NY. Upon graduation, he joined the Peace Corps and spent the next 3 years in Fiji. He returned to California and attended UC Berkeley, on a fellowship, to earn his PhD in Organic Chemistry and proceeded to become an Associate Professor of Chemistry there. His love for Fiji and the people he had met there drew him back to Fiji, where, in 1984, he first joined the Chemistry Department of the University of the South Pacific (USP) in Suva, quickly moving upwards to a full Professorship. He later moved to the Institute of Applied Sciences at USP (a scientific research and consultancy unit), becoming Director and guiding this operation most successfully for 15 years, retiring in 2016.

Bill spent 30 years as an avid environmentalist, working tirelessly to improve the cleanliness and sustainability of the local ocean systems, identifying the active compound in traditional medicinal remedies and treatments, maximizing the nutrition in the soil and also acting as a taxonomist and chemist, even having a marine sponge named after him while researching curative properties for cancer. He worked with the local communities and villages to pioneer programmes that encouraged the building of infrastructure and teamwork for resource management and the long-term health and economic benefits they could achieve as one.

He ran the Institute of Applied Sciences at USP and was revered internationally as both a humanitarian and also one of the great minds of his time, scientifically. He was recognised internationally (2005, Walter B Jones Memorial and National Oceanic and Atmospheric Administration (NOAA) Excellence Award for Coastal and Ocean Resource Management), regionally (inaugural Secretariat of the Pacific Regional Environment Program (SPREP) Award for Leadership in Environment (2014) and Japanese Nippon Award for Climate Change (2000) and locally (Inaugural USP Award for research impact). He was in constant demand to provide assistance to various agencies of the United Nations and other regional organisations. Despite this heavy consultative roll, Bill continued his own research programme, mainly through graduate students and international collaborators. He published over 200 research papers.

In addition to the attributes above, Bill was an accomplished bridge player and a keen exponent of mah-jongg. He is survived by his sister, Susie Saunders of Kula, HI, nieces Angela Saunders Koski and Sheila Siegel, great nephews Zach Siegel (who coined the family nickname name *G'unc* shortened form of Great Uncle) and Ryan Siegel, of Southern California. The world has lost a great scientific mind and a gentle soul that his family and friends will never forget.

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3

Advances in Coral Biology

Thamasak Yeemin, Vo Si Tuan, and Suharsono

Abstract

Understanding coral biology is crucial for coral reef management under the crisis of global change. This chapter provides updated knowledge on several important aspects of coral biology and existential threats to the sustainable growth of coral reefs from basic biology, including reproduction, development, and recruitment on the hard bottom to the current existential threats of coral reefs due to the prevalence of their bleaching and diseases. Advances in our knowledge on coral sexual reproduction, fertilization, hybridization, development, and recruitment are briefly reviewed. The diversity of reef-building coral species has been recently enriched with the application of molecular and population genetic investigation, and its outcome was also reviewed here. Partly due to the abrupt climate change and the increased human waste input into the coral reef region greatly increased the rate of mortality of corals arisen from the loss of their symbiont zooxanthellae to lead their bleaching or rampant disease to kill coral animals. The causes and their extents in the Indo-Pacific Oceanic region were summarized, and several case studies for prevention of coral bleaching and amelioration and cure of coral diseases were also included here.

Keywords

Coral bleaching · Disease · Molecular genetics · Reproduction · Recruitment

3.1 Introduction

Knowledge of coral biology is very important for managing coral reef ecosystems, particularly in the face of global change. During the past few decades, various aspects of coral reef biology have been studied and obviously explained. One of the critical issues in most coral reefs of tropical oceans is coral bleaching which is driven by El Niño and climate change, and it has been recognized as the major cause of coral reef deterioration in many countries. The coral-zooxanthella symbiosis and microbial consortium play significant roles on the acclimation and adaptation of the affected corals. Additionally, current understandings also reveal that some corals are more susceptible to diseases following the coral bleaching events and mass mortality. Advances in molecular genetics have been intensively applied to coral studies and provide an important explanation for other coral biology aspects, such as coral reproduction and recruitment.

In this chapter, knowledge on important aspects of coral biology, including reproduction, development, and recruitment, is updated, and we also update the causes, mechanisms, and consequences of coral bleaching and its diseases with emphasis on acclimation and adaptation of corals and their symbiosis, and we also proposed measures for prevention and therapy using coral genetics.

3.2 Coral Biology

3.2.1 Reproduction, Development, and Recruitment of Larvae

3.2.1.1 Coral Spawning

Generally, sexual reproduction of corals has two reproductive patterns (i.e., hermaphroditic and gonochoric), and two modes of sexual reproduction (i.e., brooding and broadcast spawning). Coral sexual reproduction worldwide has been

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extensively studied and reviewed (Harrison and Wallace 1990; Harrison 2011). A comprehensive review of coral reproduction in Japan has been recently made (Isomura and Fukami 2018). Coral spawning is often seen as synchronized phenomenon. During the spawning, coral colonies simultaneously release their gametes into the water column, and the sperms and eggs of corals can survive for only a few hours. Since fertilization occurs within a short period of time due to the gamete dilution, spawning synchrony has been developed to be precise to achieve successful fertilization. Besides the gamete dilution, the synchronicity of coral reproduction is also influenced by environmental factors, which are varied at different locations, including temperature, solar irradiance, wind, lunar cycles, and sunset times. It is widely believed on coral reproduction that precise within-population spawning synchrony is found with a short spawning period around a specific lunar phase. The reproduction of most coral species takes place during the warmer months of the year (Shlesinger and Loya 2019).

Coral spawning has been extensively studied across the Indo-Pacific region. The date and time of coral spawning of 18 species belonging to several families, including Acroporidae and Merulinidae around Sesoko Island in Japan, were first recorded by Heyward et al. (1987) in 1986 and 1987. They found that most coral species spawned in June, but some spawned during July, August, and September. The spawning occurred from the full moon until the last quarter moon. Hirose and Hidaka (2006) also observed the spawning of two branching corals, *Porites cylindrica* and *Montipora digitata*. The sperm or eggs of *P. cylindrica* were repeatedly released for 2–6 days after the full moon in June 2000, and the egg-sperm bundles of *M. digitata* were continuously spawned for 3–10 days after or before the full moon during May–July 1999 and June 2000. For *Acropora*, Prasetia et al. (2015) found that *Acropora tenella* living at different water depths (shallow water and at a depth of 40 m) spawned at the same time. Hayashibara and Shimoike (2002) report the difference in the timing of spawning between *A. digitifera* and the cryptic species *A.* sp.1 at Akajima Island, and it was later reconfirmed by Ohki et al. (2015). Unusual spawning in *Goniastrea aspera* was observed mainly 3–6 days after the full moon in June or July (Sakai 1997). During the reproduction, *G. aspera* first released sperm and then eggs from a single colony. Planula larvae were also released from the same colony a few days after spawning for approximately 1 month. Nozawa and Harrison (2005) also found a similar reproductive manner. For Pocilloporidae, the timing of the planula release of three brooding species, including *Pocillopora damicornis*, *Seriatopora hystrix*, and *Stylophora pistillata*, were observed by Yamazato et al. (2008) from 1993 to 1995. The planula larvae of *P. damicornis* were released from May to October, and those of the other two species were released from May to September. Additionally, no relation is found between the peak of planula release and the moon phase. For Fungiidae, the spawnings of two species, i.e., *Ctenactis echinata* and *Lithophyllon repanda* (or *Fungia repanda*), were found in the early morning, around 2:00 and 5:00 am, respectively (Loya et al. 2009). Most coral species tended to release their gametes during the period between the full moon and the last quarter moon. Some species (e.g., *Platygyra ryukyuensis*, *Favites chinensis*, *G. aspera*, and *Galaxea fascicularis*) spawned at the same timing related to the lunar phase but in different months. In addition, some species (e.g., *M. digitata*, *Platygyra pini*, and *F. chinensis*) spawned at nearly the same timing in different years (Isomura and Fukami 2018). Synchrony in gamete development and mass spawning were found among *Acropora* communities in Magsaysay reef, Bolinao-Anda Reef Complex, located in the northwestern Philippines. Jamodiong et al. (2018) conducted their studies in the area and reported that at least eight species of *Acropora* spawned between 9 and 11 days after the full moon in March 2015 and 2016.

Most studies revealed that consistent, highly synchronized spawning events were found in the corals that reproduce by broadcast spawning. However, asynchronous spawning was recorded in some reef areas, such as in lagoonal reefs adjacent to Mombasa, Kenya (Mangubhai and Harrison 2008), and in Nha Trang Bay, Vietnam (Vo et al. unpublished information). There existed the hypothesis of protracted breeding seasons and a breakdown of spawning synchrony nearer the equator (Mangubhai and Harrison 2008). In addition, the vulnerability of the synchronized spawning may occur since their reproductive phenology is possibly influenced by several environmental factors. Shlesinger and Loya (2019) investigated spawning intensity in four annual reproductive seasons and the intensity at different levels, i.e., polyp, colony, and population. They found that inability for reproductive synchrony was found in some coral species in the Red Sea compared with the historical data. This synchrony breakdown could cause a domino effect starting from the reduction of successful fertilization and reduction of new recruits, and it may lead coral populations to extinction.

3.2.1.2 Fertilization

Coral fertilization has been extensively studied, contributing to the advancement and understandings of coral biology. Crossing experiments are a primary method that has been widely applied for examining coral fertilization, particularly the observations on sperm concentration and fertilization rates within and between coral species. Several studies illustrated that the sperm concentration of approximately 106–107 sperm/ml yielded almost 100% success of intraspecific fertilization (Willis et al. 1997; Marshall 2006; Nakamura et al. 2011; Nozawa et al. 2015). Omori et al.

(2001) measured sperm concentration for corals in Okinawa and found that the sperm concentration observed within 30 min of mass spawning was 106 sperm/ml and the concentration then gradually decreased over time. Iguchi et al. (2009) also investigated the fertilization of *Acropora digitifera* at different contact times and reported that fertilization was achieved within 30 minutes for most gametes. Morita et al. (2006) examined the gamete behavior of three *Acropora* species (*A. digitifera*, *A. gemmifera*, and *A. tenuis*) in Okinawa, and they found that coral sperm were motile and moved toward intraspecific eggs. In the study, no hybridization was found among these three species in crossing experiments. Several studies also explained such phenomenon that some mechanisms of reproductive isolation exist during mass spawning events. Furthermore, crossing experiments are also beneficial for identifying species boundaries and cryptic species. For example, *Acropora* sp.1 has been recognized as a cryptic species of *A. digitifera* since the spawning of *A.* sp.1 occurs 1 month later than that of *A. digitifera*. High rates of hybrid fertilization were recorded under the crossing experiments using cryopreserved sperm from each coral species revealing a close relationship between the differences in the timing of spawning and speciation (Ohki et al. 2015). A cryptic species of *Montastraea valenciennesi* was also reported, and it was morphologically different from the original species and exhibited complete reproductive isolation (Fukami and Nomura 2009). Another example is that Zayasu et al. (2009) successfully created three morphological variants of *Acanthastrea hemprichii* belonging to the same species from the cross-fertilization. Crossing experiments are also useful for increasing the efficiency of coral seeding. The experiments conducted by Iwao et al. (2014) revealed that *Acropora tenuis* had a mixture of gametes from more than six intraspecific colonies yielding stable fertilization rates of greater than 95%. Isomura et al. (2013a) studied the fertilization *A. intermedia* in Okinawa and found a negative relationship between the fertilization rate and genetic similarity.

3.2.1.3 Hybridization

Understandings on hybridization on coral reefs have been developed, illustrating that hybridization is common and widespread (Richards and Hobbs 2015). Veron (1995) also proposed that hybrid speciation is a part of the pattern of reticulate evolution. Various studies hypothesized that the high species diversity of *Acropora* species could possibly result from the hybrid speciation. The studies on the synchronous spawning among many *Acropora* species and crossing experiments revealed the possibility of in vitro hybridization in some *Acropora* species (Wallace and Willis 1994; Willis et al. 1997; Hatta et al. 1999; Isomura et al. 2013a). Thus, the hybridization between the species is much likely to be found in nature. However, the existence of hybridization varies in different geographical areas. In the Caribbean, an F1 hybrid was found at every three *Acropora* species (Vollmer and Palumbi 2002), but no evidence supports the existence of hybrids in the Indo-Pacific. Only the colonies having their morphology intermediate between species have been reported (Hatta and Matsushima 2008; Isomura et al. 2013a). In Japan, in vitro hybridization was found for eight *Acropora* species (Hatta et al. 1999; Fukami et al. 2003). Three of them including *A. tenuis*, *A. donei*, and *A. yongei* spawned 2–3 h earlier than the other species with the fertilization rate of over 90%. Each species might have morphological variants but the variants are similar in terms of fertilization rates and genetic similarity (Fukami et al. 2003). The other five species including *A. nasuta*-A, *A. nasuta*-C, *A. muricata*-A, *A. intermedia*, and *A. florida* spawned in synchrony. *A. nasuta*-A and *A. nasuta*-C were recognized as different species since there are some differences on the key morphological characteristics (Hatta et al. 1999). The occurrences of hybridization between *A. nasuta*-A, *A. nasuta*-C, and *A. muricata*-A and between *A. intermedia* and *A. florida* were reported by Hatta et al. (1999), and later Isomura et al. (2013b) found the hybridization between *A. intermedia* and *A. florida*. Since the existence of a colony with morphology intermediate between two species was also found in the field, they believed that there is a high possibility of situ fertilization between the putative hybrid, *A. intermedia* and *A. florida*. The F1 hybrid colonies were also produced in the lab through the hybridization of *A. intermedia* and *A. florida* with high fecundity and high self-fertilization, suggesting that interspecific hybridization may continue to exist because of the offspring of self-fertilizing F1 hybrids (Isomura et al. 2016; Isomura and Fukami 2018).

3.2.1.4 Embryonic Development

The embryonic development of corals has been studied for a long history, and most of the studies focused on sexual reproduction, development, and larval biology in scleractinian corals (Fadlallah 1983). As morphological and molecular data are currently applied for the phylogeny of scleractinian corals, two major groups of the corals, the "complex" and the "robust," have been proposed (Budd et al. 2010). Okubo et al. (2013) recently conducted a histological study to describe the embryonic development of four complex species, i.e., *Pseudosiderastrea tayamai*, *Galaxea fascicularis*, *Montipora hispida*, and *Pavona decussata*, and seven robust species, i.e., *Oulastrea crispata*, *Platygyra contorta*, *Favites abdita*, *Echinophyllia aspera*, *Goniastrea favulus*, *Dipsastraea speciosa* (previously known as *Favia speciosa*), and *Phymastrea valenciennesi* (previously known as *Montastrea valenciennesi*). The histologically sectioned

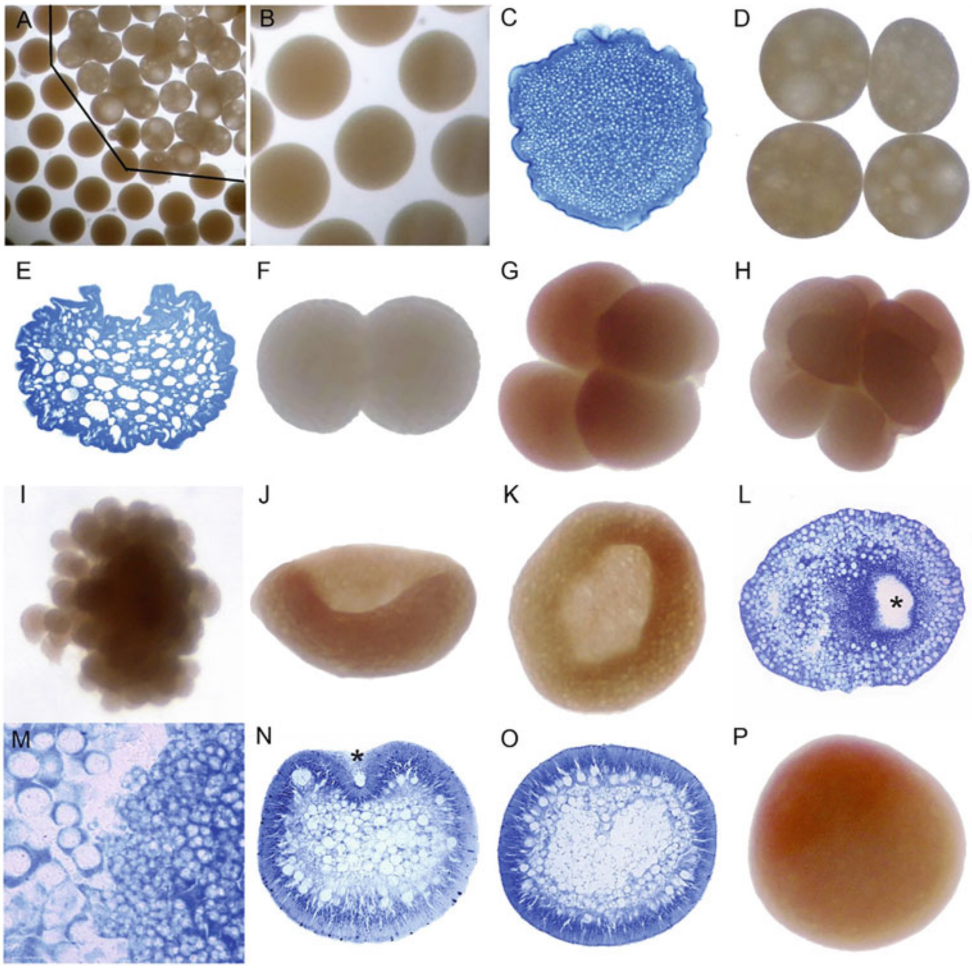


Fig. 3.1 Embryonic development of *Galaxea fascicularis*. (**a**) Eggs (darker in color) and pseudo-eggs (lighter in color), (**b**) true eggs, (**c**) a section of egg filled with small lipid bodies, (**d**) pseudo-eggs appear vacuolated, (**e**) lipid is localized to much larger bodies, (**f–h**) 2-cell, 4-cell, and 8–16-cell stages, (**i**) morula stage, (**j–k**) bowl stage, (**l**) glancing section of an embryo comparable to (**j**, **k**), (**m**) enlargement of the embryo shown in (**l**), with two sizes of lipid-containing bodies, (**n**) spheroidal embryo with closing blastopore showing center filled with lipid (**o**), formation of mesoglea, (**p**) whole mount of stage similar to (**o**). The asterisk indicates the blastopore (Source: Okubo et al. 2013)

embryos and whole mounts of *Galaxea fascicularis* and *Favites abdita* are illustrated in Figs. 3.1 and 3.2 (Okubo et al. 2013).

For complex clade, an embryo forms a prawn chip shape without having a blastocoel. Then, a bowl-shaped embryo is resulted from the cell shrinking, thickening, and inward bending. The growth of outer cells forms a concavity where lipid granules, cellular fragments, and cells stored are stored inside. For robust clade, an embryo starts developing in a cushion stage with a blastocoel. A pseudo-blastopore is then formed and later disappears. Later, a true blastopore is developed with the passage of material into the blastocoel (Fig. 3.3). A key difference distinguishing between complex and robust species is the cell shape before the gastrulation. The cells of the complex corals (mainly *Acropora* species) extend and flatten, making their shapes like a prawn chip that has no blastocoel. However, the prawn chip formation is not found in *Pavona decussata*, and the blastocoel is also well-developed. This infers that the prawn chip formation is not a synapomorphy of complex corals. Unlike complex corals, no prawn chip formation is found in robust corals, but it forms a cushion shape. The embryos of robust corals develop throughout the two periods of invagination before transforming to a spherical shape. The authors also mentioned that endoderm formation was observed only in the second period, while the first invagination is called a pseudo-blastopore (Okubo et al. 2013).

Okubo et al. (2016) studied the embryonic development of two robust corals: a massive brain coral (*Favia lizardensis*) and a solitary coral (*Ctenactis echinata*) by comparing them with the characterized complex coral (*Acropora millepora*) in terms of their morphology and key developmental genes. They found that embryonic transcriptomes consisted of 40,605 contigs for *C. echinata* (N50 = 1080 bp) and

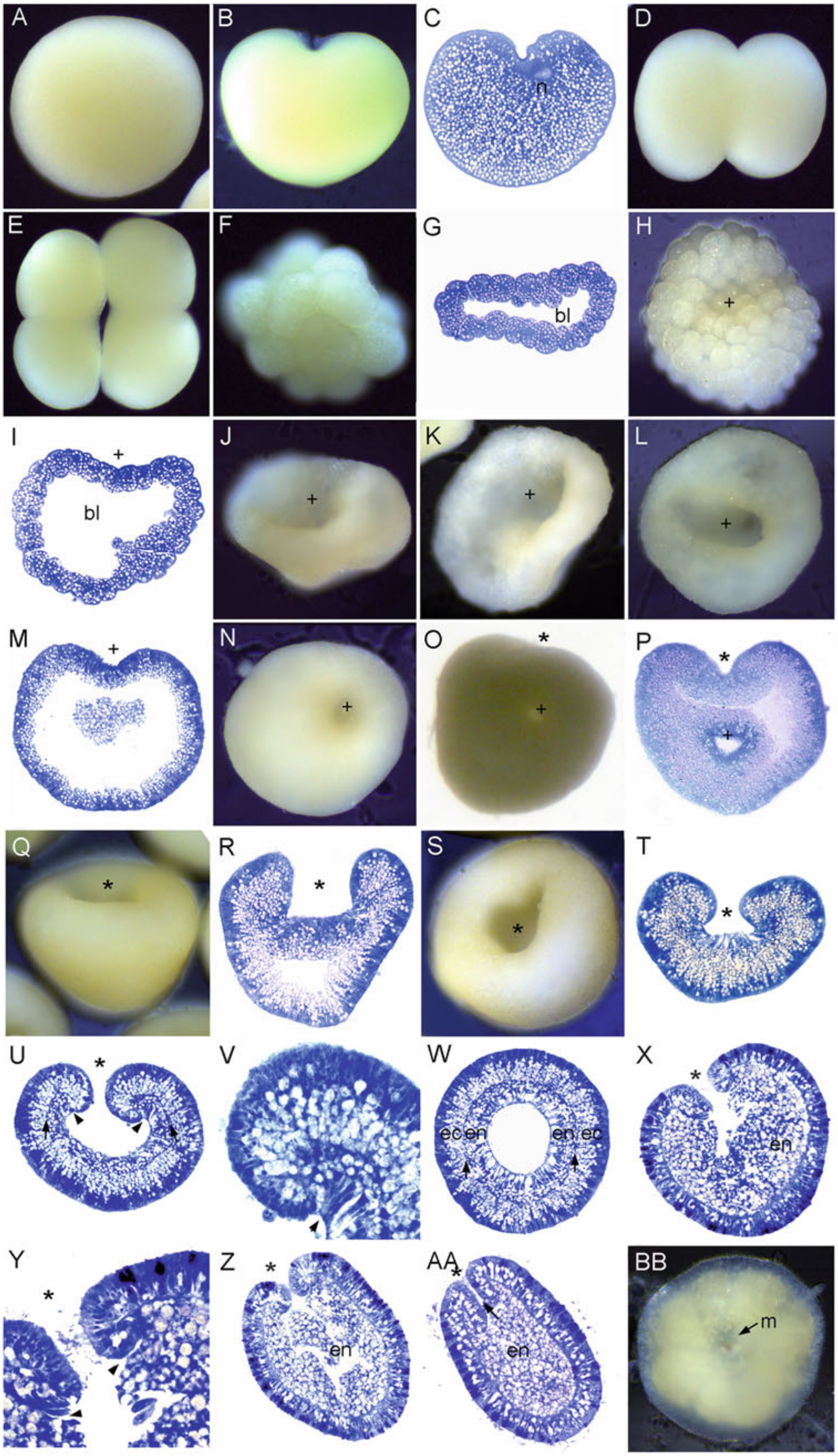
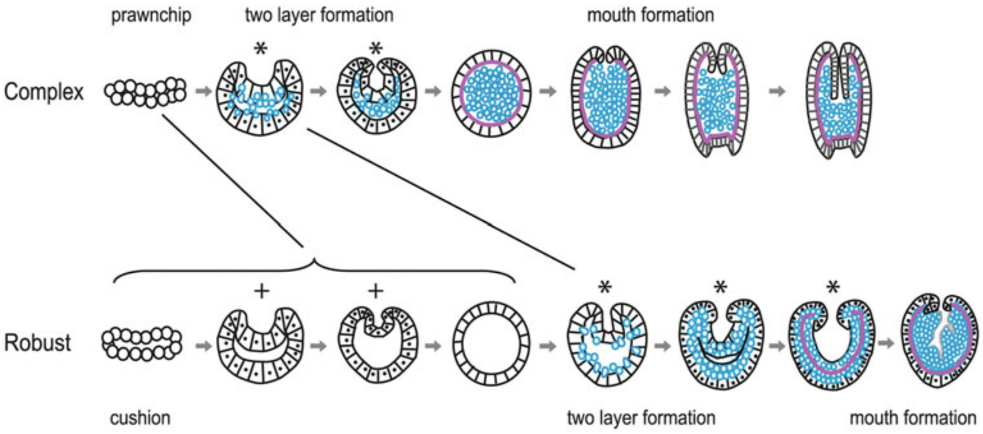


Fig. 3.2 Embryonic development of *Favites abdita.* (**a**) Spawned egg, (**b**) heart-shaped embryo in the first division, (**c**) section of a heart-shaped embryo with the appearance of a nucleus, (**d**) a 2-cell embryo, (**e**) 4-cell stage, (**f**) 16-cell stage, (**g**) the flattened shape of embryo with a blastocoel (bl in this and succeeding panels), (**h**, **i**) cushion-shaped with a depression with the pseudo-blastopore (plus sign), (**j**, **k**) embryos vary

Fig. 3.3 Coral development of "complex" (upper) and "robust" clades (lower). (Source: Okubo et al. 2013)



48,536 contigs for *F. lizardensis* (N50 = 1496 bp). Regarding the developmental series, both robust corals contained a blastocoel at early developmental stages. The expression of brachyury and forkhead confirmed that the pseudo-blastopore does not directly link with gastrulation. However, the expression of chordin for *C. echinata* differed from that found in the other two corals. Based on the expression of the key developmental genes, the expression patterns are significantly different between species in *Acropora*, *Nematostella*, and bilaterians (Okubo et al. 2016). The advancement of molecular phylogeny, particularly the information of mitochondrial 16S ribosomal gene sequences, has restructured the classification of corals. The members of order Scleractinia are currently classified into two clades, i.e., "complex" and "robust." Furthermore, morphological characteristics during embryonic development have also been applied for classifying a deeper division of scleractinian corals. Two new suborders, Refertina and Vacatina, have been established based on the embryogenetic morphological characteristics and molecular information (Okubo 2016). The families considered as the "complex" clade with no or little blastocoel were categorized in suborder Refertina, while the suborder Vacatina consists of the families considered as the "robust" clade with an apparent blastocoel (Okubo et al. 2016) (Fig. 3.4).

3.2.1.5 Recruitment

Coral recruitment and its patterns are essential for determining the population dynamic of coral reefs. Since coral reefs have been deteriorated globally due to climate change, studies on coral recruitment are also emphasized to create solutions for enhancing coral recovery and reef resilience (Hughes et al. 2010, 2019). Coral recruitment rates and juvenile coral abundance are generally considered as the key quantitative variables for the studies related to recruitment. The studies on coral recruitment in the Indo-Pacific region have been extensively conducted at different geographical scales. In Indonesia, the study on coral recruitment patterns on two reefs (Sampela and Hoga) in the Wakatobi National Marine Park, with different levels of environmental degradation (12.5% coral cover with high sedimentation rate vs 44% coral cover with low sedimentation rates) showed that there were seasonal differences in recruitment rates between the two reefs although the distance between them is only 1.5 km. Additionally, the more degraded reefs are detected, the lower the rate of recruitment and juvenile abundance. The authors explained that the patterns might be due to the settlement mortality caused by a combination of stresses, including high sedimentation rate, degraded condition, and reduction of larval supply (Salinas-de-Leon et al. 2013). In Malaysia, Faiz et al. (2017) examined a

Fig. 3.2 (continued) in shape as the pseudo-blastopore deepens, (**l**) the embryo swells to be more spherical while the pseudo-blastopore is maintained, (**m**, **n**) the embryo becomes spherical with the remains of the pseudo-blastopore, (**o**) a new invagination, the blastopore (asterisk in this and succeeding panels) starts in a different location from the pseudo-blastopore, (**p**) section of an embryo comparable to (**o**), showing that the two pores are quite distinct (labels as in **o**), (**q**, **r**) invagination has proceeded: the asterisk marks the blastopore, (**s**) the blastopore has now become smaller, (**t**) the blastocoel has now disappeared and cells at the margins of the invaginating tissue have taken on an elongate bottle shape, (**u**) the mesoglea is now clearly apparent, separating endoderm from ectoderm, (**v**) higher magnification of U, showing highly elongated cells at the margins of the invaginating tissue, (**w**) two germ layers, ectoderm (ec) and endoderm (en), are apparent surrounding the space that will eventually form the gastrovascular cavity. (**x**) Cellular differentiation is apparent in the ectoderm and lipid-filled endodermal cells have invaded the central cavity. (**y**) Higher magnification of the oral pore region showing sharply invaginated margins of the pharynx (arrowheads), (**z**) section of the elongating planula showing the central cavity filled with lipid-containing endodermal cells (en). (AA) The pharynx (arrow) has elongated. (BB) Primary polyp immediately after settlement. The ectoderm is translucent, whereas the endoderm is opaque white. The mouth (m) is central (Source: Okubo et al. 2013)

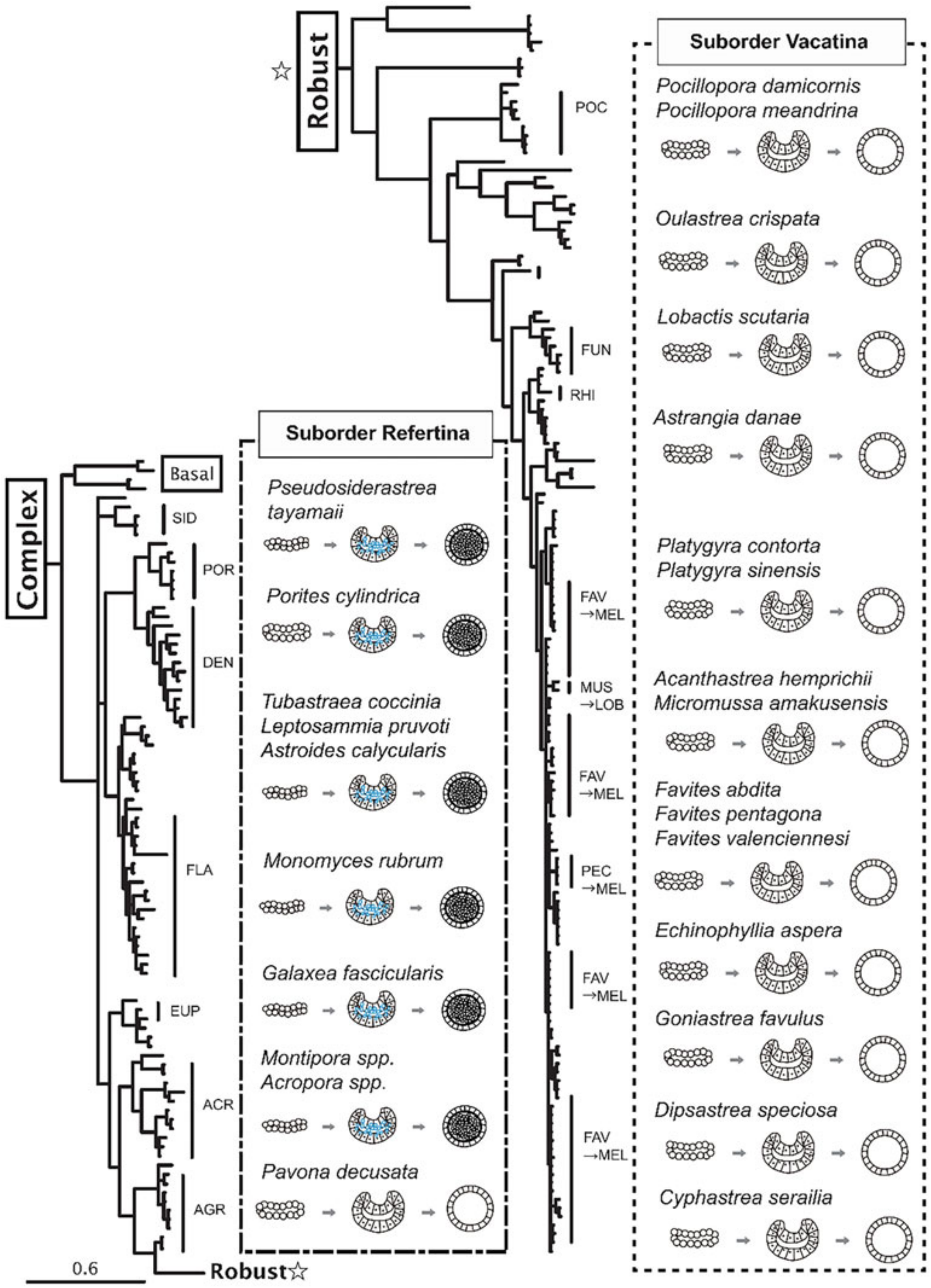


Fig. 3.4 The reconstructed coral phylogeny based on the sequence of the mitochondrial CO1 gene and the occurrence of blastocoel. The family names revised recently are explained using arrows. ACR, Acroporidae; AGA, Agariciidae; CAR, Caryophylliidae; DEN, Dendrophylliidae; EUP, Euphylliidae; FAV, Faviidae; FLA, Flabellidae; FUN, Fungiidae; LOB, Lobophylliidae; MEL, Meruliniidae; MUS, Mussidae; PEC, Pectiniidae; POC, Pocilloporidae; POR, Poritidae; RHI, Rhizangiidae; SID, Siderastreidae. (Source: Okubo et al. 2016)

comparative study of recruitment success between terracotta tiles and the artificial substrates made of coral rubble, sand, and plasters' cement at four reef sites in Tioman Island between April 2012 and June 2013. They found that Acroporidae (65.48%) were mostly observed, followed by Pocilloporidae (31.4%), Faviidae (2.34%), Poritidae (0.89%), and Fungiidae (0.19%). The recruitment densities found on the terracotta tiles were higher than those on the artificial reef plates during the initial settlement period. However, the recruitment densities on both types of plates during the post-settlement period were similar. However, the mean total benthic percentage cover seemed higher on artificial reef plates than terracotta tiles during both settlement periods.

Besides, the understanding of coral recruitment may enable to predict the potential for coral recovery from the impacts of various disturbances, particularly coral bleaching events, as well as knowing more on a spatiotemporal variability in coral community structure. The elevation of seawater temperatures induced by global warming generates extensive impacts on various marine lives. The recent review indicated that the decline in larval recruitment in the Great Barrier Reef due to heat stress resulted from global warming, which caused the mass bleaching events and mass mortality of adult broodstock (Hughes et al. 2019). In Thailand, the elevated seawater temperatures in the summer months of 2010 caused widespread coral mortality throughout the Thai waters. Mass mortality of corals was observed in various areas of Mu Ko Surin, located in the Andaman Sea, following the bleaching event. Yucharoen et al. (2015) observed the composition, abundance, and growth rate of juvenile corals and analyzed the reef recovery potential at Mu Ko Surin. They detected temporal and spatial variations of coral recruitment. The coral recruitments recorded in 2012 were higher than those observed in 2011. Coral recruits were dominated by *Fungia*, *Acropora*, *Porites*, and *Favites*. The size ranges of *Acropora* recruits at Ko Torinla in 2012 (13–54 mm) had a larger size than what was observed in 2012 (4–30 mm). Six species of *Acropora* recruits were found, including *Acropora intermedia*, *A. nasuta*, *A. cerealis*, *A. subulata*, *A. muricata*, and *A. latistella*. The growth rates of such recruits varied spatially, ranging from about 2.1 to 7.5 cm per year. This study sees the possibility for coral reefs around Mu Ko Surin to be recovered after the bleaching event.

3.2.2 Coral Taxonomy and Species Identification

3.2.2.1 Molecular Taxonomy and Systematics

Indo-Pacific region is one of the richest global biodiversity hotspots harboring as many as about 720 species of scleractinian corals, 690 species of Alconarian corals, and thousands of various marine species (Spalding et al. 2001). Traditionally, corals are classified mainly by their morphological characteristics and some ecological functions. The advancement of molecular genetics improves the understanding of coral reef history and evolution, coral taxonomy, and classification system in which molecular and morphological information are integrated (Knowlton and Leray 2015). For example, Budd et al. (2012) proposed the revised monograph of scleractinian corals' classification based on the taxonomic relationships of 55 zooxanthellate genera in seven families. The higher-level classification system for the 46 genera was introduced and a new family-level was also established. Ten genera and 26 species were assigned to the family Mussidae and one of the genera was newly created (Table 3.1). The phylogeny reconstruction integrated 38 morphologic characters (macromorphology, micromorphology, and microstructure) and molecular information of 67 species of corals. Based on the ancestral state reconstructions, extensive homoplasy appeared in almost all morphological characters.

Budd et al. (2012) recommended that morphological characteristics, especially septal teeth, are the most useful for classifying family- and subfamily-level molecular clades. The family Mussidae has septal teeth with regular pointed tips (a symplesiomorphy) and a stout blocky appearance. Two subfamilies, Mussinae and Faviinae, belong to the family Mussidae. The subfamily Mussinae is characterized by spine-shaped teeth and widely spaced costoseptal clusters of calcification centers, while the main characteristics of the members in subfamily Faviinae include blocky, pointed tricorne or paddle-shaped teeth with elliptical bases, transverse structures such as carinae that cross the septal plane, and well-developed aligned granules. The authors also mentioned that morphological phylogenetic analyses were useful to classify the families Mussidae (XXI) and Lobophylliidae (XIX). Also, two subfamilies (Mussinae, Faviinae) belonging to the family Mussidae were distinguished by this approach except for *Homophyllia australis*. Compilation of the entire 67-species dataset can be applied for classifying the family Lobophylliidae (XIX), but not for others. Additional molecular and morphological information is needed for classifying some lower-level relationships within the family Merulinidae (XVII) and Mussidae (XXI).

Huang et al. (2014) illustrated their reconstructed monograph taxonomic classification of three coral families, including Merulinidae, Montastraeidae, and Diploastraeidae (Cnidaria: Anthozoa: Scleractinia), by focusing on the disarray within the clade is epitomized by its informal name "Bigmessidae." The morphological traits at three different scales of the coral skeletal structure of 84 living merulinid species were examined, yielding 44 morphological characters. Phylogenetic reconstructions were then performed using the parsimony and maximum likelihood criteria. The revised classification explains 139 species in 24 genera revealing the synonymization of *Barabattoia* as *Dipsastraea*, and *Phymastrea* as *Favites*, the resurrection of two genera (*Astrea* and *Coelastrea*) and a new genus, *Paramontastraea*. The examination based on morphological characters was well applied to all the genera in Merulinidae, monotypic Montastraeidae, and Diploastraeidae.

Schmidt-Roach et al. (2014) revised the taxonomic classification of species closely related to and within the *Pocillopora damicornis* species complex (Scleractinia; Pocilloporidae) using both the new datasets on morphometrics (i.e., fine-scale corallite and coenosteum

Table 3.1 Comparison of cited classifications of recent reef corals

Wells (1956)	Veron (2000)	Budd et al. (2012)
Family Mussidae	**Family Mussidae**	**Family Mussidae (clade XXI)**
Genus *Mussa*	Genus *Mussa*	**Subfamily Mussinae**
[=Scolymia]	Genus *Isophyllia*	Genus *Mussa*
Genus *Isophyllia*	*[=Isophyllastrea]*	Genus *Isophyllia [=Isophyllastrea]*
Genus *Isophyllastrea*	Genus *Mycetophyllia*	Genus *Mycetophyllia*
Genus *Mycetophyllia*	Genus *Mussismilia*	Genus *Scolymia* (Atlantic only)
Genus *Mussismilia*	Genus *Lobophyllia*	**Subfamily Faviinae**
Genus *Lobophyllia*	Genus *Acanthastrea*	Genus *Favia* (Atlantic only)
Genus *Acanthastrea*	Genus *Symphyllia*	Genus *Colpophyllia*
Genus *Symphyllia*	Genus *Australomussa*	Genus *Diploria*
?Genus Cynarina	Genus *Micromussa*	Genus *Pseudodiploria*, new
Genus *Homophyllia*	Genus *Cynarina*	Genus *Manicina*
Genus *Parascolymia*	Genus *Scolymia*	Genus *Mussismilia*
Genus *Blastomussa*	*[=Homophyllia,*	**Family Lobophylliidae, new (clade XIX)**
Family Faviidae	*Parascolymia]*	Genus *Lobophyllia*
Subfamily Faviinae	Genus *Blastomussa*	Genus *Acanthastrea*
Genus *Favia*	Genus *Indophyllia*	Genus *Symphyllia*
Genus *Colpophyllia*	**Family Faviidae**	?Genus *Australomussa*
Genus *Diploria*	Genus *Favia*	Genus *Micromussa*
Genus *Manicina*	Genus *Colpophyllia*	Genus *Cynarina*
Genus *Barabattoia*	Genus *Diploria*	Genus *Homophyllia* (part Indo-Pacific *Scolymia*)
Genus *Bikiniastrea*	Genus *Manicina*	Genus *Parascolymia* (part Indo-Pacific *Scolymia*)
Genus *Caulastrea*	Genus *Barabattoia*	Genus *Oxypora*
Genus *Favites*	[=*Bikiniastrea*]	Genus *Echinophyllia*
Genus *Goniastrea*	Genus *Caulastrea*	?Genus *Echinomorpha*
Genus *Leptoria*	Genus *Favites*	Genus *Moseleya*
Genus *Oulophyllia*	Genus *Goniastrea*	**Family Montastraeidae (clade XVI)**
Genus *Platygyra*	Genus *Leptoria*	Genus *Montastraea* (*M. cavernosa* only)
Genus *Hydnophora*	Genus *Oulophyllia*	**Family Diploastreidae (clade XV)**
Genus *Plesiastrea*	Genus *Platygyra*	Genus *Diploastrea*
Subfamily Montastreinae	Genus *Australogyra*	**Family Merulinidae (clade XVII)**
Genus *Montastrea*	Genus *Erythrastrea*	Genus *Merulina*
Genus *Diploastrea*	Genus *Montastrea*	?Genus *Boninastrea*
Genus *Cyphastrea*	Genus *Diploastrea*	?Genus *Paraclavarina*
Genus *Echinopora*	Genus *Cyphastrea*	Genus *Scapophyllia*
Genus *Cladocora*	Genus *Echinopora*	Genus *Hydnophora*
Genus *Solenastrea*	Genus *Cladocora*	Genus *Barabattoia*
Genus *Leptastrea*	Genus *Solenastrea*	Genus *Caulastraea*
?Genus *Oulastrea*	Genus *Leptastrea*	Genus *Favites*
Subfamily Trachyphylliinae	Genus *Oulastrea*	Genus *Goniastrea*
Genus *Indophyllia*	Genus *Plesiastrea*	Genus *Leptoria*
Genus *Trachyphyllia*	Genus *Parasimplastrea*	Genus *Oulophyllia*
?Genus *Moseleya*	Genus *Moseleya*	Genus *Platygyra*
Family Pectiniidae	**Family Trachyphylliidae**	?Genus *Australogyra*
Genus *Pectinia*	Genus *Trachyphyllia*	?Genus *Erythrastrea*
Genus *Mycedium*	**Family Pectiniidae**	Genus *Cyphastrea*
Genus *Oxypora*	Genus *Pectinia*	Genus *Echinopora*
Genus *Echinophyllia*	Genus *Mycedium*	Genus *Dipsastraea* (Indo-Pacific "*Favia*")
Family Merulinidae	Genus *Oxypora*	Genus *Phymastrea* (Indo-Pacific "*Montastraea*")
Genus *Merulina*	Genus *Echinophyllia*	Genus *Orbicella* ("*Montastraea*"
Genus *Boninastraea*	Genus *Echinomorpha*	*annularis* complex)
Genus *Clavarina*	**Family Merulinidae**	Genus *Trachyphyllia*
Genus *Scapophyllia*	Genus *Merulina*	Genus *Pectinia*
Family Oculinidae	Genus *Boninastrea*	Genus *Mycedium*
Genus *Galaxea*	Genus *Paraclavarina*	**Family Meandrinidae (clade XII)**
Genus *Simplastrea*	Genus *Scapophyllia*	Genus *Meandrina*
Family Meandrinidae	Genus *Hydnophora*	Genus *Dichocoenia*
Genus *Meandrina*	**Family Oculinidae**	Genus *Dendrogyra*
Genus *Dichocoenia*	Genus *Oculina*	Genus *Eusmilia*
Genus *Dendrogyra*	Genus *Schizoculina*	[a]**Family Euphylliidae (clade V)**
Genus *Ctenella*	Genus *Galaxea*	Genus *Ctenella*
[a]**Family Caryophylliidae**	Genus *Simplastrea*	?Genus *Gyrosmilia*
Genus *Eusmilia*	**Family Meandrinidae**	?Genus *Montigyra*

(continued)

Table 3.1 (continued)

Wells (1956)	Veron (2000)	Budd et al. (2012)
Genus *Gyrosmilia* Genus *Montigyra*	Genus *Meandrina* *[=Goreaugyra]* Genus *Dichocoenia* Genus *Dendrogyra* Genus *Ctenella* Genus *Eusmilia* Genus *Gyrosmilia* Genus *Montigyra*	Genus *Galaxea* ?Genus *Simplastrea* [a]**Family *Incertae sedis*** Genus *Blastomussa* (clade XIV) Genus *Cladocora* (clade XIII) Genus *Leptastrea* (clade XI) Genus *Oulastrea* (clade XI) Genus *Parasimplastrea* Genus *Plesiastrea* (clade XIV) Genus *Solenastrea* (clade XIII)

Source: Modified from Budd et al. (2012)

[a] This list includes only recent genera that were previously assigned to the families Faviidae, Meandrinidae, Merulinidae, Mussidae, Oculinidae, Pectiniidae, or Trachyphylliidae

structure) and molecular genetic information. The integrated consideration of mitochondrial molecular phylogenies and gross-morphological characteristics was beneficial on species-level differentiation. To find the differences between clades, the authors suggested using fine-scale morphological characteristics, particularly the shape and type of columella. It also provided the key characteristics for examining evolutionary relationships among genetic lineages. The authors also recommended applying the Unified Species Concept for revising the *Pocillopora* taxonomy in case the introgressive hybridization and incomplete lineage sorting occur. The authors also created a haplotype network of eight species including *P. damicornis*, *P. acuta*, *P. aliciae*, *P. verrucosa*, *P. meandrina*, *P. eydouxi*, *P.* cf. *brevicornis*, and *Pocillopora bairdi* sp. nov. (new taxon) based on ORF DNA sequence data and incorporating published *Pocillopora* sequence data from other locations across the Indian and Pacific Oceans (total alignment length 594 bp) (Schmidt-Roach et al. 2014).

3.2.2.2 Population Genetics

Population genetic studies based on genotypic information using molecular markers have explained genetic diversity and connectivity, clonality, and species diversity, particularly cryptic species and coral population adaptations (Hedgecock et al. 2007; Lowe and Allendorf 2010; Nakajima 2018). Alleles, and their frequencies, are important in determining inherited traits. Their variation is based on the differentiation among populations which are influenced by both historical and ecological factors. Gene flow is also applied in various reef studies, particularly the expression of population dynamics and the cohesion of population between reefs (Lessios and Baums 2017). For example, low (restricted) gene flow among reefs reflects the lower possibility of long-distance larval dispersal through multiple generations of coral species. Having a large genetic differentiation between two sites indicates a short larval dispersal distance which is found in brooding corals. On the other hand, broadcast-spawning corals that have a longer larval dispersal distance are able to maintain genetic connectivity among reef sites. Thus, population genetic studies are useful for explaining the population dynamics of reefs at different habitats (Nakajima 2018).

Multilocus genotyping also provides significant information on the aspect of clonality in coral populations. The effective population size seems to be smaller and susceptible to environmental changes if the population has a low clonal diversity or a high rate of clonemates. Restricted population size increases inbreeding resulting in low genetic diversity. Mitochondrial DNA is one of the genetic markers in population studies. Since mitochondrial DNA shows higher mutation rates than nucleic DNA, it is used to examine the mechanism and variations of genotypes among individuals and their frequency among study sites. Unfortunately, this analysis is not suitable for coral species because the corals have low mutation rates (van Oppen et al. 1999, 2001; Fukami et al. 2000).

Allozymes and microsatellites serve as essential tools for population genetic studies of corals. Allozymes, or isozymes, are variant forms of enzymes having a polymorphic characterization but lack functional differentiation. The allozyme locus is comparatively conserved among coral species. The microsatellite is a highly polymorphic DNA marker recognized as a convenient method for genetic analyses since the DNA is more stable than proteins. The numerous microsatellite loci are found and widely distributed in genomic DNA. Because of the high species specificity and high resolution, microsatellite loci can provide adequate genetic variability and differentiation among coral species and colonies (Van Oppen et al. 2007). Null alleles and size homoplasy should also be concerned when choosing markers as they might cause scoring errors (Putman and Carbone 2014).

Most population genetic studies of corals have been conducted in the Great Barrier Reef, Australia (Ayre and Dufty 1994; Ayre et al. 1997; Ayre and Hughes 2000, 2004; Miller and Ayre 2008; van Oppen et al. 2008, 2011). On a wide geographic scale, Baums et al. (2012) reported a population genetic study of *Porites lobata* across the central Pacific and the Eastern Tropical Pacific (approximately

18,000 km). The population genetics of corals in Japan and the northwestern has also been reported (Nakajima 2018). *Acropora* is a highly diversified genus of corals (Richards and Hobbs 2015). Several studies use microsatellite markers to differentiate the cryptic species of corals. Nakajima et al. (2012) found genetic differentiation between two sympatric *Acropora* species in Japan, *A. digitifera* and its cryptic species *Acropora* sp. 1 aff. *digitifera* with two different genetic clusters. The clusters were different because of the reproductive isolation caused by differences in the spawning season in Japan. Four genetic lineages of *Acropora hyacinthus* were reported using mitochondrial putative control region (Suzuki et al. 2016). Hybridization of some *Acropora* species might occur in the field (Isomura et al. 2016; Kitanobo et al. 2016).

The studies conducted in Japan and the Philippines reported that brooding blue coral *Heliopora coerulea* can be grouped into two genetic lineages based on branch morphotypes (small-branch shape and flat shape). Yasuda et al. (2014, 2015) explained that the differences in branch morphotypes are related to the genotypic composition of an internal transcribed spacer region of nuclear ribosomal DNA (ITS) and microsatellite markers. In the Philippines, two genetic lineages may be occurring because of the reproductive isolation that the planula is released at different times within a reef site (Villanueva 2015).

The genetic differentiation between types was observed for *Galaxea fascicularis*, based on the intergenic region between cytochrome b (cytb), NADH dehydrogenase subunits 2 (nad2) on mitochondrial DNA, and microsatellite markers (Nakajima et al. 2015, 2016; Watanabe et al. 2005). The shape of the nematocysts is characterized by two genetic types (mt-L and mt-S) (Watanabe et al. 2005; Abe et al. 2008). The genus *Galaxea* might have reproductive isolation caused by a shift in its spawning season (Watanabe et al. 2005), but this is an unusual event since there is an overlap in the spawning seasons (Abe et al. 2008). An unexpected genetic lineage might occur when using both mitochondrial DNA and microsatellite markers (Nakajima et al. 2016).

The genus *Pocillopora* from the family Pocilloporidae remains an unclear distinction with high variability in colony shape and branch size. The well-known variants of *Pocillopora* seem to be not correlated with genetic variation (Pinzón and LaJeunesse 2011; Pinzón et al. 2013; Schmidt-Roach et al. 2013, 2014). For genus *Seriatopora*, the genetic study on *Seriatopora hystrix* in the Ryukyu Archipelago showed that three genetic lineages were detected based on mitochondrial DNA and microsatellite markers (Nakajima et al. 2017). As mentioned earlier, mitochondrial DNA and microsatellite are beneficial for constructing genetic lineages (Pinzón and LaJeunesse 2011; Pinzón et al. 2013) using the open reading frame (ORF) of unknown function between atp6 and nad4 and the D-loop, which is the control region between atp8 and cox1 (Flot and Tillier 2007).

Population genetics can also be applied to investigate the migration of benthic marine organisms. In the case of reef-building corals, the migration occurs during the pelagic larval stage. For most coral species, gametes are released during the spawning season (Harrison and Wallace 1990). Long-distance dispersal of broadcast-spawning coral species contributes to genetic connectivity among reefs. Nishikawa et al. (2003) illustrated that the broadcast-spawning species, *A. tenuis*, exhibited lower genetic differentiation than the brooding species, *S. pistillata*. Based on the genetic differentiation of *Acropora tenuis*, *A. digitifera*, *Stylophora pistillata*, and *G. aspera*, broadcast-spawning corals showed the lower genetic differentiation among regions, compared with brooding corals (Nakajima 2018). Nakajima et al. (2015) developed 27 amplifiable and polymorphic microsatellite markers for studying the broadcast-spawning species *Galaxea fascicularis*. Eleven of the markers were cross-type microsatellite loci in the mt-Long and mt-Short colonies showing that many clonemates were found in Zampa, Okinawa, for both mitochondrial DNA types (clonal diversity R = 0.189 in mt-L and R = 0.159 in mt-S). Clonal colonies of blue coral *H. coerulea* were also observed in Oura Bay, Okinawa, with only one genotype (Yasuda et al. 2012).

3.3 Current Threats on the Health of Reef Corals

3.3.1 Coral Bleaching

3.3.1.1 Spatial and Temporal Variation

Climate change affects coral reefs around the world, resulting in coral bleaching and mortality. Coral bleaching was most common in localities where high intensity and frequency anomaly elevated sea surface temperature are recorded. The patterns and severity vary spatially and temporally (Sully et al. 2019). On a global scale, the coral bleaching event was first documented during 1982–1983, and the bleaching records started from 1982 onward (Donner et al. 2017; Oliver et al. 2018; Eakin et al. 2019). Historically, the first coral bleaching event was probably recorded in the Great Barrier Reef in 1929. Yonge and Nicholls (1931) reported that some corals, particularly *Goniastrea* spp. and *Favia* spp., lost their zooxanthellae and became bleached, while many corals died due to elevated water temperature at Low Isles, the Great Barrier Reef. Coral recovery was found some weeks after the bleaching event since their color and zooxanthellae populations became normal. In Japan, the first record of coral bleaching occurred around Sesoko Island, Okinawa, in 1980 (Yamazato 1999). The bleaching events that occurred before 1982 were published in several papers (e.g., Mayer 1914; Goreau and Hayes 1994; Shinn 1966;

Williams and Bunkley-Williams 1990; Coffroth et al. 1990; Glynn 1991, 1993; Goreau and Hayes 1994).

According to Oliver et al. (2018), two peaks of moderate to severe coral bleaching were observed during 1979–2016, corresponding to the two major El Niño events in 1997–1998 and 2015–2016 affecting coral reefs in most regions. Several studies illustrate that two peaks of coral bleaching events and mass coral mortality were correlated (Wilkinson 1998; Hughes et al. 2017; Kimura et al. 2018). The 2010 coral bleaching event extensively occurred in Southeast and East Asia due to elevated sea surface temperatures. The event was also synergized by the intense La Niña event that started in early 2010 within the regions and continued until late 2010. Many coral reefs in the regions were impacted by the coral bleaching event. Several countries reported that this event was more severe than the 1998 bleaching event, resulting in coral mortality of about 18%. In most locations, sea surface temperatures declined to normal seasonal levels by November 2010. Yet, corals in many reefs continued to bleach. The initial mortality of about 10% to 90% was estimated in Indonesia, Malaysia, and Thailand. In Indonesia, however, no bleaching was reported on the coral reefs in the Raja Ampat Archipelago, the West Papua Province, even though the temperature in the central Dampier Straits region largely fluctuated. The comparative study in Vietnam (Phan et al. 2020) showed severe bleaching at Phu Quoc islands (Gulf of Thailand), with 56.6% hard coral bleached but less susceptibility in other reefs in southern waters (Western South China Sea). The repeated surveys showed the rapid recovery of bleached corals in Singapore with less than 10% mortality resulted from the bleaching event in November 2010 (Tun et al. 2010; Hoeksema et al. 2012; Sutthacheep et al. 2013). In China, the coral communities in the mainland have been degraded mainly by anthropogenic impacts over the last decades. Reports on mass coral bleaching in China are limited with a record of the bleaching event during 1997–1998 in Weizhoudao (Guangxi).

The global surface temperature anomalies that occurred during 2014–2017 caused the most severe, widespread, and longest-lasting coral bleaching events across the globe. Similarly, the satellite records revealed spatial scale, duration, intensity, and repetition of such coral bleaching. The impacts of bleaching due to heat stress have been the most severe at many reefs, and the level of impacts varied globally and locally. Generally, heat stress and bleaching result in coral mortality and coral diseases (Eakin et al. 2019).

Coral bleaching events in East Asia in 1998 and 2010 were limited only to those years, but from 2015 to 2017, the coral bleaching events were continuously reported expanding for 3 years, beginning from mid-2014 to mid-2017. It is the most extensive and harmful for many reefs due to high seawater temperatures. In 2016, the impact of coral reefs in East Asian countries, i.e., Cambodia, Indonesia, Japan, South Korea, Singapore, Taiwan, Thailand, and Vietnam, was extensively assessed, showing the widespread bleached coral reefs. In Indonesia, 21 out of 22 monitoring sites covering most of the major islands had impacts due to the bleaching event. In West Papua, no bleaching was reported. In Thailand, the early start of the southwest monsoon in 2016 helped to lower the coral bleaching impacts resulting in less coral mortality compared to that observed in 2010. In Japan, the highest coral mortalities were recorded at Sekisei Lagoon and the outer reef of Miyako Island, with the mortality rates of 67.9% and 67.5%, respectively. During the years 2016 and 2017, the coral communities were mainly damaged by crown-of-thorns starfish predation and typhoon rather than the impacts of bleaching events. In Taiwan, between 2014 and 2017, no extensive coral bleaching was reported because it was limited to specific locations at different times except at Kenting National Park and Hsiaoliuchiu where the coral bleaching was observed in 2017. In 2014 and 2015, the severity of coral bleaching in some countries was mild to moderate. In South Korea, no coral bleaching was reported because few species of zooxanthellate corals have adapted to live in warmer seawater temperature. The patterns of coral bleaching can be seen from the bleaching severity, which is different among reef sites, and the level of susceptibility is greatly influenced by the coral taxa. In Thailand, the experiment revealed that some coral species that were under the shade tended to have a higher rate of survival and bleaching recovery. The lower mortality rate of *Acropora muricata* in shaded areas after the bleaching event was also observed (Kimura et al. 2018).

Overall, there have been global-scale coral bleaching events formally recorded during 1983–2017, and the most severe ones occurred in the years 1998 and 2014–2017 (Table 3.2). The multiple consequences due to global warming continue to increase, particularly elevated sea surface temperatures, and the severity is also synergized by the weather variation of El Niño-Southern Oscillation phases. The high intensity and frequency of annual coral bleaching could occur in the next decades (Hughes et al. 2018).

Coral bleaching occurred in 2019, but only few recent publications reported it. In Vietnam, it was recorded (Phan et al. 2020) high ratio of bleached hard corals in southern waters (39.5% at Nha Trang Bay, 32.9% at Ninh Thuan coastal area, and 25% at Con Dao islands) but less bleaching at Phu Quoc islands (7.3%). The study on genus-specific bleaching at Con Dao islands (Vo et al. 2020) highlighted apparent shifts in susceptibility of some genera, especially *Acropora*, to the bleaching events from 1998 to 2019. Whether these shifts are related to adaptation or acclimation is still questionable.

Table 3.2 The occurrence of global bleaching events during 1983–2017

Year	Severity	Additional information
2014–2017	Severe	Bleaching occurred from 2014 to 2017 with the highest impacts in 2016 and most of the major mortality impacts already reported in some areas. The very high frequency was reported at 19 grid and regional scale.
2010	Moderate	The severity of this bleaching event was lower than those occurred in 2016 and 1998 with the occurrence of coral mortality was reported in some areas.
1998	Severe	One of the most severe bleaching events that coral mortality was observed.
1987	Possible moderate	A discrete peak in bleaching frequency at moderate severity. Heat stress reached critical levels in a small percentage of global reefs.
1983	Possible moderate	The bleaching with mortality in the Great Barrier Reef occurred in 1982. Similar to the occurrence in 1987, heat stress reached critical levels in a small percentage of global reefs.

Source: Modified from Oliver et al. (2018)

3.3.1.2 Causes, Mechanisms, and Consequences

The coral-zooxanthella symbiotic relationship serves as an energetic foundation of coral reef ecosystems. The relationship consists of two distinct organisms in which biological processes are evolutionarily and metabolically integrated. Zooxanthella is a photosynthetic single-celled dinoflagellate living in the gastrodermal layer of corals. At least one million cells of zooxanthellae are generally found in a square centimeter of coral tissue. Intercellular nutrient exchange is the main benefit from this symbiosis, supporting the growth and reproduction of both coral and zooxanthellae (Weis et al. 2008; Davy et al. 2012). The cellular mechanisms of the coral host and zooxanthellae symbiont yield higher productivity under the high irradiance and warm waters, particularly in tropical regions. Although the complex mechanisms and the nutritional and immunological interactions in the coral-zooxanthella symbiosis have been developed and successful for millions of years, they are still susceptible to external stresses, particularly heat stress and rapid changes of other environmental conditions like salinity, sedimentation, etc. The symbiosis can be disrupted by such stresses leading to bleaching and further mortality of corals. Coral bleaching highly depends on periods of both high seawater temperature and irradiance (Hoegh-Guldberg et al. 2007; Hughes et al. 2017). Most mass coral bleaching events caused by severe and prolonged elevated seawater temperatures usually occurs in summer months, which has been reported at a global scale (Hughes et al. 2017).

Typically, symbiosis relies on the productivity yielded from the photosynthetic process of zooxanthellae living inside each coral cell. In the bleaching event, the loss of zooxanthellae from the coral host due to heat stress and the direct generation of reactive oxygen species (ROS) have been considered (Warner and Suggett 2016). Some physiological studies indicate the physiological impairment and the expulsion of the zooxanthellae during the bleaching as well as a coral host immune response may relate to the level of harmful reactive oxygen species (ROS) produced from the coral host and zooxanthellae (Weis 2008). Regarding the oxidative theory of bleaching, ROS generation is likely to be induced by thermal stress. Detoxification of ROS is needed for coral hosts and zooxanthellae to repair oxidative damage (Weis 2008).

Oakley and Davy (2018) described the mechanisms of thermal stress that link with coral bleaching as follows:

(A) Derived from photosystem II (PSII) and photosystem I (PSI), superoxide (O_2) is produced from photosynthetic O_2 via the Mehler reaction.
(B) Photosynthetic O_2 may react with singlet oxygen sensitizers (Sens.) to form the highly reactive singlet oxygen (^{1}O2).
(C) Peroxynitrite (ONOO) is produced from the reaction between photosynthetic O_2 and nitric oxide (NO), inhibiting mitochondrial electron transport.
(D) Thermally induced high respiration and electron transport inhibition induce an increase of respiratory electron transport chain, and producing mitochondrial reactive oxygen species (ROS).
(E) High temperatures cause endoplasmic reticulum (ER) stress which leads to protein misfolding, releases of calcium (Ca^{2+}) to the mitochondria, and promotes the release of cytochrome c (cyt c). Repair of the misfolded proteins also generates ROS.
(F) As the release of cyt c induces apoptosis, the host cell has a mechanism to regulate the apoptosis by the function of mitochondrial B-cell lymphoma 2 (BCL2) protein. Under heat stress condition, the excessive generation of NO and ROS or by mitochondrial Ca^{2+} uptake can promote the host apoptosis (Oakley and Davy 2018).

As mentioned earlier, high water temperature and irradiance provide a large quantity and rate of energy, stimulating photosynthetic processes in zooxanthellae, primarily the light-harvesting complexes and photosynthetic electron transport chain. The coral host membranes and tissues limit the photosynthetically generated oxygen (O_2) generated from the zooxanthellae. At the same time, the dissolved inorganic carbon is infused into the zooxanthellae to sustain photosynthetic carbon fixation (Kuhl et al. 1995; Tansik et al. 2017).

These factors explain how thermal stress affects the photosynthetic process in the zooxanthellae and leads to oxidative damage (Weis 2008). When the corals and zooxanthellae fail to moderate these stresses, dysfunction of symbiotic relationship is initiated and consequently, corals become bleached (Oakley and Davy 2018).

As climate change and its impacts have been increasingly in societal attention, numerous studies regarding the photobiology of zooxanthellae have been conducted aiming to understand cellular mechanisms of stress and reaction to climate change. An integrated approach is focused to corporate several key processes relate to photosynthesis to further how photobiological findings support the ecological success of the zooxanthellae (Warner and Suggett 2016). A recent comparative study on the dissolved inorganic carbon-associated photosynthetic kinetic parameters on corals and zooxanthellae illustrates that different species of corals had a different rate of photosynthesis (Tansik et al. 2017). According to the study, *Orbicella faveolata* had the maximum rates at current seawater conditions than *P. astreoides* or *S. radians*. Furthermore, CO_2 was more produced by *O. faveolata* at the coral surface than that produced by the others. The zooxanthellae of all the corals had a very low dissolved inorganic carbon half-saturation constant for photosynthesis but high levels of internal carbonic anhydrase activity. It means that the zooxanthellae need to use lots of energy to acquire carbon for photosynthesis. Thus, host regulation of dissolved inorganic carbon delivering to the zooxanthellae is crucial for photosynthesis. Rosset et al. (2017) suggested that the coral-zooxanthellae symbiosis may be interrupted by phosphorus starvation. They conducted long-term experiments by providing zooxanthellae with imbalanced N/P ratios, and found that the undersupply of phosphate greatly disturbed the symbiosis leading to the loss of coral biomass, malfunctioning of photosynthesis and bleaching of corals. The corals were adaptable with nitrogen limitation as they can tolerate and did not show any negative effects at lacking of nitrogen at high phosphate concentrations. Transmission electron microscopy analysis under the study also confirmed the nutrient stress in zooxanthellae, and the accumulation of uric acid crystals indicated the high N/P ratios in the water (Rosset et al. 2017).

To date, the cellular mechanisms of coral and its zooxanthellae responding to high temperatures have been well-documented. However, the downstream mechanisms regarding the loss of zooxanthellae from host cells during the bleaching are still questionable (Weis 2008; Bieri et al. 2016). Relevant studies have been conducted on the fate of the zooxanthellae during the coral bleaching process in different organisms and environments (Gates et al. 1992; Ainsworth et al. 2008; Tchernov et al. 2011; Hanes and Kempf 2013). However, the causes of coral bleaching at each natural bleaching event are still unclear. Researchers believed that it could be derived from a combination of multiple stressors, particularly the intensity and duration of the thermal stress (Gates et al. 1992; Brown et al. 1995; Bieri et al. 2016). The other possible mechanisms explaining the loss of symbiotic zooxanthellae have been proposed, including exocytosis, symbiophagy, host cell detachment, host apoptosis and autophagy (Baghdasarian and Muscatine 2000; Sawyer and Muscatine 2001; Davy et al. 2012; Strychar et al. 2004; Fujise et al. 2013; Bieri et al. 2016; Downs et al. 2009; Paxton et al. 2013; Oakley et al. 2016). The possible mechanisms of symbiont loss from cnidarian host cells after the initiation of bleaching were reviewed by Oakley and Davy (2018), including (1) exocytosis in which symbionts are expelled from the host cells; (2) symbiophagy occurs when the hosts degrade symbionts within the host cells through host autophagic pathways; (3) host cell detachment occurs when entire host cells detach from the gastrodermal layer; (4) host apoptosis refers to the symbiont expulsion due to host cell death; and (5) autophagy breaks down compromised or extraneous organelles and cells of host corals using the fusion of the autophagosomes with lysosomes containing digestive enzymes.

Quigley et al. (2018) explained some existing knowledge and research gaps regarding the roles of zooxanthellae on coral bleaching, as the following points:

(a) Zooxanthellae are essential for studying the coral physiology since the molecular mechanism and feedbacks signaling between coral and zooxanthellae during cell expulsion are unclear.
(b) Zooxanthellae are diversified in phylogenetic clades, which express in different physiological tolerances. The development of molecular techniques such as qPCR, microsatellite and NGS techniques increases the understanding of intra-cladal diversity within zooxanthellae and holobiont physiology. It could help to understand the holobiont physiology and its bleaching response. Additionally, the current genome sequencing can be applied to seek for single-copy markers and further studying on the resolution of zooxanthellae taxonomic diversity.
(c) Corals can host many different types of symbionts. The zooxanthellae community observed in the Caribbean has a single genotype per zooxanthellae type, while multiple genotypes per type are found in the Indo-Pacific. However, genetically distinct symbionts have been detected at lower abundance within coral colonies. Sequencing technology also improves the detection and characterization of symbiont types, such as their prevalence and roles in bleaching recovery. Some research questions are still raised whether the background types and variants play important roles in bleaching and recovery.

(d) Although the symbiont shuffling can increase thermal tolerance for some coral species, this still fails to handle under extreme conditions with increased and prolonged higher seawater temperatures. Thus, mass mortality of corals following the bleaching events was globally reported during 2014–2016. The studies on symbiont shuffling are required to seek for potential corals that can shuffle symbionts and the ecological trade-offs between growth and reproduction associated with hosting altered symbionts with the current rate and severity of ocean warming.

(e) Currently, the knowledge of adaptive potential and limits of corals are well-documented. Researches also demonstrate that zooxanthellae had both positive acclimatory and adaptive potential at the type and community level to heat stress. Extended studies are required to prove that holobionts can survive over long timescales. The new research idea should also be formulated by integrating these findings to support the evolution of zooxanthellae.

The ability of the holobionts to adapt and/or acclimate to the changes in environmental conditions may possibly be associated with the division rate and evolution of symbiotic microbes. Researchers hypothesized that modification of the microbiome may be an alternative to potentially enhance transgenerational acclimatization of coral reef organisms (van Oppen et al. 2015). Later, Damjanovic et al. (2017) proposed a series of manipulative experiments to explore whether microbial mediation enhances long-term coral stability. Also, the importance of microorganisms to corals has also been extensively discussed to seek adaptive mechanisms coping with climate change stressors (Torda et al. 2017; Webster and Reusch 2017). Community shuffling has also been discussed on both the microbiome and zooxanthellae populations on the idea of getting the new genetic material via mutation and/or horizontal gene transfer. Researchers hypothesized that holobionts may or may not transfer advantageous microbial alterations to new generations that are able to tolerate coral bleaching events. Coral holobionts could possibly be developed to be heat tolerant and more resilient to future bleaching events through shifting in the coral microbiome and zooxanthellae populations and obtaining new genetic materials through mutation and/or gene transfer. Conversely, such mechanisms may cause negative impacts to the next generation of holobionts, leading to greater mortality and algal and sponge domination (Morrow et al. 2018). This theory corresponds to the founder effect, which may result in speciation and further enhance the evolution (Barton and Charlesworth 1984). At this point, either vertical or horizontal transmission of the founder populations from acclimated coral holobionts may be beneficial to the improvement of future generations (Morrow et al. 2018).

A consortium of corals, macroalgae and benthic invertebrates has a complex reef structure that plays important roles in maintaining organic and inorganic forms of coral reef productivity and balance (Finelli et al. 2006). Various reef animals, particularly reef fishes, obtained benefits from these benthic organisms in terms of shelter and food supplies. Reefs are formed by calcium carbonate skeletons through a calcium deposition process made by corals and some macroalgae, contributing to shoreline protection from storm damage and erosion. Thus, the loss of zooxanthellae due to bleaching events leads to coral mortality, thus affecting other consequences such as reef growth, productivity, biodiversity, and the functions and services of the coral reef ecosystem. Physiologically, thermal stress affects coral-zooxanthellae metabolism and physiological functions. The evidence shows that the expulsion of zooxanthellae significantly reduces the translocation of photosynthetic products to the coral host cells (McClanahan et al. 2018). Such dysfunction has a great impact on corals because zooxanthellae supply approximately 30% of the total nitrogen and 91% of the carbon to the coral host (Bythell 1988).

Large-scale environmental disturbances, particularly elevated seawater temperature, have caused mass coral mortality on coral reefs for over a century across tropical and subtropical waters worldwide. Various model projections have been made to predict coral bleaching and its impacts. However, it is challenging because there are still some uncertain factors, especially the ability of coral adaptation/acclimation to the elevation of seawater temperatures (Buddemeier et al. 2004; van Oppen et al. 2015). Bleaching events due to thermal stress are mostly found on the hydrocorals, scleractinians, and octocorals as well as some macroalgae, such as *Halimeda* (Vicente 1990). Most studies confirm that there is a highly significant association between the scale/severity of thermal stress and the degree of bleaching mortality (Glynn 1984; Hughes et al. 2017). Coral mortality following bleaching also depends on habitat characteristics; for example, coral mortality tends to decline on deeper areas and lower light intensity. Some studies report that less coral mortality was found in the habitat that has a high natural background temperature variability (Brown et al. 1996; McClanahan et al. 2007a; Bridge et al. 2014). Higher intensity of bleaching events was found in windward habitats compared with leeward habitats since the natural background temperature variability in the windward habitats was relatively less (McClanahan et al. 2005). At a community level, coral bleaching also varies spatially depending on the community structure. For example, the coral communities dominated by susceptible coral species had a higher coral bleaching tendency (Marshall and Baird 2000; Shuail et al. 2016; Heron et al. 2016). Environmental factors are also important in strengthening coral acclimation to extreme conditions such as temperatures, irradiation, and UV levels. Such corals surviving in habitats with extreme conditions may tolerate the effects of coral bleaching (Ainsworth et al. 2016).

In the Indo-Pacific region, patterns of susceptibilities and bleaching to heat stress found among coral species are quite similar (McClanahan et al. 2004), but rates of acclimation of the same coral species over time in each region are still different (McClanahan 2017). Besides, some explanations on how the bleaching susceptibility hierarchy changes over time and with temperature severity histories are still required. Since coral mortality rates and bleaching intensity are not always related, only the information on bleaching surveys may be difficult to reflect natural selection and genetic adaptation rates (McClanahan et al. 2004; McClanahan 2017). Hughes et al. (2017) also supported that the past history and severity of the coral bleaching are the critical information; for example, some coral species that were previously experienced with the less severe bleaching events can tolerate the greater severe events. Some coral species were bleached, but they were well-recovered (Baird and Marshall 2002). On the other hand, some species can die of heat stress and disease without showing any bleaching-related symptoms (McClanahan et al. 2004; Weil and Rogers 2011). It is quite difficult to determine the impacts of elevated seawater temperature by only considering the coral bleaching pattern like partial and whole colony mortality because of the different abilities of each coral species. Compared to most branching corals, massive corals seemed to be more tolerant to heat stress, taking longer time to bleach and die (Brown and Suharsono 1990; McClanahan et al. 2001; Baird and Marshall 2002). For *Acropora hyacinthus*, the predominant transcriptome response due to bleaching events (involving up to 20% of the transcriptome) was disturbed to 6 months after bleaching and 4 months after the symbiont recovery. Also, the genes were not recovered to normal expression levels within 12 months (Thomas and Palumbi 2017). The response pattern of each coral also relies on their previous experience (Brown et al. 2000; Oliver and Palumbi 2011; Guest et al. 2012; McClanahan 2017). As corals have different abilities to adapt or acclimate to the changes due to global warming, the projections of coral reef status should also include those factors (adaptation/acclimation) in the models (Baird et al. 2007; Logan et al. 2014).

Some coral colonies surviving after the coral bleaching may suffer from sublethal negative impacts, e.g., reduced reproductive output, reduced growth, increased susceptibility to diseases, etc. (Lesser et al. 2007). The effects of bleaching on coral reproduction output have been reported in several ways, such as changes in egg size and quality and reduced polyp fecundity, number of polyps with eggs and number of eggs per polyp, and number of whole breeding colonies (Baird and Marshall 2002; Mendes and Woodley 2002). Typically, the effects on reproduction vary among coral species (Baird and Marshall 2002). No effect on reproductive output was reported in some coral species, e.g., *Montipora capitata*, since they can acquire some more food through heterotrophic feeding to compensate for the food imbalance due to the loss of zooxanthellae (Cox 2007). Reduction in coral growth rate is one of the effects of bleaching on corals (Pratchett et al. 2015). The effects of coral mortality following the bleaching event on the size structure of coral populations have been hypothesized (Baird and Marshall 2002). The coral colonies with large sizes are likely to be harmful when they are exposed to the anomaly elevated seawater temperature (Nakamura and van Woesik 2001). A study suggests that no bleaching sign is detected on the coral recruits (diameter <20 mm) compared to the larger corals (Mumby 1999). Many field surveys mention that the survival rate of small coral colonies is higher than that of the larger colonies (Loya et al. 2001; Nakamura and van Woesik 2001; Bena and van Woesik 2004; Shenkar et al. 2005). Furthermore, the coral bleaching decreases the coral settlement rate and loss of live coral cover leading to an imbalance of the predator-prey relationship of corals (Gilmour et al. 2013). Such imbalance is derived from the loss of live coral cover and more feeding activities of coral predators on the surviving corals.

Environmental change and global climate change possibly create synergistic impacts of elevation of seawater temperature, coral bleaching, and disease, severely affecting the coral reef ecosystem (Baird 2000; Willis et al. 2004; Miller et al. 2006; Bruno et al. 2007; Weil et al. 2009, 2017; Cróquer and Weil 2009a, b; McClanahan et al. 2018). Elevation of seawater temperature may stimulate and accelerate the prevalence of new coral diseases (Rosenberg and Ben-Haim 2002; Lesser et al. 2007; Weil and Rogers 2011; Weil et al. 2017) and may affect the corals' immune system making them unhealthy and susceptible to the disease. Moreover, a physiological equilibrium between the coral host and resident microorganisms such as bacteria may also be destabilized by anomaly environmental changes. Either coral hosts become susceptible or such bacteria become virulent, or both can affect the physiological equilibrium and coral health (Harvell et al. 1999; Rosenberg and Ben-Haim 2002; Ritchie 2006; Ward et al. 2007; Harvell et al. 2009; Burge et al. 2014; Page et al. 2016; Weil et al. 2017; McClanahan et al. 2018).

Each coral species or population has differential susceptibility to elevated seawater temperatures. Such heat stress can change the abundance of coral population leading to the coral community change such as lower species richness, species diversity, changing community composition, and the life history characteristics of the coral communities (Jokiel and Coles 1990; Warwick et al. 1990; Loya et al. 2001; Kayanne et al. 2002; McClanahan and Maina 2003; McClanahan et al. 2007a, b; Weil et al. 2009; Kuo et al. 2012; Darling et al. 2013; Harii et al. 2014). The coral community can be changed short- or long-term depending on several factors

(Glynn 1994; Brown 1997; McClanahan and Maina 2003; Berumen and Pratchett 2006; McClanahan 2014). Changes in a coral population can also change competitive interactions because each coral species has a different heat-tolerant ability (Alino et al. 1992).

Climate change impacts can change a coral species composition and can also cause coral community changes on a larger scale (Langmead and Sheppard 2004; van Woesik et al. 2012; Edmunds et al. 2014; McClanahan et al. 2014). In the Indo-Pacific, loss of coral has been reported, while coral recovery and responses vary spatially (Ateweberhan et al. 2011; Selig et al. 2012; McClanahan et al. 2014). Brown and Suharsono (1990) report that 92% of the coral cover of reef flats at the islands in Pulau Seribu, Indonesia, were affected by the elevated seawater temperature of about 2–3 °C in 1982. Almost of the *Acropora* colonies were greatly devastated due to such heat stressor. In Japan, the species richness and coverage of the coral reefs at Sesoko Island after the 1998 coral bleaching decreased by 61% and 85%, respectively (Loya et al. 2001). In Thailand, many reefs across the Gulf of Thailand were affected by severe bleaching during the summer months of 2010. Coral taxa were bleached with different levels of intensity, and many coral species, particularly *Acropora* spp., had high mortality. Yeemin et al. (2013) report the impacts of the 2010 bleaching event on coral communities at Kut Island, located in the eastern Gulf of Thailand, found that the live *Acropora* cover observed before the 2010 bleaching event (0.35–1.46%) significantly decreased to 0.1% after the 2010 bleaching event. They also mention that the significant decrease in the live *Acropora* cover implies the possible local extinction of this coral species in this area.

Calcium carbonate accretion and primary productivity have been on the top concerns regarding coral bleaching impacts. Some studies reveal that coral bleaching can decrease calcium carbonate accretion and the primary productivity of coral reefs. Perry et al. (2013, 2015) illustrate that the net calcification rate becomes negative when the coral cover declines below 10%. Thus, the reefs cannot grow to correspond to sea-level rise. The obstruction of coral reef growth results from the decline of dominant coral species that grow fast, but it is sensitive to thermal stress, for example, *Acropora* spp. (McClanahan et al. 2018). After bleaching, some corals die, but some other species start to grow. Epilithic turf and encrusting coralline algae overgrow on dead coral reefs and become the main players for productivity and calcification in deteriorated reefs. However, the algae do not build up the structural complexity as corals do (McClanahan 2008; Alvarez-Filip et al. 2011). Coral mortality following bleaching events helps to open up benthic areas where some herbivores and macro-invertivores access to feed on the areas. Some small-sized species relying on the reef microhabitats are risky from predators or fishers (Graham et al. 2008, 2011; McClanahan et al. 2014). The abundance and diversity of coral reef fishes depend on both ecological and human factors such as live coral cover, diversity of corals, coral reef complexity and fishing practices and intensity. Extensive studies indicate that coral bleaching affects not only corals but also the reef fish community. Coral mortality, the collapse of reef structures, synergized by ecological phase shift, may result in a decline in abundance and species richness of reef fishes of more than 60% (Wilson et al. 2006; Graham et al. 2006, 2008; Pratchett et al. 2018).

3.3.2 Coral Diseases

3.3.2.1 Identification and Prevalence

As coral reefs around the world have been unhealthy due to increasing multiple stressors, studies on coral health have been growing in the previous decades. Coral diseases are also discussed as they potentially affect coral health and their community structures. Disease outbreaks have been reported from many locations from the Red Sea, Caribbean, Mediterranean, Gulf of Mexico, Japan, and western Indian Ocean (Rosenberg and Loya 2010). In Indo-Pacific reefs, coral diseases have been prevalent across the region, as illustrated by some studies, which are also linked to local anthropogenic disturbances, for example, land-based pollution, sedimentation, eutrophication, marine debris, and elevated seawater temperatures (Pollock et al. 2019). Table 3.3 provides a list of coral diseases and syndromes reported from various locations worldwide. Historically, the first coral disease study was conducted in Belize in 1973, reporting the identification of black band disease (BBD) (Antonius 1973). Later from 1980 to 1990, white band disease was identified as a major cause of the 95% decline in the Caribbean corals dominated by *Acropora palmata* and *A. cervicornis* (Aronson and Precht 2001). Predicting the disease outbreak is somewhat challenging and prediction models have some limitations; thus, understanding the disease-inducing factors is crucial to prevent the outbreak and to mitigate its impacts (Wada et al. 2018).

Six unhealthy characteristics of corals and their causes have been proposed as the guidelines for coral disease classification (Woodley et al. 2008): (a) bleaching due to loss or degradation of the dinoflagellate symbiont caused by biotic (bacteria) and abiotic (temperature, UV radiation, salinity, toxicants, etc.) factors; (b) physiological and morphological abnormalities caused by noninfectious stressors (toxicants, sedimentation, and pollution); (c) physical damage caused by predators; (d) parasitic infestation caused by protozoans, metazoans, or sponges; (e) growth abnormalities caused by hypertrophy, hyperplasia, neoplasia, or tumors; and (f) partial or whole colony infections caused by bacteria, fungi, virus, or other microorganisms potentially leading to colony mortality.

Table 3.3 Common coral diseases identified worldwide

Disease (acronym)	Coral affected	Location
Black band disease (BBD)	Massie corals	Belize
White plague type I (WPL I)	*Agaricia agaricites*	Florida
Shut down reaction (SDR)	*Acropora cervicornis*, *Montastraea annularis*, and *Siderastrea siderea*	Belize and Florida
White band disease type I (WBD I)	*Acr. palmata*	Caribbean Sea
Growth anomalies (GAs)	*Acr. palmata*	Venezuela
Dark spot disease (DSD)	*Orbicella annularis*	Colombian Caribbean
Caribbean yellow band disease (CYBD)	*Orb. annularis* and *Orb. faveolata*	Florida
White pox (WP)	*Acr. palmata* and *Acr. cervicornis*	Florida Keys
Vibrio shiloi-induced bleaching (VSB)	*Oculina patagonica*	Mediterranean coast, Israel
Yellow blotch/band (YBL)	*Orb. faveolata*	Florida Keys
White plague type II (WPL II)	*Millepora alcicornis* and *Dichocoenia stokesi*	Florida Keys
White band disease type II (WBD II)	*Acr. cervicornis*	San Salvador and Bahamas
Arabian yellow band disease (AYBD)	*Acr. clathrata*, *Acr. pharaonis*, *Acr. tenuis*, *Acr. valida*, *Acr. florida*, *Porites lutea*, *P. lichen*, *P. nodifera*, *Turbinaria reniformis*, and *Cyphastrea*	Persian Gulf
Skeletal eroding band (SEB)	*Massive* and *branching corals*	Indo-Pacific
Growth anomalies (GAs)	*Montipora informis*	Sesoko, Okinawa
White plague type III (WPL III)	*Orb. annularis* and *Colpophyllia natans*	Florida Keys
Pink-line syndrome (PLS)	*P. lutea*	Lakshadweep island
Vibrio *coralliilyticus*-induced bleaching (VCB)	*Pocillopora damicornis*	Red Sea
Porites ulcerative white spot disease (PUWS)	*Porites* spp.	Philippines
Black band disease (BBD)	*n.d.*	Sekisei Lagoon, Okinawa
Brown band disease (BrBD)	Acroporidae	Great Barrier Reef
White syndrome (WS)	Acroporidae and Poritidae	Great Barrier Reef
White syndrome (WS)	Table *Acropora* spp.	Sekisei Lagoon, Okinawa
Red band disease (RBD)	*Pachyseris speciosa* and *Porites* sp.	Palau
Tissue loss	*Porites cylindrica*	Sekisei Lagoon, Okinawa
White spot syndrome (WPS)	*Turbinaria peltata*	Miyazaki
Pigmentation response	*P. lutea* and *P. lobata*	Zamami and Ginowan, Okinawa
Porites ulcerative white spot disease (PUWS)	*P. lutea* and *P. lobata*	Zamami and Ginowan, Okinawa
Brown band disease (BrBD)	*A. nobilis*	Zamami and Ginowan, Okinawa
Compromised health conditions (CH)	*Oxypora lacera*	Zamami and Ginowan, Okinawa
Skeletal eroding band (SEB)	*Montipora* spp.	Aka, Okinawa

Source: Modified from Bruckner (2016) and Wada et al. (2018)

In some studies, Koch's postulate has been applied to identify the causative agent that causes coral disease signs. A rod-shaped gram-negative bacterium, *Serratia marcescens*, causes a white pox (WP) found in *Acropora palmata*, whereby distinct white patches occur throughout a distressed colony (Patterson et al. 2002). White plague type II (WPL II) is caused by a rod-shaped gram-negative bacterium *Aurantimonas coralicida* that can cause whitening and tissue mortality at the base of coral colonies *Dichocoenia* and *Orbicella* (Denner et al. 2003). A rod-shaped gram-negative bacterium, *Thalassomonas loyana*, can cause infection in *Favia* spp., called white plaque type I (WPL I), which can be seen similarly to WPL II (Thompson et al. 2006). An infection found in *Acropora*, *Montipora*, and *Pachyseris* species is caused by a gram-negative *Vibrio* species, which promotes faster loss of tissue resulting in the exposure of the coral skeleton, diagnosed as white syndromes (WS) (Sussman et al. 2008). Several species of *Vibrio* have been recognized, causing bleached corals. Bleaching signs found in *Oculina patagonica* and *Pocillopora damicornis* are caused by *V. shiloi* and *V. coralliilyticus*, respectively (Kushmaro et al. 2001; Ben-Haim and Rosenberg 2002). A cyanobacterium *Phormidium valderianum* can also cause infection by promoting a pink discoloration found on the tissues of *Porites*. This infection is known as pink-line syndrome (PLS) (Ravindran and Raghukumar 2002). Growth anomalies (GAs) are the first sign of coral disease reported in Japan in 2000 (Yamashiro et al. 2000). Coral diseases have been reported worldwide. In the Indo-Pacific region, various types of coral diseases have been identified in Japan and Australia (Table 3.3).

Sabdon et al. (2019) report that nutrients in the seawater can be enriched by human activities, like aquaculture, but they do not promote the prevalence of coral diseases. The study was conducted at three study sites (Genting, Sambangan, and Seruni) in Karimunjawa National Park, Java Sea, Indonesia, to find the possible effects of nutrient enrichment caused by floating fish cages. They found six signs of diseases, including white band disease, black band disease, white plague, pigmented response, ulcerative white spot, and growth anomaly as well as the signs from predation and bleaching. The nutrient concentration in the seawater tended to increase due to fish culture activities, but no significant correlation between the nutrient (N and P) concentrations and coral disease prevalence was found.

Samsuvan et al. (2019) provide an extensive study on coral diseases in Thai waters by conducting surveys in the Gulf of Thailand and the Andaman Sea during 2010–2015. Nine signs in four main categories are observed, including pigmentation responses (pink lines, pink patches, pink spots, and pink borers), white syndromes (white patches, white bands, and ulcerative white spots), growth anomalies, and unusual bleaching patterns. The highest severity of coral diseases and signs of compromised health is found in the inner Gulf of Thailand, while the Andaman Sea remains the lowest one. The authors also highlight the association of disease severity and composition and the level of human impact that the study sites located near the shores and/or the areas with intensive tourism tend to have a higher human impact due to mainly poor water quality. According to the study, the severity of fish bites tends to increase within marine national park boundaries.

Some studies highlight nutrient loading as a stressor on coral health. For example, Oberle et al. (2019) identify the factors determining spatial patterns of coral health and diseases, including water circulation, residence times, and submarine groundwater discharge (SGD). They explain that submarine groundwater discharge causes high nutrient and low salinity affecting coralline health as well as promoting the prevalence of black band disease. The nutrient level is relatively high during low tide and is associated with nearby upstream cesspools and drain fields.

Due to the growing plastic use worldwide and ineffective or waste mismanagement, lots of plastics have been dumped into the ocean and distributed globally. As many as 11.1 billion plastic wastes are found on coral reefs in the Asia-Pacific, and the amount of plastic continues to increase to 40% by 2025, according to the projection (Lamb et al. 2018). The impacts of plastic waste or marine debris are well-documented. Furthermore, some studies show that plastic waste can possibly promote outbreaks of disease in marine ecosystems. Lamb et al. (2018) illustrated the influence of plastic debris and coral disease risk by conducting surveys in 124,000 reef-building corals from 159 reefs in the Asia-Pacific region. When corals contact with plastic waste, the likelihood of disease infection sharply rises from 4% to 89%. Corals with complex structures (tabular and branching) are eight times of chance to contact with plastics higher than corals with less complex structure like massive corals. However, the microhabitats inside the reefs may be disproportionately affected.

3.3.2.2 Disease Transmission

Understanding coral disease transmission is crucial for understanding disease ecology, identifying risk and factors at both species and population levels, and formulating interventions to prevent and mitigate the impacts of coral diseases. Examining coral disease transmission has been developed in different approaches ranging from laboratory and field experiments to modeling. The advancements and techniques have been proposed and enhanced the understanding of disease ecology. To date, three hypothesized modes of coral disease transmission have been introduced, including direct contact, waterborne, and vector-borne transmission (Shore and Caldwell 2019). Diseases can be directly transmitted to corals via physical damages and/or chemical reactions during competition, colony fusion, and fragmentation. Waterborne transmission occurs because of free-living pathogens or any free-floating vectors or infected coral tissue or mucus. Coral pathogens can be transported through water movement (rivers and oceanic currents) and the discharge of untreated ballast water. Vector-borne transmission may be promoted via predation by corallivores (such as snails, worms, or fishes), or by interactions with non-corallivorous marine organisms. Hypothesized modes of transmission in coral diseases of some coral species are described in Table 3.4.

Table 3.4 Hypothesized modes of transmission in coral diseases

Disease system	Coral species	Mode of transmission		
		Direct contact	Waterborne	Vector-borne
Tissue loss[a]	*Acropora cervicornis*	e	e	e
	Acropora clathrata	e		
	Acropora cytherea	e		
	Acropora hemprichii			f
	Acropora hyacinthus	e		
	Acropora muricata			m
	Acropora palmata			f
	Colpophyllia natans			f
	Dendrogyra cylindrus			f
	Dichocoenia stokesi		e	
	Diploria labyrinthiformis			f, e, m
	Favia favus		e	
	Montipora capitata	f, e	e, s	f, m
	Oculina patagonica			e, m
	Orbicella annularis	e	e	f, e
	Orbicella faveolata			f, e, m
	Orbicella franksi			f
	Pocillopora damicornis	e		
	Porites andrewsi	e		
	Porites cylindrica	e	e	f, e
	Pseudodiploria strigosa			f, e, m
	Turbinaria mesenterina	f, e		e
Multifocal tissue loss[b]	*Acropora palmata*		m	m
	Porites attenuata	e	e	
Black band disease	*Acropora abrolhosensis*			f
	Acropora muricata	e		f, m
	Acropora intermedia			f
	Pseudodiploria strigosa	f	s	
	Montastraea cavernosa	f	s	
	Montipora patula			f
	Montipora spp.	f		
	Orbicella annularis	f	s	
	Orbicella faveolata			e
	Siderastrea siderea	f	s	
Arabian yellow band disease	*Acropora* spp.	f		
	Acropora clathrata	f, e		
Caribbean yellow band disease	*Orbicella faveolata*			m
Brown band disease	*Acropora abrolhosensis*			f
	Acropora cytherea			f
	Acropora hyacinthus			e
	Acropora muricata			f
	Acropora intermedia			f
	Acropora surculosa		e	
Skeletal eroding band	*Acropora* spp.	e		
	Acropora muricata		e	
	Agaricia tenuifolia	e	e	
	Pocillopora spp.	e		
	Pocillopora damicornis		e	
	Porites cylindrica		e	
	Stylophora pistillata	e		

(continued)

Table 3.4 (continued)

Disease system	Coral species	Mode of transmission Direct contact	Waterborne	Vector-borne
Dark spot disease	*Siderastrea siderea*			f
Porites trematodiasis	*Porites compressa*			f, e
Aspergillosis	*Gorgonia* spp.	e, s	f, s	m

Source: Modified from Shore and Caldwell (2019)

Remarks: Evidence from field observations (f), in situ or laboratory manipulative experiments (e), microbial analysis (m), and spatial analysis (s)

[a] Includes diseases referred to as white band disease, white plague disease, white plague-like disease, and white syndromes

[b] Includes diseases referred to as white pox disease and *Porites* ulcerative white spot disease

3.3.2.3 Prevention and Therapy

Coral diseases have become a significant threat to coral reefs. However, knowledge and understanding in various aspects of coral diseases are still limited. It is necessary that more studies should be conducted to fill up the knowledge gap, supporting the establishment of prevention and mitigation measures for coral diseases. The idea of enhancing immunization of corals has less possibility in practice because of the restricted adaptive immune system. Applying antibiotics to corals is still questionable whether it is safe for the environment or it can be applied in the coral reefs, which are an open system. Phage therapy has been studied to hope that it is an alternative method for treating diseases on infected corals. For example, Atad et al. (2012) applied phage therapy to treating white plague-like disease infected on *Favia favus* colonies in the Gulf of Aqaba, Red Sea. The successful results reveal that phage BA3 can inhibit white plague-like disease caused by the pathogen *Thalassomonas loyana* and terminate the transmission to healthy corals. The lower infection proportion (5% of total healthy coral colonies) is found when treating with phage, and the infection proportion increases to 61% in the no-phage control.

Control and prevention of coral diseases are important, particularly for coral aquaculture. Sheridan et al. (2014) provide a comprehensive review on the causes, implications, and preventions of diseases in a coral aquaculture system. In coral aquaculture, corals are usually kept in dense culture facilities, making them vulnerable to coral diseases and outbreaks. Likewise, the corals cultured in the natural environment are also vulnerable to the exposure of various diseases in the marine environment. Although preventing coral disease outbreaks in culture systems much important, scientific knowledge regarding the diseases and coral aquaculture is still scarce. Treatment methods are being developed, such as tinctures of iodine, freshwater dips, and the addition of antibiotics (Sweet et al. 2012). The use of probiotic bacteria is under investigation to inhibit coral pathogens and strengthen coral health (Teplitski and Ritchie 2009). In most coral aquaculture practices, fragmentation techniques are popular to propagate corals. However, concerns regarding the loss of genetic diversity and the decrease of disease resistance have still arisen. Studies suggest using sexual reproduction techniques for coral restoration and aquaculture as this method is relatively efficient compared with fragmentation techniques. Besides, sexual reproduction maintains genetic variability and enhances coral resistance (Petersen, 2008). Sheridan et al. (2014) also recommend the measures for preventing coral diseases in coral aquaculture that should consider on (a) policy, management, and good practice, (b) technical methods, and (c) coral genetic selection.

The advances of biomedical science, as well as molecular biology, should be applied to develop a multifunctional toolbox and useful applications for investigating the state and severity of disease as well as supporting research on coral diseases (Work et al. 2008). Researches in molecular genetic serve the understanding the mechanism of coral resistance. For example, a study conducted by Miller et al. (2019) on genotypic variation in disease susceptibility of cultured stocks of elkhorn (*Acropora palmata*) and staghorn corals (*A. cervicornis*) in the Caribbean reveals the significant genotypic variation in disease susceptibility of both species. This is beneficial for further developing mechanistic studies and supporting effective disease management tools (Miller et al. 2019).

3.4 Management Consideration Based on Coral Biology

Coral reefs have been experiencing an increasing magnitude of impacts resulting from multiple anthropogenic and natural stressors at local and regional/global scales (Muthukrishnan and Fong 2014; Good and Bahr 2021). The anthropogenic activities synergize the impacts of global climate change, deteriorating coral reef ecosystem function and services (Hughes et al. 2017). Fortunately, coral biology has been developed, contributing to the understanding of coral from molecular to ecosystem levels and the links between corals with other species and ecosystems. Molecular genetics enables us to comprehend the molecular information of corals and the relevant aspects such as identification of cryptic species and microbes, determination of relationships among populations and species, and characterization of reproductive and dispersal patterns, mechanisms of speciation, evolutionary relationships, etc. (Knowlton and Leray 2015). The advancement of coral genes may also provide understandings of species-specific adaptations (Cleves et al. 2020). The knowledge on coral biology serves as key information for coral reef conservation and management for sustainable utilization and the enhancement of coral resilience and recovery during climate change.

Climate change causes various impacts on coral reefs, particularly anomaly elevated seawater temperature, resulting in coral degradation in many reefs worldwide. Coral recovery and resilience have been discussed with the hope of helping corals survive after experiencing thermal stress as well as strengthening them to be able to cope with disturbances. In this matter, coral biology is highly significant to enhance coral recovery and resilience. Knowledge of a symbiont-host relationship, bleaching mechanism, and the relationship with the environment helps determine the impact severity and recovery ability. Each ecosystem has a different buffering capacity to disturbances. It is generally controlled by genetic variability, species diversity, functional groups of species, and habitat variability (Chapin et al. 2000). Such biological information should be incorporated into resilience-based management as ecological aspects to elevate tolerance and recovery and facilitate coral adaptation (McLeod et al. 2019). The concept of coral reef refugia has been proposed to protect corals and other species under climate change, particularly thermal stress and acidification. Some reefs showed fewer impacts of climate change than others. They could potentially be a refuge for corals and other marine species. Some criteria have been proposed to assess the capacity of refugia, including long-term buffering, protection ability from climate-related stressors, accessibility, microclimatic heterogeneity, size, and exposure to non-climate-related disturbances (Kavousi and Keppel 2017).

Coral restoration is a human effort aiming to rebuild and enhance coral reef health and biodiversity in response to the degradation of coral reefs. Coral restoration projects have been extensively found worldwide using different restoration techniques (both sexual and asexual) applied. However, most coral restoration projects revealed low survivorship of colonies, fragments, or sexual propagules (Omori 2019). The advancement of coral biology may help increase the success of coral restoration. Nowadays, molecular tools have been developed; thus, population genetic information of corals has been applied for coral restoration to maintain genetic diversity and to enhance reef resilience to future disturbances (Omori 2019; Boström-Einarsson et al. 2020). It is reported that poor design of restoration projects, i.e., lack of experimental controls and inappropriate reference systems, was one of the causes of failures of coral restoration projects worldwide (Boström-Einarsson et al. 2020). Thus, it is important that a review of advanced existing techniques and relevant information should be incorporated into the planning and decision-making process to ensure that project objectives and methodologies are properly designed and selected.

The advancement of coral biology serves as valuable information for planning and decision-making for coral reef management and governance in which many stakeholders (government, private sector, nongovernment organizations (NGOs), communities, etc.) are involved. In addition, systemic social science and the understandings of local context are also needed (Aswani et al. 2015). However, difficulties in knowledge exchange and communication between scientists and other stakeholders are generally found, making it difficult to transfer research into practical implementation (Selmoni et al. 2020). Information access and effective communication play a vital role in the reef management process, enhancing the engagement of local people. Content extracted from original research should be prepared to be appropriate and understandable for general people. Educators, community leaders, and volunteers can be mediums for knowledge transfer. In some areas, community leaders become a "bridge" to transfer global science for local people to build up their awareness on coral reefs (Trialfhianty and Suadi 2017). Scientific information on coral reefs is also essential for designing a marine protected area (MPA). The MPA is generally established based on the best readily available science. Scientists are engaged with other stakeholders throughout the planning process (Saarma et al. 2013) to provide consultation and relevant information such as coral biology, population dynamics, community ecology, oceanography, etc. Furthermore, the information on ecological connectivity can indicate the locations/boundaries that are ecologically important, and it also helps the design of MPA (Balbar and Metaxas 2019).

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4 Reef Ecology in the Western Pacific for Adaptation to Global Change

Makamas Sutthacheep, Thamasak Yeemin, and Porfirio M. Aliño

Abstract

Coral reefs are critically important to the economic development of most tropical countries. However, they have faced multi-stressors from natural and anthropogenic disturbances, particularly from coastal development, tourism, overfishing, and coral bleaching. Consequently, the loss of vulnerable species from coral communities is occurring at an accelerating rate. Many coral species are particularly at risk. Coral reef recovery following severe disturbances depends on several complicated factors, including resistance and tolerance to stresses, recruitment rate, reef connectivity, and local stressors. Maintaining reef framework is also very important, particularly bioerosion rate at a degraded reef. As global climate change potentially causes more frequent and severe coral bleaching events, identifying and conserving coral reef refugia is critically important. Most coral reefs are in a type of marine protected areas that intensively require scientific data for management. The achievements of passive and active coral reef restoration projects in the Western Pacific are necessarily considered for the improvement of coral reef management plans. In this chapter, we synthesize important information on coral reef biodiversity decline and extinction risk; coral reef recovery after disturbances; coral reef resilience; coral reef connectivity; coral reef bioerosion; coral reef refugia under global change; marine protected area networks; and passive and active restoration of degraded coral reefs.

Keywords

Coral ecology · Biodiversity · Extinction risk · Recovery · Resilience · Connectivity · Bioerosion · Refugia · Climate change · Marine protected area · Restoration

4.1 Introduction

The ecological and socioeconomic significance of coral reefs has stimulated marine researchers and conservationists around the world to deepen the understandings of the coral reefs in various aspects. They are recognized as the most biologically diverse habitat among marine ecosystems and the ancient structure created by living organisms (Carpenter et al. 2008; Budd and Pandolfi 2010). Coral reefs provide significant ecosystem services to human societies in different forms, for example, source of food, structural materials, and biochemicals; job and revenue from marine tourism; environmental regulation such as coastal protection, nutrient cycling, and carbon sequestration; and so forth (Souter and Lindén 2000). Yet, coral reefs have been affected by both natural and anthropogenic disturbances with different types, intensities, and frequencies. Many recent studies show major threats to coral reefs, including global warming, ocean acidification, overfishing, coastal development, land-based and marine-based pollution, and unmanaged tourism (Wilkinson 1999; Wear 2016). Such threats, particularly anthropogenic ones, have significant impacts on the structures and function of coral reefs, affecting biodiversity and quality of ecosystem services provided by the coral reefs at both local and global scales. Consequently, the livelihoods and well-being of the people who depend on coral reefs are inevitably degraded (Cinner et al. 2016; Edmunds 2017). Many studies illustrate that human disturbance and climate change can cause some ecological and physiological changes in corals (Hoegh-Guldberg et al. 2007, 2017; Baker et al. 2008). Adaptation and acclimation mechanisms are needed for coral reefs around the world to be able to survive in a global change

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where natural and anthropogenic disturbances, particularly the climate change impacts, are increasing (Hoegh-Guldberg et al. 2014). Coral reef scientists, managers, practitioners, and policy makers worldwide have been questioning on how coral reefs and their associated biodiversity are viable in the future. The emerging reef studies in various aspects have elevated our understandings that coral reef ecosystems may potentially adapt or acclimate to environmental changes (Camp et al. 2017). In this chapter, we review and synthesize existing and most recent knowledge on reef ecology in the Western Pacific for adaptation to global change. We summarize the research results on coral reef biodiversity decline and extinction risk; coral reef recovery after disturbances; coral reef resilience; coral reef connectivity; coral reef bioerosion; coral reef refugia under global change; marine protected area networks; and passive and active restoration of degraded coral reefs.

4.2 Coral Reef Biodiversity Decline and Extinction Risk

4.2.1 Coral Reef Biodiversity Loss

Coral reefs, a highly diverse ecosystem providing marine products and services in tropical countries, have been increasingly disturbed by natural and human activities (Graham et al. 2015; Hughes et al. 2017a, b; Brandl et al. 2019). Negative impacts generated by local and global stressors must be minimized in order to maintain their functions and services (Odum and Odum 1955). Such stressors that are harmful to coral reefs include coastal development, land-based pollution, marine-based pollution, unmanaged tourism, overfishing, destructive fishing, elevated seawater temperature, and ocean acidification (Burke et al. 2011; Bruno et al. 2019).

Ecological processes and functions are highly related to the ecological structure, particularly species composition and its interactions among biotic components and abiotic environment. Biodiversity also influences the rates of production, consumption, or decomposition, shaping the quality of biodiversity and ecosystem functioning (Hooper et al. 2012; Gamfeldt et al. 2015; Duffy et al. 2017). The ecosystem functioning of coral reefs relies on the species richness and the ecological roles and contributions of those species to the coral reef ecosystem (McWilliam et al. 2018; Clements and Hay 2019; Lefcheck et al. 2019; Brandl et al. 2019). The ecosystem functioning consists of several processes such as calcium carbonate dynamics, herbivore-algae interactions, predator-prey interactions, and nutrient cycling, resulting in the gain and loss of primary habitat, biomass production, energy transfer through trophic levels, and nutrient uptake and release. A number of researches regarding the coral reef ecosystem functioning are focused on herbivory, followed by primary and secondary production (Brandl et al. 2019).

The South China Sea is a part of the Indo-Pacific region and has a large marine area of more than 3 million km^2 in which ten Asian countries and numerous small islands are located (Huang et al. 2015). Coral reefs of scleractinian corals are generally found across the South China Sea, particularly in Southeast Asia. Approximately 20% of the reefs in Southeast Asia are highly diverse, having more than half of its coral species. At least 50 locations of coral reefs are found with the species richness ranging from 12 to 351. Coral reefs in Nha Trang (Vietnam) and El Nido (Palawan) have been recognized as one of the highly diverse reefs in this region (UNEP 2004). The South China Sea is connected to the Coral Triangle, one of the global marine biodiversity regions. Even though the coral reefs in the South China Sea are less than 17% compared to those in the Coral Triangle, they are comparable in terms of biodiversity. According to the existing dataset on comprehensive species distribution in the South China Sea, as many as 571 known species of scleractinian corals are found. Reef compositions in most areas are different from one another, and they are influenced by latitude rather than longitude (Huang et al. 2015).

Coral bleaching events can cause coral mortality in many reef areas worldwide. It may lead to the biodiversity loss of corals as well as other reef-associated organisms, i.e., reef fish diversity (Pratchett et al. 2011). For example, the 2010 coral bleaching event caused extensive coral bleaching and mortality across Thai waters affecting various coral species, particularly *Acropora* spp. A long-term decline in *Acropora* species was observed at Kut Island, located in the eastern part of the Gulf of Thailand. The live cover of *Acropora*, observed before the 2010 bleaching event, was very low with the average live cover of 0.35–1.46% because of a result of the previous 1998 massive coral bleaching event. Later, the 2010 bleaching event sharply decreased the live cover to 0.1%. Juvenile *Acropora* colonies were also impacted from the bleaching event showing extremely low densities of 0.01–0.03 m^{-2}, and no recruitment was observed for up to nearly 2 years. Importantly, several *Acropora* species that were previously found at Kut Island are currently risky for local extinction leading to the loss of biodiversity in this area (Yeemin et al. 2009, 2013a).

4.2.2 Extinction Risk of Corals

The decline and deterioration of coral reef ecosystems have been globally observed, stimulating a global concern on coral extinction. Regarding that, the Red List Categories and Criteria have been developed by the International Union for Conservation of Nature (IUCN), serving as a guideline for setting priority for biodiversity conservation. It has been globally applied to help identify the extinction risk of reef-building coral species, which is based on the reduction of population size and geographic range information (Carpenter et al. 2008). The IUCN Red List Categories has nine tiers, including "Not Evaluate" (NE), "Data Deficient" (DD), "Least Concern" (LC), "Near Threatened" (NT), "Critically Endangered" (CR), "Endangered" (EN), "Vulnerable" (VU), "Extinct in the Wild" (EW), and "Extinct" (EX). "Critically Endangered" (CR), "Endangered" (EN), and "Vulnerable" (VU) are included in the "Threatened" categories (IUCN 2012). Corals have evolved and existed on the earth for a long time. Scientists suggest that some widespread coral species may not be necessarily listed for extinction. Yet, studies of the fossil record reveal mass coral extinctions occurred in ancient time (Veron 2000, 2008), reflecting that there were unsuitable conditions that caused a drastic impact on the viability of coral populations. Although as many as 45% of coral species were extinct during Cretaceous-Tertiary boundary (66 million years), considered as the last major extinction, the extinction of zooxanthellate corals was greater than that of azooxanthellate corals (Kiessling and Baron-Szabo 2004). Coral species with survival traits (cosmopolitan distributions; non-symbiotic, solitary, or small colonies; and coral bleaching-resistant) tend to have stable populations; otherwise, the populations have less abundance and diversity. This reveals that some corals have a mechanism enabling them to survive after the major mass extinction. As mentioned, some corals with the survival traits might survive during the Anthropocene extinction (Dishon et al. 2020).

Coral reefs around the world have been deteriorating, and the population of some coral species continues to decline. The assessment of the global conservation status of corals using the IUCN Red List Criteria is vital to understand whether the present environmental conditions may accelerate the extinction of corals (Aronson and Precht 2001; Aronson et al. 2002). The extinction status of about 845 zooxanthellate reef-building coral species, including scleractinian corals, reef-building octocorals, and hydrocorals (families Helioporidae, Tubiporidae, and Milleporidae), was assessed by using the IUCN Red List Criteria. The conservation status of 704 species was successfully established, while 141 coral species were excluded from the assessment due to information insufficiency, of which about 33% (231 species) are identified in the categories of extinction risk. Almost 50% of coral species in the families Euphylliidae, Dendrophylliidae, and Acroporidae and 40% for the families Meandrinidae and Oculinidae are listed in a "Threatened" category. The blue coral *Heliopora coerulea*, the member of the ancient family Helioporidae, is also in "Vulnerable" category. The coral species in the families Caryophyllidae, Astrocoeniidae, Merulinidae, and Fungiidae exhibit the lowest proportions of "Threatened" species. None of the coral species inhabiting in deeper areas and lower reef slopes are listed in "Threatened" categories. In terms of the vulnerability to impacts, about 40% of the coral species are primarily reef-restricted, shallow water corals (<20 m depth). They are more vulnerable to anthropogenic disturbances compared to the coral species (60%) inhabiting the deeper reef areas or outside reef areas (Carpenter et al. 2008).

As many as 303 coral species are highly vulnerable to thermal stress leading to coral bleaching and mortality. However, only 102 species of them have a relatively high growth rate, and their population can be recovered within a few years after bleaching (Hughes et al. 2003). Half of the corals that are vulnerable to thermal stress, mainly Acroporidae, are also susceptible to several ecological stresses, i.e., diseases and predation from the crown-of-thorns starfish, *Acanthaster planci*. Although acroporid corals are generally abundant, the proportion of the threatened coral species is relatively high. Only eight species, most are in genera *Favia* and *Porites*, are relatively resistant to coral bleaching.

Globally, an increase in the extinction risk of corals has been reported over the past decades. The many coral reefs in the Indian Ocean had the most severe impacts from the 1998 mass coral bleaching event, deteriorating many shallow coral reefs such as degradation of reef structures, cascading trophic and ecological effects, a decline in fish populations, etc. (Graham et al. 2006). In the Coral Triangle, one of the global marine biodiversity hotspots including Indonesia, Malaysia, Papua New Guinea, the Philippines, the Solomon Islands, and Timor-Leste (Veron 2000), the proportions of "Vulnerable" and "Near Threatened" coral species are quite high. Many reefs in this region are impacted by a combination of anthropogenic disturbances and the effects of climate change. In Oceania, the coral reefs have the lowest proportion of "Threatened" species. The coral reefs in Hawaii have less impact from coral bleaching or diseases (Jokiel and Brown 2004; Friedlander et al. 2008; Aeby 2006; Kenyon et al. 2006), but several rare endemic species might be vulnerable to future threats (Jokiel and Brown 2004). Several studies reported that massive coral bleaching is one of the significant causes triggering loss of coral biodiversity and extinction risk. Adaptation and acclimation are highly needed to make them resilient for future disturbances; otherwise, the coral reefs will continue to decline, degrading their structure, functions, and ecosystem services. Furthermore, such coral degradation would disrupt inter-ecosystem linkage and lead to global biodiversity loss.

Conservation priorities, which are important to help prevent biodiversity loss of coral species, should consider both the contribution of coral species to evolutionary diversity and their risk of extinction. The phylogenetic study of corals is useful to understand how coral species contribute to evolutionary diversity. Huang (2012) constructed the phylogenetic tree of 1296 species of scleractinian corals and identified the most endangered lineages using a combination of phylogenetic distinctiveness and extinction risk. The phylogeny-associated patterns illustrate that no clear cluster of the corals with elevated extinction risk was found on the tree, but the clusters of the coral species that are susceptible, resistant, or resilient to impacts, particularly bleaching and disease, became clearer. The author emphasized that the preservation of these coral lineages should be integrated with extinction risk to conserve evolutionary diversity. Huang et al. (2016) also estimated the changes in species and evolutionary diversity during projected anthropogenic extinctions using the species information and phylogenetic diversity among the 571 reef coral species collected from 16 reefs in the South China Sea. The differences in richness, rarity, and phylogenetic diversity are found among the coral reefs. Species-rich areas (e.g., West Malaysia and the Philippines) have relative rarity and threat levels, but the reefs that have less species richness (e.g., northern Vietnam and the Paracel Islands) seem to face the loss of disproportionately large amounts of phylogenetic diversity. The information on species diversity alone is not enough for determining extinction risk. Importantly, the information of various biodiversity components and phylogenetic diversity of each coral reef is important for planning and prioritizing the most urgent reefs to be managed, supporting the management of marine protected areas.

Quantitative data on coral species population is generally required for assessing the extinction risk of coral species. However, in a sparse data situation, expert opinion regarding coral species, abundance, distribution, and threats as well as other relevant existing knowledge are commonly applied for the assessments. Species traits can be generally used to identify extinction risk because of their high correlation between them. However, life history traits (such as stress tolerance, fecundity, and habitat specialization) and the IUCN conservation status are not significantly correlated. This is because (1) the traits recognized as significant predictors for other taxa are not suitable for assessing corals or (2) the assigned conservation status may not provide enough accuracy of extinction risk (Bridge et al. 2020). For a global assessment, the authors also recommended that the conservation status for most coral species should be assigned as “Data Deficient” (DD). In addition, the assessment of the status and trends of coral populations seem to be more reliable at smaller scales (Bridge et al. 2020).

4.3 Coral Reef Recovery After Disturbances

4.3.1 Disturbance Types and Impacts

Disturbance and recovery become the significant aspects that have been applied in community ecology and management of coral reefs to understand the origin and maintenance of ecological balance in communities (Miller 2015). Disturbance refers to an event or change in environmental conditions that cause ecological change altering the physical structure or biotic or abiotic components in an ecosystem. Disturbance damages individuals or populations that may enable new individuals or populations to settle (Sousa 1984). The impacts resulting from a disturbance are influenced by the types of disturbances and the previous experience of the present community (Hughes and Connell 1999; Mumby et al. 2011). In addition, the impacts also vary on different species and individuals, depending on their tolerance which is linked to their physiological adaptation and evolution. At a community level, changes in species composition may enhance community tolerance. Changing the environment, caused by natural and anthropogenic disturbances, e.g., climate change, may stimulate the shifts in species and community. Like other regions of the world, anthropogenic disturbances on the coral reefs in the Western Pacific include physical destruction from tourism, fisheries, pollution from tourism, industry, agriculture, mining, mariculture, sedimentation, eutrophication, coastal development, and so forth. The impacts are also synergized by natural disturbances, particularly elevated seawater temperature and ocean acidification (Morrison and Aalbersberg 2006; Yeemin et al. 2011). The disturbances on coral reefs can be chronic or acute. Chronic disturbances include water quality degradation, fishing and trophic changes, and ocean acidification, while acute disturbances include hurricanes, tropical storms, severe coral bleaching events, and disease or predator outbreaks (Connell 1997).

Land-based pollution is mainly generated by human activities from various sources, i.e., communities, tourism, industries, agriculture, aquaculture, coastal development, mining, etc., driving into the sea through sewage discharge and runoff. It contains different forms of pollutants in general, i.e., sewage, solid waste, nutrients, heavy metals, microbes, sediment, pharmaceuticals, persistent organic substances, oils, etc. (UNEP 2007; Vo et al. 2013). Land-based pollutants degrade seawater quality leading to reef degradation, particularly in nearshore coral reefs, whereas the impacts in offshore reefs are difficult to observe due to the combined impacts of other factors (Fabricius 2005). The degraded seawater quality may affect coral health, which further leads to disease vulnerability (Aeby et al. 2011; Haapkylä et al. 2011; Samsuvan et al. 2019). It can alter the reproductive system of corals since poor water quality causes a direct stress on both planulae, juvenile, and adult coral colonies (Miller 2015). Heavy sedimentation is caused by inappropriate land use, mangrove deforestation, and unmanaged coastal development in many countries, affecting various coral species (McKergow et al. 2005; Yeemin et al. 2013b). The level of water quality is directly related to human population densities. The coral reefs near the areas with dense populations or dense tourists are likely to expose more pollution unless environmental management systems are well maintained and operated.

The impacts of fishing on coral reef ecosystems have been documented, mostly caused by destructive fishing practices and overfishing. Some fishing practices, such as blast fishing, cyanide fishing, and fish trap fisheries, may generate some physical damages on coral reefs (Fox and Caldwell 2006; Suebpala et al. 2021). Overfishing may lead to a decline in fish population and diversity and indirectly affect coral reef ecosystems. It reduces species diversity and leads to local extinctions, both target species and the bycatch species (Roberts 1995). Overfishing of grazers, particularly herbivorous fishes, causes the imbalance of algae in coral reefs, making them more susceptible to algal-dominated reefs (Jackson et al. 2001; Hughes et al. 2007, Shantz et al. 2020). Increased algal biomass can have effects on coral growth and tissue mortality (Lirman 2001; Bulleri et al. 2013) as well as reduced fecundity and reduced egg sizes (Monteil et al. 2020). Macroalgae can generate some dissolved organic carbon (DOC), stimulating microbial activity living on live coral surfaces and then causing tissue mortality. Since the higher level of DOC can foster the shift from coral to macroalgal dominance, the level of DOC is recommended to include this parameter in long-term coral reef monitoring (Kline et al. 2006; Smith et al. 2006). The study using a dynamic food web model on the Raja Ampat Archipelago, Indonesia, explains that coral-algal phase shifts can change in fish communities and reduce fisheries productivity (Ainsworth and Mumby 2015). Several studies reveal the density of coral-feeding butterflyfishes is positively correlated with coral disease prevalence due to the transmission through feeding. However, the overall coral disease prevalence in marine protected areas, where fish diversity is relatively high, is low, compared with unprotected areas suggesting that fish diversity may help diminish coral diseases (Raymundo et al. 2009).

Ocean acidification has been arisen due to the concern of the climate change impacts. It may affect many marine species, particularly calcifying species such as corals and bivalves, in various ways such as reduction of calcification, dissolution of calcium carbonate structure, the interruption of physiological processes (e.g., reproduction and nutrition), and behavioral change of marine organisms (Nakamura et al. 2011; Allemand and Osborn 2019). Corals, one of the calcifying organisms, are vulnerable to ocean acidification. The study conducted in the coral reefs in Papua New Guinea shows that massive corals are more tolerant to ocean acidification (up to the pH of 7.7) than branching corals which are very susceptible. The reef morphology can be directly disturbed, then leading to a decrease in coral biodiversity and an algal-coral phase shift (Fabricius et al. 2011). Some studies illustrate that ocean acidification does not affect the growth of some resistant species, but it makes the corals to be more porous, increasing the fragility of coral reefs (Tambutté et al. 2015; Rippe et al. 2018). The long-term effects of ocean acidification synergizing with the impacts of coral bleaching may weaken the resilience of coral reef ecosystems (Allemand and Osborn 2019).

Coral reefs can be degraded by short-term or acute disturbances, including physical disturbances, thermal stress, diseases, and predator outbreaks. Tropical storms and cyclones are the major physical disturbance, resulting in coral mortality, reef destruction, and substrate modification. Other natural disasters and accidents like tsunamis, earthquakes, and ship groundings can also cause physical disturbances. The effects of such physical disturbances can cause serious damages depending on various factors such as storm severity, depth, habitat types, and the history of coral reefs experiencing storms. Hughes and Connell (1999) conducted a study at Heron Island in Australia and in the north coast of Jamaica, providing a clear illustration in which the impacts of repeated storms depend on the habitat characteristics; the exposed areas seem to have a greater amount of impact than protected areas. Furthermore, the impacts also depend on the exposure of previous perturbations. Coral morphology is an important factor in the impact severity. Coral species with tabular structure, particularly *Acropora* and *Pocillopora* corals, are the most vulnerable to storms, followed by bushy and encrusting structures, whereas massive corals have the least impacts of storms (Hughes and Connell 1999; Miller 2015). Multiple stressors, in that case, the recurrent hurricanes and human impacts, also cause crucial impacts on coral recruitment and growth, leading to changes in the dynamics of coral communities over longer time scales (Hughes and Connell 1999). However, such physical disturbances are generally patchily distributed (Connell et al. 1997).

Long-term monitoring of acute disturbances on the Great Barrier Reef, Australia, showed that the coral mortality during 1985–2012 was mainly induced by cyclones (1.63% of coral cover per year), followed by predation (1.42% per year) and coral bleaching (0.34% per year) (De'ath et al. 2012). Such physical disturbance may be associated with the occurrence of coral diseases and predation outbreaks (Knowlton et al. 1981; Bruckner and Bruckner 1997; Brandt et al. 2013), because a storm can potentially cause coral fragments, injury, and slowing coral recovery. Storms may disperse some benthic invertebrates, which are coral predators, leading to the outbreaks of coral predators (Miller 2015). Tropical storms in the south of the South China Sea and the Gulf of Thailand are relatively low compared to other regions. There were critical storms causing significant damages on coral reefs in this region, for example, a tropical storm, Pabuk, passed through this region in January 2019. Coral cover was clearly affected, decreasing the live coral cover from 47.9 ± 5.02% to 28.75 ±

3.9% and increasing the dead coral cover from 26.3 ± 3.8% to 65.09 ± 3.77%. The most impacts were observed on the corals, particularly *Acropora* and *Fungia*, at shallow areas (the depth of less than 3 m) where more than 60% of live coral covers were disappeared. However, coral community changes were not detected. Reviews of thermal stress derived mass coral bleaching and coral disease outbreaks are provided in Chap. 3 and other published papers (e.g., Brown 1997; Kushmaro et al. 1997; Antonius 1999; Yamashiro et al. 2000; Raymundo et al. 2003; Baker et al. 2008; Weil et al. 2012).

The outbreak of crown-of-thorns starfish (COTS; *Acanthaster planci*) is considered an acute disturbance in the Indo-Pacific region (Birkeland and Lucas 1990; De'ath and Moran 1998; Kayal et al. 2012; Yasuda 2018). COTS prefer to consume the tissues of acroporids and other tabular corals deteriorating coral reefs (Miller 2015). Generally, the consumption rate of COTS is greater than the recovery rate of corals. In the Great Barrier Reef, the total coral cover declines approximately 1.43% due to the COTS outbreaks (De'ath et al. 2012). The causes of the outbreak are still questionable, but scientists have hypothesized that COTS outbreaks might be induced by local environmental factors, particularly excessive nutrient loads resulting in high planktonic productivity and high larval recruitment (Birkeland 1982; Brodie et al. 2005; Fabricius et al. 2010). Reef fisheries are possibly linked with the COTS outbreak due to the removal of some predators that control the COTS' population dynamics in a coral reef ecosystem. Some observations conducted in the Great Barrier Reefs showed that the limit of fishing activities could lessen the occurrence of COTS outbreaks. The occurrence of the COTS outbreaks in the areas with fishing was 3.75 times higher than that in the area where fishing is prohibited. The fishes may not prey on the COTS directly, but those fishes may enhance the viability of some other organisms that prey on juvenile starfish (Sweatman 2008). The COTS outbreaks in Moorea, an island in French Polynesia, reduced the coral cover and further affected various marine species, particularly sessile organisms and coral-feeding fishes (Kayal et al. 2012). Two major COTS outbreaks were reported in Japan during 1969–1991 and 1995–2018. The secondary COTS outbreaks within Japan were possibly originated from the western Okinawa population. The outbreaks occurring in temperate regions may possibly from Amami population (Yasuda 2018).

Drupella snails are a small gastropod, generally found in the shallow waters across the Indo-Pacific region (Robertson 1970; Claremont et al. 2011). Since they feed on the living tissue of corals, the outbreaks of corallivorous *Drupella* snails can cause a widespread decline in live coral coverage reported in this region (Pratchett et al. 2014; Babcock et al. 2016). Several reports reflect the high positive correlation between the outbreaks of *Drupella* and coral mortality. For example, coral degradation in Japan was linked with the high density of *Drupella* of about 5.12 individuals m^{-2} (Moyer et al. 1982; Fujioka and Yamazato 1983; Ayling and Ayling 1987; Turner 1994; Antonius and Bernhard 1997; Shafir et al. 2008). A massive outbreak of *Drupella*, with its density of more than 200 individuals per a 30-cm-diameter circle, devastated multiple coral genera in the Red Sea. All of the coral colonies at the study site, a 150-m artificial limestone quay, were died (Shafir et al. 2008). Generally, a higher density of *Drupella* was observed in areas with higher coral cover. An observation in Ningaloo Reef, Western Australia, showed the lower density of *Drupella* (0.95 individuals m^{-2} of reef area) at the relatively low coral cover of 17.6 ± 13.7%, whereas the higher density (2.83 individuals m^{-2} of reef area) was found at the reef with the high coral cover (60%) (Bessey et al. 2018). The corallivorous *Drupella* snails also prey on free-living mushroom corals, according to Hoeksema et al. (2013) who conducted a study at Ko Tao, a touristic island in the western Gulf of Thailand. Coral communities in this area were impacted by the severe mass coral bleaching events in 2010 and 2011, resulting in the mortality of Acroporidae and Pocilloporidae corals, the most preferred prey species. Consequently, the dietary shift of *Drupella* snails was observed, tending to prey on other less-preferred species, i.e., Fungiid species (Hoeksema et al. 2013).

4.3.2 Coral Reef Recovery

Coral recovery potential depends on multiple factors, including disturbance characteristics (both natural and anthropogenic), reef characteristics, reef connectivity, and ecological characteristics as well as management interventions (Graham et al. 2011). The rate of coral reef recovery depends on the types of disturbances. Coral reefs with the physical damages caused by disturbances, such as storms or other activities removing corals or/and destroying reef structures, seem to have a lower recovery rate compared with those experiencing the disturbances that do not destroy coral skeleton, such as coral bleaching. Furthermore, coral reefs facing anthropogenic disturbances, particularly pollution and exploitation, may have a slower recovery (Sandin et al. 2008; Graham et al. 2011). High coral reef connectivity enhances the coral recovery process because the other reefs connected with the damaged reefs may help to restock the population of corals and other marine organisms (Graham et al. 2006; Jones et al. 2009). The ecological characteristics of reefs play an important role in promoting the ecological structure and function. The reefs with high functional diversity accelerate the recovery of disturbed reefs (Mumby et al. 2007; Burkepile and Hay 2008). Importantly, coral recovery can also be enhanced by management interventions through various strategies such as the designation of marine protected areas, reef restoration, reduction of human pressures, etc. (Graham et al. 2008; McClanahan 2008; Mumby and Harborne 2010; Sutthacheep et al. 2012).

The recovery of disturbed coral reefs is generally slow, and it relies on coral recruitment rather than coral growth (Connell et al. 1997). The recovery also depends on the impact severity of disturbances reducing the coral cover; for example, the reef with 10% reduced coral cover has the greater recovery than the reef with 20% reduced coral cover (Emslie et al. 2008). However, the recovery dynamics of coral cover is generally nonlinear, depending on several factors (Emslie et al. 2008). Little difference in coral recovery rates between biological and physical disturbances is reported. Biological disturbances, such as coral bleaching events, diseases, and COTS outbreaks, affect only coral tissue; on the other hand, physical disturbances, particularly tropical storm damage and destructive fishing practices, generate damages on both live coral cover and coral structures (Wilson et al. 2006). Some studies have revealed that the coral recovery rate after COTS outbreaks was higher because of the maintenance of reef structural complexity and the herbivorous fish population that promotes macroalgae herbivory in coral reefs (Graham et al. 2007, McClanahan 1999). There is high recovery rate of coral reefs after COTS outbreak since the COTS do not destroy the structural integrity of coral reefs (Colgan 1987). Although the biological disturbances may spatially generate extensive disturbances, a large area of undamaged reefs still exists to enhance coral recovery (Bythell et al. 2000; Halford et al. 2004). Some dead coral cover that is a stable substrate can also serve as an available substrate for coral recruitment (Bellwood et al. 2004).

Coral covers typically among reef zones, reef crests, and slopes have higher coral cover than reef flats; however, the recovery rates among reef zones might not be different (Connell et al. 1997). The variability of recovery potential can be different by reef types. Fringing reefs have a lower level of recovery potential than atolls and barrier reefs since fringing reefs have greater exposure to various pressures from the mainland. At a regional scale, the fastest and slowest recoveries of coral reefs have been reported in the western Pacific and the eastern Pacific, respectively. Coral recovery in the Indian Ocean seems to be faster than that in the eastern Pacific. Such recovery potentials are influenced by the functional diversity of corals and fish. Among these regions, the western Pacific exhibits the highest functional diversity, followed by the Indian Ocean, while the Caribbean and eastern Pacific remain low, reflecting that high diversity helps promote ecosystem functioning and recovery potential (Bellwood et al. 2004; Hooper et al. 2005; Allen 2008). Coral reproduction can also influence its recovery potential in an area. The dispersal of brooding corals is relatively limited, but spawning corals can disperse coral larvae with a longer distance to other reefs (Jones et al. 2009). In isolated reefs, local recruitment rates are typically high, but the recovery rate may be low if their local parent colonies or associated organisms are disappeared, making them vulnerable to local extinction (Ayre and Hughes 2004; Cowen et al. 2006; Graham et al. 2006). Some semi-isolated reefs can be quickly recovered from acute disturbances if they have less exposure to chronic disturbances and have enough local brood stock to restore coral population (Connell 1997; Graham et al. 2008; Sheppard et al. 2008; Smith et al. 2008; Halford and Caley 2009; Sutthacheep et al. 2014). The establishment of protected areas helps increase the coral cover, particularly corals that are vulnerable to disturbances. The declines in coral cover in protected areas were higher than those in the adjacent reefs where fishing activities that are found were reported. It is because the marine protected areas have higher values of starting coral cover than the adjacent reefs (Graham et al. 2008; McClanahan 2008; Darling et al. 2010; Selig and Bruno 2010).

Structural complexity is the key characteristic of coral reefs fostering the recovery of corals and fish communities as documented in many reef sites, for example, the Great Barrier Reef (Emslie et al. 2008) and Guam (Colgan 1987). Destruction of the coral reef structure can reduce the number of crevices or holes affecting the survival of newly coral recruits (Connell et al. 1997). The coral rubber can be generated from the destruction, limiting the settlement of new coral recruits and juvenile colonies and slowing down a reef recovery (Victor 2008). Reef fish, particularly herbivorous fishes, are essential in recovery dynamics by regulating benthic algae biomass and fostering coral recovery (Andres and Witman 1995; Bellwood et al. 2004; Mumby and Harborne 2010). The high diversity of reef fishes may also enhance the functioning ecosystem (Bellwood et al. 2004; Burkepile and Hay 2008; Palumbi et al. 2008). The larger size structure of the coral community may have more chances to increase the recovery potential for corals after facing disturbances since the remaining live corals can be a major contributor to the recovery processes, especially local coral recruitment (Hughes and Tanner 2000; Done et al. 2010). An acute and widespread heat stress event that hit the Great Barrier Reef (GBR), Australia, in 2002 decreased the recovery rate of both Acroporidae and hard corals, and the recovery time was doubled to reach the modest level of recovery. Furthermore, the recovery times may be increasing for the reefs experiencing more frequent and intensive acute disturbances (Osborne et al. 2017). In Singapore, two-thirds of the coral reefs were bleached due to the 2010 bleaching event, but they were rapidly recovered. In terms of species composition, the coral community structure before and after the bleaching was not significantly different although the total cover decreased. The shallow coral communities in

Singapore illustrated their high resilience to acute thermal stress even though they have been exposing to local environmental stress such as high turbid environments (Guest et al. 2016).

Overgrowth of macroalgae can lead to the loss of coral cover, reducing biodiversity and deterioration of habitat complexity. A study in the Red Sea reported that crustose coralline algae and other calcifying organisms were recognized as an important colonizer, accumulating inorganic carbon in that healthy reef area. However, turf algae mostly colonized on the substrates in degraded reefs, decreasing the accumulation of inorganic carbon by 178%, and the coral recruitment was lowered by 50%. In this regard, the restocking of coral populations seems to be decreasing due to low recruitment and grazing pressure, affecting the potential for coral reef recovery (Roth et al. 2018). Robinson et al. (2019) studied a long-term recovery dynamic of coral reefs in Seychelles, illustrating that the coral covers in 12 coral reefs where more than 95% mortality was reported resulting from the 1998 bleaching event were fully recovered to pre-bleaching cover, of which 6 reefs with initially low coral cover (<25%) fully recovered (100% of the pre-bleaching cover) within 7–12 years and the coral cover increased by 132–305% after 16 years. However, other six reefs with initially high coral cover (20–60%) failed to fully recover and remained at 48–93% baseline cover; and they recovered within 17–29 years. The authors mentioned that the coral recovery rate depends on both abiotic and historical factors. High juvenile coral densities and low nitrogen levels facilitate coral recovery rates. The reefs that suffered from bleaching events can recover to a moderate level. However, repeatedly high coral mortality due to coral bleaching may limit coral recovery, transiting to non-coral-dominated reefs (Robinson et al. 2019).

4.4 Coral Reef Resilience

4.4.1 Ecological Resilience

Ecological resilience or ecosystem resilience concept refers to the ability of a system to experience changes but still maintain its structure and functions as well as the system's capability to adapt to changes (Holling et al. 1995; Gunderson 2000). The ecosystem resilience concept has been applied to determine the dynamics of complex adaptive ecosystems (Levin 1998), for example, coral reefs which are complex, adaptive, nonlinear dynamic, having multiple stable states (Hughes 1989, 1994; Done and Potts 1992; Knowlton 1992; Holling et al. 1995; Levin 1998). Coral reef resilience ability regulates the state or functions of coral reefs whether its locally stable equilibrium shifts into another stability domain (Holling 1986). The resilience capacity of coral reefs depends on various factors such as genetic variability, species diversity, functional groups of species, ecological interaction, and habitat variability (Naeem et al. 1994; Done et al. 1996; Chapin et al. 2000). Ecological resilience may also provide opportunities for ecosystems to reorganize, renew, and develop themselves after disturbance as well as to build an adaptive capacity to respond to future environmental changes (Gunderson 2000; Nyström and Folke 2001).

Ecological resilience is derived from species diversity and their interactions. An ecosystem in which dominant and minor species have overlapping functions may have a higher level of ecological resilience (Peterson et al. 1998; Walker et al. 1999). When experiencing any environmental changes or disturbances, the dominant species are generally impacted and depleted. Consequently, the ecosystem function tends to be maintained by some minor species that have a similar function of the dominant species. Thus, species diversity within functional groups is essential at all scales ranging from genes to biogeographic regions to elevate the capacity of coral reef resilience to cope with disturbances and changing environmental conditions (Nyström et al. 2000; Nyström and Folke 2001). Some coral species harbor multiple types or species of zooxanthellae. However, the composition of these symbiont communities depends on the environmental gradient and coral hosts that provide a suitable environment for those to live (Rowan and Knowlton 1995; Baker and Rowan 1997; Rowan et al. 1997). Ecological functions can still be maintained in the coral reefs with low diversity within functional groups, but facing additional or repeated disturbances may drive them to a critical threshold, leading to ecosystem shifts (Kinzie 1999; Nyström et al. 2000). Loss of ecological resilience facilitates the phase shifts in coral reef communities from coral-dominated into algae-dominated (Knowlton 1992; Hughes 1994). The coral-algal phase shifts can also be synergized by the declines of herbivorous fishes or other organisms that regulate macroalgae cover. Overgrowth of macroalgae inhibits coral recruitment, and the growth of juvenile corals destabilizes microbial communities and promotes disease outbreak (Carpenter and Edmunds 2006; Ledlie et al. 2007; Smith et al. 2006; Birrell et al. 2008a, b; Mumby and Steneck 2008; Ainsworth et al. 2010; Hughes et al. 2010).

Coral reefs worldwide have been deteriorated due to several stressors, particularly anthropogenic stressors. Yet, some ecological factors can limit the ability of coral reefs to experience disturbance as well as their recovery, including (a) lack of adaptive capacity to cope with many current disturbances; (b) anthropogenic disturbances affecting life history, reducing larval supply and recruitment; (c) the loss of few species may affect the entire functions of coral reefs because niche specialization or temporal and spatial segregation can make each species unique or narrow ecological redundancy; and

Table 4.1 Proposed indicators for assessing coral reef resilience

Semi-quantitative indicators	Quantitative indicators
Habitat environment – Physical site parameters – Substrate and reef morphology – Connectivity	–
Coral community – Population – Individual condition	– Cover, genera, size classes, recruitment – Bleaching, mortality, disease, threats
Interactions/responses – Benthic interactions – Coral interactions – Fish functional groups	– Algae community, competition – Competition – Herbivore functional groups
Anthropogenic influences	–
Climate/thermal stress – Cooling and flushing – Shading and screening – Extreme conditions and acclimatization	–

Source: Modified from Obura and Grimsdith (2009)

(d) feedback loops and extinction vortices that remain or accelerate degradation may exist after the disturbance (Mora et al. 2016). It is important that the mechanisms that corals respond to thermal stress should be well understood to elevate coral reef resilience on various factors, including microbial composition, *Symbiodinium* clade, *Symbiodinium* adaptation, coral morphology, tissue thickness, heterotrophic feeding, upwelling reefs, turbid-zone reefs, remote reefs, high-latitude populations, heat-selected populations, and temporary refugia. Coral resilience can be considered at different spatial scales ranging from the microbiome, coral colony, and archipelago reef to biogeographic region. Some factors can be possibly used within a certain event, while others could be applied for a longer time scale (Roche et al. 2018).

4.4.2 Coral Reef Resilience Indicators

Obura and Grimsdith (2009) developed a protocol for assessing reef resilience to coral bleaching and thermal stress, consisting of semi-quantitative indicators and quantitative samples (Table 4.1). Semi-quantitative assessment includes key groups of indicators regarding habitat and environment, coral community, interaction/responses, anthropogenic influence, and climate/thermal stress. Quantitative information is useful, enabling the more in-depth assessment of coral status and health.

McClanahan et al. (2012) identified 11 key resilience indicators affecting the ability of coral reefs to resist and recover from climate disturbance based on expert opinion and existing scientific evidence. The key indicators include resistant coral species, temperature variability, pollution or nutrients, sedimentation, coral diversity, herbivore biomass, physical human impacts, coral disease, macroalgae, recruitment, and fishing pressure. Of those, resistant coral species and temperature variability were recognized to provide the greatest resistance to climate change. Coral recruitment and macroalgae abundance were the greatest influencing factors on coral recovery. The authors also mentioned that few strong variables are still useful to determine the ecosystem dynamics despite high ecological complexity (McClanahan et al. 2012). Coral reef resilience indicators and criteria have been developed with different purposes and applied many areas, for example, Maynard et al. (2015) applied indicators of resilience process in combination with the data on anthropogenic stress and larval connectivity to prioritize some reef sites in the Commonwealth of the Northern Mariana Islands, in terms of conservation, reduction of land-based pollution, and fishery management and enforcement. They found the high spatial variation in relative resilience potential. The reef sites near Saipan exhibited high resilience, whereas the sites with low resilience were found near Rota.

The recent studies suggest that resilience indicators and anthropogenic indicators should be considered for resilience assessment. Six essential resilience indicators should be incorporated, including resistant coral species, coral diversity, herbivore, biomass, coral disease, macroalgae cover, and recruitment, while other indicators (temperature variability, herbivore diversity, habitat complexity, mature colonies, light, coral size-class distribution, substrate suitability) should be considered if they are important for local context or assessment purpose. Importantly, the key anthropogenic stressors, i.e., nutrients (pollution), sedimentation, physical human impacts, and fishing pressure, should not be negligent (Maynard et al. 2017). For some developing countries, particularly those in Southeast Asia, where line-intercept transect (LIT) has been used for coral reefs for a long time, such information can be incorporated into the coral reef resilience assessment. The modified resilience index was developed by Orwin and Wardle (2004), suggesting that six indicators can be applied in the resilience assessment, including coral functional group, coral habitat quality, sand-silt cover, coral cover, coral small-size number, and algae other-fauna cover. These indexes are useful to assess and compare the level of coral reef resilience among reef sites and times (Bachtiar et al. 2019).

4.4.3 Coral Reef Resilience Assessment

As mentioned earlier, coral reef resilience reflects the ability of corals to acclimatize and resist disturbances, particularly bleaching events, illustrated by several studies. Coral reefs in Kāne'ohe Bay, Hawaii, have experienced two severe bleaching events and the increase of 0.96 °C seawater temperature from 2000 to 2018. Interestingly, no significant changes in coral cover and species composition of dominant corals, e.g., *Porites compressa* and *Montipora capitata*, in the fringing reefs were detected. Two coral species *Pocillopora meandrina* and *Porites lobata* were lost, while a new species, *Leptastrea purpurea*, was found, reflecting that the shift in coral species composition may occur in this area. The overall algal cover increased during that time, but two species, *Gracilaria salicornia* and *Kappaphycus alvarezii*, previously found in the early observation were disappeared in 2018. Likewise, the cover of *Dictyosphaeria* sp., which was previously a dominant species, decreased over time (Barnhill and Bahr 2019). The study reflects that coral reefs in Hawaii are dynamic and they are able to acclimatize to bleaching events.

Fringing reefs along the coast of Nanwan, southern Taiwan, have been experienced with fluctuating thermal environment influenced by various factors, e.g., Kuroshio Current, the monsoon-induced South China Sea Surface Current, a tide-induced upwelling, and the cooling water released from a nuclear power plant. The coral communities in the areas seem to be having more thermal-resistant capability, particularly those inhabiting nearby a nuclear power plant in the west Nanwan. The temporal variation of live coral cover in these areas was due to typhoons and corals that occurred during 1986 and 2019, while recovery of such live coral cover has been observed with a spatial heterogeneity pattern. The spatial variation of coral reef resilience is also detected among subregions in Kenting National Park. Thermally tolerant zooxanthellae *Durusdinium* spp. have been dominantly found in thermal-resistant corals. Besides, the thermal-resistant corals can tolerate bleaching by re-shuffling their symbiont communities to be viable in seawater temperature changes. Coral reefs surviving in unique environmental conditions and having special ecological characteristics are possibly resilient to bleaching, and those should be conserved to be a thermal refugium (Keshavmurthy et al. 2019).

The coral reef resilience assessment framework has been applied to coral reefs across the world to support resilience-based coral reef management. In Indonesia, the assessment was conducted in four major reefs in Wakatobi islands (i.e., Wangi Wangi, Kaledupa, Tomia, and Binongko) with several stages of implementation, i.e., indicator selection, data collection, data analyses, and management target identification. The reefs in the group with high relative resilience are characterized by high values of coral bleaching resistance, herbivore biomass, coral cover, and coral diversity. The reefs membered in the group with mid-high relative resilience are contributed by coral recruitment and coral diversity. The group with mid-low relative resilience is influenced by some indicators like coral disease and algal cover. The authors also mentioned that resilience assessment is helpful to prioritize reefs in various management actions, including conservation, fisheries management, bleaching monitoring, coral recovery and restoration, setting appropriate tourism development measures, and pollution reduction and prevention (Minsaris et al. 2019). In Vietnam, the concept of reef resilience has been applied to support adaptive management and rehabilitation of diverse and abundant coral reefs in Khanh Hoa Province, located in the western South China Sea. The resilience of 15 reef sites against elevated surface water temperature and the anthropogenic impact was assessed using various relevant factors, including coral covers, coral diversity, coral recruitment, substratum heterogeneity, depth, water exchange level, sediment deposit, and water temperature. Such parameters were considered together with coral susceptibility-related factors, including reef health, adaptability to environmental change, recruitment potential, and the influences of physical factors that help reduce bleaching severity and protect corals from bleaching. Based on the study, those observed reefs can be grouped into four categories with different levels of reef health and physical conditions, enabling such reefs to be managed with appropriate interventions (Vo et al. 2019).

Several studies of reef resilience to climate change in Thai waters reflect how reef resilience promotes coral recovery and sustainable coral reef utilization. Twenty sites in the Gulf of Thailand and the Andaman Sea were assessed approximately 2 years after they had experienced the 2010 severe bleaching event, considering the percentage of non-bleached coral colonies, the percentage of surviving coral colonies, and the density of juvenile corals. Spatial variation of coral reef resilience was detected among locations and major reef groups due to different community structures. A reef that has thermal-resistant dominant coral species tends to be resilient. Coral recruitment rates of most reefs in the Gulf of Thailand were considerably low compared to those in the Andaman Sea. However, the reef sites with the highest resilience were observed in the Inner Gulf of Thailand, while reef sites in the Andaman Sea exhibited the lowest resilience (Yeemin et al. 2013a; Sutthacheep et al. 2018a, b). Sutthacheep et al. (2019)

assessed the resilience potential of offshore (Ko Losin) and nearshore reef sites (Mu Ko Chumphon); both are located in the Gulf of Thailand. Live coral cover, hard substratum composition, and diversity and density of juvenile corals were used in the assessment, revealing that several reef sites at Ko Losin and Mu Ko Chumphon exhibited a high resilience potential to bleaching events and anthropogenic stressors influenced by high survival rates and higher percentages of live coral cover. The density of the juvenile corals, particularly for the *Acropora* communities, at most reef sites was not correlated to the availability of live coral cover of adult colonies in a reef. The authors suggested that Ko Losin should be designated as a marine protected area and Mu Ko Chumphon National Park should be properly managed in accordance with its management plans to support coral recovery and promote sustainable utilization of coral reefs.

Manikandan et al. (2017) compared the recovery and resilience of three reef sites in Palk Bay, India, by considering the recruitment pattern and survival of juvenile corals, available substrate, live coral cover, and herbivorous reef fish stock. The fishing pressures in Mandapam, Vedalai, and Pamban are severe, moderate, and low, respectively. Turf algal overgrowth affected live coral cover in Vedalai and Mandapam where a low density of herbivorous fishes was observed. The Pamban reef has a high diversity and density of juvenile corals, but the other sites remained low. It is because the other connected reefs supply coral larvae to the Pamban reef. This study illustrates that human activities, particularly reef fishing, can degrade live coral cover and consequently affect juvenile coral recruitment, especially in an isolated reef that has less connectivity to other reefs (Manikandan et al. 2017). The resilience of coral recruits in the Gulf of Mannar Marine Biosphere Reserve (GOMMBR), India, was mapped, using a wide range of resilience indicators, i.e., macroalgae, sedimentation, substratum, herbivore biomass, bleaching prevalence, coral diseases, temperature, photosynthetically active radiation, and depth. About 12 percent of all observed reef sites was identified as high resilience, 16 percent belonged to low resilience, and the remaining had medium resilience. Coral recruitment in these areas was mainly inhibited by some macroalgae such as *Caulerpa scalpelliformis*, *C. racemosa*, *Ulva reticulata*, *Turbinaria ornata*, *T. conoides*, *Chaetomorpha linum*, and *Kappaphycus alvarezii*. Additionally, sedimentation and temperature variability are also the factors contributing to the spatial variation of resilience (Machendiranathan et al. 2020).

Urbanization becomes an important consideration in reef resilience as it causes significant pressures on coral reefs. The magnitude of the pressures is increasing due to the urbanization occurring across the world, particularly in tropical and subtropical regions. Heery et al. (2018) illustrated how urbanization affects hard coral assemblages using the information of 11 cities in East and Southeast Asia, particularly Singapore, Jakarta, Hong Kong, and Okinawa. Urbanization influences coral reefs nearby in different ways, including (1) urban coral reefs are generally dominated by dome coral growth forms with low complexity; (2) there are variable city-specific inshore-offshore gradients of the severity of stressors; (3) there is a temporal decline due to acute impacts, but urban coral reefs are rapidly recovered, and colonization of urban infrastructure by hard corals; and (4) reef compression which refers to a decline in bathymetric range with poorer seawater quality, particularly turbidity. This reflects that the understandings of urban reef community dynamics are important for planning and the establishment of appropriate management actions for urban coral reef conservation (Heery et al. 2018).

4.4.4 Coral Reef Resilience-Based Management

Resilience-based management (RBM) has been introduced in coral reef management, focusing on the use of knowledge of existing and possible drivers that potentially influence the functions and structure of coral reef ecosystem, e.g., climate change, coral disease outbreaks, land-use change, coastal development, reef fisheries, etc. The RBM can be used to prioritize, plan, and implement management actions, achieving reef ecosystem sustainability and human well-being. The main goal of this approach is to strengthen the reef resilience, the ability of coral reefs to withstand and recover from disturbances, by prioritizing and implementing any actions to maintain ecological processes and to protect species that support coral reefs' resilience. Such actions vary over time and depending on global and local contexts, most of which focus on controlling and minimizing threats, for example, land-based and sea-based pollution, fishing activities, tourism, and coastal development. RBM should also foster the development of adaptive capacity and adaptation for society, for example, providing alternative livelihoods to those who mainly utilize coral reefs. Importantly, knowledge, both scientific and local knowledge, should be shared and exchanged among relevant sectors/institutions to increase societal capacity for supporting an ecosystem sustainability (Folke 2016; Mumby et al. 2014a, b).

Management objectives and actions might be different depending on the local context. However, baseline information (both existing and projected), stakeholder needs, and expected state of the coral reef ecosystem should be integrated into the management objectives (Anthony et al. 2015). The RBM enables proactive decision-making that concerns risks and uncertainties in a changing environment. It is also important to understand mechanisms regarding how the coral reef ecosystem interacts or responds to disturbances that differently occur among locations and periods of time (Mumby et al. 2014a, b). Designing effective RBM also requires management strategies that can cope with conflicting objectives under different scenarios. Tradeoffs and prioritization are key processes for this approach. Scientific information in different aspects is highly required to support resilience-based management. Mcleod et al. (2019) proposed the research priority supporting RBM implementation, including (1) biodiversity and habitat protection; (2) ecological connectivity; (3) reduction of stressors/threats; (4) marine protected areas; (5) adaptive management under uncertainty and change; (6) prioritization of reef sites that have low environmental risk, but high social adaptive capacity; (7) application of social-ecological indicators in planning and monitoring to detect early warnings and social-ecological changes; (8) experimental approaches to support resilience; (9) enhancement of social and ecological adaptive capacity; and (10) strategies to facilitate adaptation and transformation (Mcleod et al. 2019).

4.5 Coral Reef Connectivity

4.5.1 Concepts of Marine Population Connectivity

Connectivity refers to the flow of items (organisms, larvae, nutrients, pollutants, etc.) among or between location types of ecosystems that are similar or different, for instance, the flow of fishes between coral reefs and seagrass beds or the flow of coral larvae between coral reefs. Knowing the connectivity is important for marine and coastal resources management, particularly fisheries resources, while quantification of the connectivity is challenging. Transfer of non-living materials, like sediments, water mass, pollutants, etc., is primarily influenced by hydrodynamics, while the transfer of marine organisms depends on various factors including hydrodynamics, dispersal pattern, sensory, and behavior of each marine species. Connectivity among populations should reflect both dispersal patterns and successful recruitment of larvae from donor to receiving population (Sale et al. 2010). Advancement of geochemical and genetic techniques plays important roles in fulfilling the understanding of the connectivity of marine populations, revealing that there is a wide range of their connectivity, from fully open to fully closed. Measurements and modeling of ecological connectivity need various information, such as empirical data, biophysical process, and post-settlement survival, to increase the accuracy of predicted ecological connectivity (Cowen and Sponaugle 2009).

Population genetics has been applied to explore connectivity. By looking at the larval connection between populations, the scale of its connectivity can be determined using the pelagic larval duration of marine species. Knowledge on ecology, oceanography, and geography is integrated, called “seascape genetics,” which has been introduced as an important approach of population genetics to comprehend marine connectivity on different aspects, e.g., taxonomic and geographic coverage, sampling and analytical methodology, seascape drivers, etc. To date, it is believed that spatial genetic patterns are influenced by temperature, oceanographic, and geographic conditions with equal prevalence. Yet, there are other drivers affecting connectivity at different spatio-temporal scales. Fortunately, advancement in statistical analysis helps extract the mechanism and effect of each driver on connectivity from multiple drivers. The application of GIS and molecular technologies improves the understandings on population connectivity from correlation to the patterns and processes of the connectivity as well as its adaptation. Knowing the differences in demographic, functional, and genetic connectivity is valuable for policy setting and management of marine reserve, fisheries resources, reef resilience to climate change and anthropogenic impacts, etc. (Selkoe and Toonen 2011; Selkoe et al. 2016).

Some locations, e.g., coral reef islands, where physical and ecological characteristics are unique, have different connectivity patterns compared with those of the larger continental reefs, due to the complex flow patterns of seawater flows resulting from different shapes and underwater topography (Baums et al. 2006; Paris et al. 2002; Kendall et al. 2013; Lindo-Atichati et al. 2016; Vaz et al. 2013). Edmunds et al. (2018) conducted a comprehensive review on larval connectivity among coral reef islands, illustrating that multiple pathways of the larval connectivity among near-shore reefs are from the diversity of marine species with different life history strategies. To comprehend the connectivity and its contributions to coral reef resilience, eight components of studies should be conducted, covering in three major phases as follows (Fig. 4.1): (a) in propagule and organism levels (tracking a long-term biological phenomenon, quantification of connectivity following natural disturbance); (b) pelagic larval transport and movement (quantification of location of larvae in seawater and dispersal polymorphisms, measurement of physical oceanography at a high resolution); and (c) post-settlement and recruitment patterns (differentiation between self-recruits and distance recruits, temporally consistent measurement of recruitment, time series analysis of benthic population structure (Edmunds et al. 2018)). Both physical and ecological characteristics can influence the coral reef resilience, and they are also essential factors regulating the population dynamics of fundamental species and supporting their recovery after the disturbance (Munday et al. 2009). Coral reef dynamics in a location with unique characteristics, in this case coral reef islands, are complex; determining such dynamics is challenging and required an

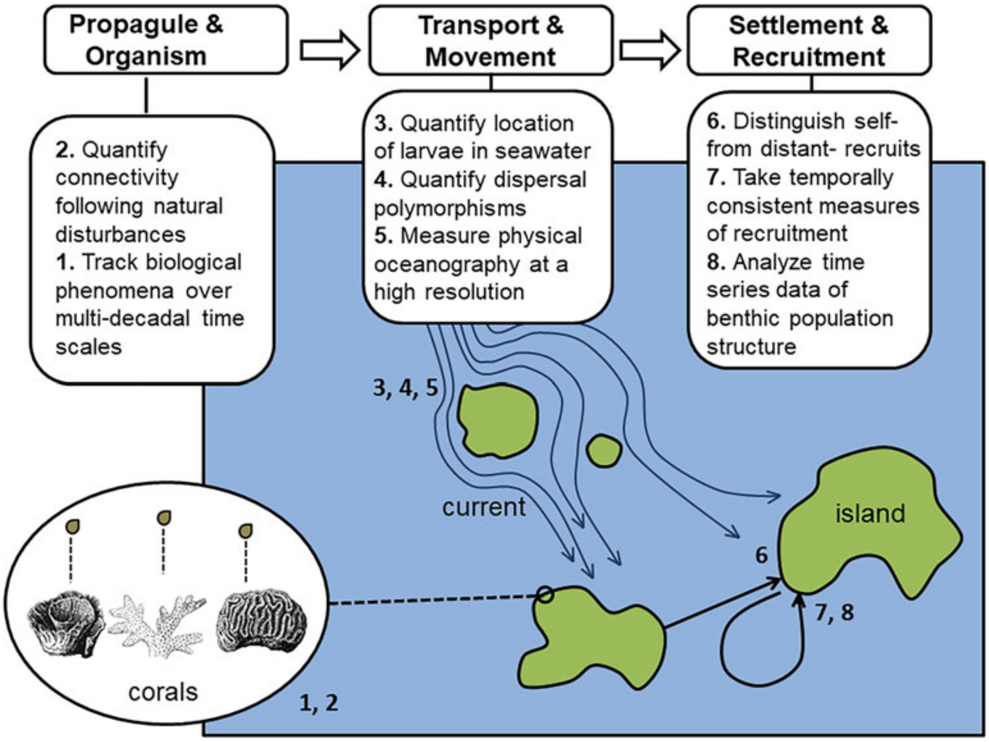

Fig. 4.1 Recommended research components to understand the connectivity and its contributions to coral reef resilience (Source: Modified from Edmunds et al. 2018)

integrated approach rather than only an ecological aspect. To understand its complexity, more studies should focus on other processes, e.g., settlement success, impacts of disturbances, factors determining adult mortality, etc. (Edmunds et al. 2018).

4.5.2 Ocean Circulation Drives Population Connectivity

Physical characteristics of the marine environment, particularly ocean circulation, play important roles in determining population connectivity. Wood et al. (2014) developed the first global model explaining the connectivity of a generic broadcast spawning coral and proposed connectivity indices to describe the connectivity between locations in terms of their potential sources of coral larvae and relative isolation. The simulation of coral larvae was performed integrating an individual-based biophysical dispersal model with surface ocean current data (1°/12°-resolution) and individual trait variability information, revealing standardized dispersal paths and reef connectivity level between source and destination reefs. They found that about 50% of the linkages were found within a range of 50–100 km. In the Pacific, the central Pacific acted as a main barrier to the larval dispersal in which only the connectivity between the Galapagos and Marquesas Islands, in French Polynesia, was observed. Some areas, for instance, Hawaii, Easter Island, the Red Sea, and the eastern Atlantic, seemed primarily isolated. The highest level of connectivity was observed in the Indo-West Pacific and Great Barrier Reef, followed by the reefs in the western Indian Ocean. The reefs in the central Indo-Pacific generally play a vital role as a source of larval supply rather than a sink (Wood et al. 2014).

The Coral Triangle (CT) is the global marine biodiversity hotspot located in the western tropical Pacific. The coral reefs across this region have been threatened with multiple disturbances, particularly coral bleaching due to global climate change, leading to a high proportion of coral mortality. As larval dispersal and recruitment enhance reef recovery after the disturbances and the knowledge on reef connectivity in this region is limited, oceanographic modeling has been applied to comprehend such connectivity. A recent study conducted by Thompson et al. (2018) exhibits larval transport of a typical broadcasting coral using the information on surface current velocity and direction from the Coral Triangle Regional Ocean Modeling System (CT-ROMS). Long-term simulations (1960–2006) were performed via TRACMASS, a Lagrangian trajectory code for the ocean and atmospheric general circulation models, to explore the connectivity, the physical drivers, and its variability. Long-term simulations are essential for studying reef connectivity because of the high interannual variation. They found that self-seeding was found in most coral reefs in the Coral Triangle, while long-distance dispersal events were relatively rare. The coral sub-population, categorized based on the potential connectivity between coral reefs, had a similar pattern compared to what was observed on the regional-scale patterns of biodiversity. Coral larval dispersal and biodiversity in this region may be significantly influenced by the physical barriers (Thompson et al. 2018).

Useful applications such as dispersal kernels, temporal variability maps, and reef clustering can be integrated in an individual-based Lagrangian biophysical model to determine population connectivity patterns that can further be applied to spatial management of coral reefs (Pata and Yñiguez 2019). In the simulation, they applied the model to simulate connectivity between reefs in the North Indo-West Pacific for three organisms: a branching coral (*Acropora millepora*), a sea urchin (*Tripneustes gratilla*), and a reef grouper (*Epinephelus* sp.). The dispersal kernels illustrated that the larvae of those species tended to settle within a third of their maximum settlement distances. Regarding *A. millepora* larvae, about 95% of them settled within 171 km from their source reefs, similar to the settlement distance patterns of *Tripneustes gratilla* and *Epinephelus* sp. However, the connectivity magnitude can be different depending on the types of organisms and seasonal variation. Also, cluster analysis can be useful to explore the inherent variability of sink and source connections. The similarities in regional connectivity patterns can be categorized based on the desirable cluster sizes and the scale of interest. The results obtained from the model were verified by comparing with previous literature revealing that the simulated larvae dispersals are in the range of the previous parentage analyses and the clusters reflecting the dispersal barriers are in accordance with published population genetic studies (Pata and Yñiguez 2019).

A particle tracking model was applied to explore the population biology of the coral *Acropora millepora* in the Spratly Islands which are an archipelago located in the South China Sea, and the islands are believed as an important source of coral larvae for the coral reefs in the South China Sea and the Palawan reefs in the Philippines. Using the oceanographic data and the spawning information of the coral *A. millepora* during 1960–2005 to simulate the reef connectivity by considering acquisition and loss of competency, settlement, and mortality, it was illustrated that the coral reefs in the western Spratly Islands had limited source reefs and less success of recruitment. Based on the particle dispersal, there are some possible connectivities among the reefs in the South China Sea, and they may also be a significant source of larval supply for the Coral Triangle region. However, further studies on coral spawning dynamics are highly required to understand why the coral larval connectivity and dispersal in this region are different between the spring and fall (Dorman et al. 2016).

Feng et al. (2016) provided a comprehensive illustration explaining how shelf circulation influences coral recruitment and connectivity using the case of the North West Shelf (NWS), Australia, where the fringing coral reefs are significant with high endemism and they have been designated as marine parks. Two major currents, i.e., Holloway Current during austral autumn-winter and the northeastward monsoon currents during austral summer, have a major influence on the shelf circulation on the NWS. Based on the shelf circulation model and particle tracking model, the larvae of *Acropora millepora* tended to move southwestward and settle on a desirable coral reef within 10 days after spawning, and the coral larval settlements varied spatially. Interannual variations of coral larval dispersals were mainly caused by the seasonal and intraseasonal wind variations. They also found that the rate of self-seeding within 47 subregions ranged from 99% to <1% with a mean rate of 22%. Subregions with high retention may not be those with the highest level of coral larval settlement. Some subregions with high recruitment could also be the most significant source of larval supply. Even though most of the important source and sink reefs were not located in marine parks, some reefs located in marine parks had the highest levels of self-seeding and coral larval retention (Feng et al. 2016).

4.5.3 Population Connectivity Among Corals and Reef Fishes

The understanding of the coral reef connectivity supports the establishment of appropriate actions and conservation efforts to enhance the resilience and recovery of coral reef meta-populations. Larval retention within and dispersal among isolated coral reef populations enable us to comprehend the ability of reefs on self-recruitment and connectivity. In the past, studies focused on the processes limiting populations and structuring coral reef communities, but recent researches have illustrated the importance of dispersal information for MPA design. New methodologies, particularly population genetics, have been introduced to reef connectivity studies, and biophysical circulation models have been applied for a larger-scale observation. Most studies tend to use multiple methods for validating the simulated larval dispersal results to be more accurate and realistic. Researches on ecological connectivity among corals and fishes have been progressive, providing the understandings of local-scale patterns of self-recruitment and the larger-scale (ten to hundreds of kilometers) of their connectivity among fishes and reefs. The levels of larval retention and connectivity boundaries mainly depend on various factors, e.g., larval duration, reef size, geographic conditions, etc. (Jones et al. 2009).

Molecular genetics have become important tools for marine population connectivity research. For example, Huang et al. (2018) applied molecular genetics to investigate the connectivity of broadcast spawning coral *Porites lutea* in 20 reefs in the South China Sea (SCS). They found that most coral populations had high genetic diversity, while the lower diversity was found in Daya Bay, the south coast of Guangdong Province in China. The slow development of *P. lutea* populations observed in this region may link to the decreases in the coral community. Genetic homogeneity among populations of *P. lutea* covered an area as large as about 1500 km. They also detected a genetic-level adaptation of the coral populations to lower winter temperatures in Daya Bay. The coalescent migration analysis illustrated that high levels of gene flow were observed among all adjacent populations except between Daya Bay and Taiwan. The northward gene flow was also found inferring the tendency of northward migration, which may be resulted from global warming. In this region, the populations of *P. lutea* are considered as one large panmictic meta-population. The low-diversity populations of *P. lutea* observed in Daya Bay indicated a higher level of their susceptibility to anthropogenic disturbances (Huang et al. 2018).

Split spawning can also be found in some corals to increase their reliability of larval supply. Since mass synchronous spawning events produce a large number of coral larvae, their larval dispersal and the reliability of coral larval supply varied considerably depending on oceanographic circulation. Coral colonies from the same population can split their spawning to match favorable conditions. The model developed by Hock et al. (2019) illustrates the dispersal of coral larvae across the Great Barrier Reef, highlighting that split spawning can increase the diversity of sources and reliability of coral larval supply. The split coral spawning event can be beneficial for enhancing inter-reef connectivity, and it can provide a more reliable larval supply to some coral reefs with low and intrinsically variable connectivity, contributing to reef resilience to climate change and anthropogenic disturbances.

Besides coral reef connectivity, the information on fish connectivity among habitats is essential for ecosystem-based management, particularly supporting the design of marine protected areas and sustainable fisheries. Diverse communities of fish on coral reefs are highly dynamic, non-equilibria communities. The fish community structure is influenced by patterns of recruitment and mortality, rather than by patterns of resource allocation among differently adapted phenotypes. In addition, the local community structure of fish varied spatially and temporally due to ecological interaction with other species (Sale 2004). The connectivity of fish among mangrove, seagrass beds, and coral reef habitats has been studied in various locations. For example, Du et al. (2020) used gillnets to explore the fish community structure in Wenchang, Hainan Province, China, revealing that mangroves exhibited the most diverse and abundance of fishes, followed by coral reefs, and seagrass beds. Most fishes are habitat-specific and can be broadly categorized into three groups according to the habitats, coral, seagrass, and mangrove habitats. About 35% of observed species lived in multiple habitats (24% and 11% of the fishes resided in two and three habitats, respectively). Some fish species, i.e., *Mugil cephalus*, *Gerres oblongus*, *Siganus fuscescens*, *Terapon jarbua*, *Sillago maculata*, *Upeneus tragula*, *Lutjanus russellii*, and *Monacanthus chinensis*, exhibited ontogenetic shift in habitat use from mangrove or seagrass beds to coral reefs. This reveals the fish connectivity among habitats, emphasizing the habitats/areas to be included in MPA network (Du et al. 2020).

4.5.4 Applied Population Connectivity

As mentioned, population connectivity is an important input for designing and decision-making of marine protected areas as well as predicting and evaluating the outcome of MPAs. Several studies on MPAs modeling have found that population persistence in MPAs is influenced by the size and spacing of MPAs as well as the intensity of threats outside the MPAs, particularly from fishing practices. Additionally, the patterns of connectivity linked by larval dispersal play a major role in the model uncertainty. A dispersal matrix containing the quantity of larvae exchanged among locations, the fraction of larvae transporting between each location, and local retention become the important information for determining the population persistence that enables us to understand larval transport dynamics. To date, the understandings on larval dispersal have been improved by researches using different approaches and advanced analytical tools, including population genetics, parentage analysis, and geochemical and artificial marks in calcified structures, modeling of biophysical circulation, etc. Besides, larval particle tracking has been incorporated into biophysical models to determine the sensitivity of larvae to flows and larval behavior. To enhance the advancement on connectivity, communication between empiricists and modelers should be promoted to help improve the characteristics of the dispersal matrix and exchange on their perspectives as well as the need of information/empirical results for effective modeling (Botsford et al. 2009).

Global warming has accelerated its impacts on coral larvae and reef connectivity in various ways with different magnitude of the impacts. Elevated seawater temperatures resulting from global warming may cause impacts on coral larvae such as accelerating larval development, reducing pelagic durations, and earlier coral reef-seeking behavior. Consequently, a reduction in dispersal distances and scale of connectivity are expected to occur. Coral larvae can be promoted to survive during pelagic phase with small elevated seawater temperatures, but they are prone to reduced reproductive output and mortality with the higher temperature. Changed ocean currents and circulation affect the larval dynamics and planktonic productivity, which may further lead to larval survival and their condition at settlement. However, there are still some spatial and temporal variations of these patterns and the uncertainties of the future projections if the oceanographic characteristics and other factors are changed. Coral bleaching and ocean acidification possibly alter the structure of coral reefs, making them fragile and become fragmented. These impacts cause changes in the spatial and temporal scales of connectivity. MPAs and MPA networks should be properly designed with appropriate size and space to maintain their ecological connectivity under climate change (Munday et al. 2009). Additionally, reef connectivity is also important among reefs with different thermal regimes. Corals have different abilities to adapt and acclimate to coral bleaching depending on the local maximum temperature regime. The inherited heat-tolerant corals that are able to adapt or tolerate to bleaching can be an important source of coral larvae for other impacted areas. The information on reef connectivity is crucial for conservation planning and the establishment of marine protected areas as well as the prediction of bleaching and recovery (Kleypas et al. 2016).

Reef connectivity highlights the need for networks of no-take marine reserves (NTMRs), which are a crucial tool for protecting coral reef biodiversity and enhancing coral recovery from natural and anthropogenic disturbances. Generally, the shorter distance between marine reserves reflects the higher connectivity. Thus, the information on larval dispersal in corals, reef fishes, and reef-related organisms is critical for determining the appropriate location, size, and spacing of marine reserves to achieve effective network design. Tradeoffs between connectivity and conservation objectives (representation and risk-spreading) should also be conducted to integrate the connectivity into NTMR decision-making processes (Almany et al. 2009). In the case of the Philippines, Abesamis et al. (2017) explored the connectivity of coral reef fish (*Chaetodon vagabundus*) among NTMRs and fishing grounds using genetic parentage analysis, revealing the dispersal connections among the NTMRs, while self-recruitment was found in some areas. The simulated larval dispersal illustrated that that 50% and 95% of larvae tended to settle within 33 and 83 km, respectively, from the origin of their parental population with a mean larval dispersal distance of 36.5 km. The study suggests that a closely spaced NTMR can promote recruitment and the population of marine species, particularly those with short dispersal distances. Collaborative management should also be promoted to enhance connectivity over multiple political boundaries (Abesamis et al. 2017).

4.6 Coral Reef Bioerosion

4.6.1 The Role of Bioerosion in Reef Development

Coral reefs are formed by the carbonate accumulation processes of corals and other calcifying organisms, becoming a major marine habitat for benthic carbonate production in tropical and subtropical marine ecosystems (Milliman 1993; Kleypas et al. 2001; Montaggioni and Braithwaite 2009). The net accumulation rate depends on a wide range of biological, physical, and chemical factors, influencing the production and erosion processes (Scoffin 1993; Perry and Hepburn 2008; Montaggioni and Braithwaite 2009). Scleractinian corals are a major reef framework producer, and various calcareous encrusters, particularly crustose coralline algae, help support calcification. Skeletal cementation binds reef materials together, strengthening reef stability (Chave et al. 1972; Scoffin 1992; Payri 1997; Perry and Hepburn 2008). On the contrary, coral reefs can be biologically or mechanically eroded. Extensive bioerosion is due to the feeding activities of various marine organisms, for example, parrotfishes (Bellwood and Choat 1990) and sea urchins (Ruengsawang and Yeemin 2000; Alvarado et al. 2016), and through the boring activities of endolithic macro- and microboring organisms (Vogel et al. 2000; Tribollet and Golubic 2005). Tropical storms can also cause physical erosion of coral reefs, influencing sediment balance and the production of coral rubble in coral reef ecosystems (Scoffin 1993). Carbonate sediments and structures can also be dissolved chemically depending on the aragonite saturation state of seawater (Eyre et al. 2018; Langea et al. 2020).

The net rate of carbonate production is the sum of gross carbonate production, primarily by reef-building corals and coralline algae, minus the carbonate loss from erosion and dissolution (Chave et al. 1972). The carbonate budget of a coral reef is essential quantitative information used to indicate a functional state of coral reefs at a given time and a capacity of reef sites to build reef structures, to explain reef complexity and maintenance (Kleypas et al. 2001; Perry and Hepburn 2008; Kuffner and Toth 2016; Perry and Alvarez-Filip 2018). Thus, the carbonate budget is a key information illustrating the maintenance of biodiversity and ecosystem functions (Mace et al. 2014). Additionally, such biodiversity and ecosystem functions are highly linked to the ecosystem services they provide, particularly the provisional services as food sources for people, shelter and habitat for various marine species, coastal protection by reducing energy from waves and storms, and nourishment of beaches by sediments produced from coral reefs (Perry et al. 2011; Graham and Nash 2013; Ferrario et al. 2014; Beetham et al. 2017; Langea et al. 2020). To assess the carbonate budget at any areas, information on local coral growth and erosion rates of dominant coral species is gathered as well as environmental conditions. Carbonate budget assessment has been applied in many reef sites across the world, particularly in the Indo-Pacific. Several predictive models have been developed to overcome the challenges on the geographic and environmental variations that influence the calcification and erosion rates. Such models require sufficient input information and some conversion factors on species-specific responses to environmental variations, e.g., depth, temperature, nutrients, and other physical, chemical, and biological characteristics of seawater (Langea et al. 2020).

Bioerosion simply refers to the corrosion of reef hard structures caused by living organisms (Neumann 1966). Reef hard structure is eroded through various activities of bioeroders, either feeding strategies, such as grazing activities of fishes and sea urchins, or inhabiting within the coral reef substrate, such as internal substrate living of borers (sponges, bivalves, worms, and microorganisms), leading to the modification and degradation of the deposited skeletal framework. Both primary and secondary reef producers (corals and crustose coralline algae) have a direct impact from this process. The bioeroders can break down the skeletal framework into small fragments and sediment. Generally, the impacts of bioerosion occur at a small-spatial and short-temporal scale on coral reef ecosystems. However, bioerosion occurring over long time scale can cause significant changes on coral reefs such as reef structure, net accretion rates, etc. In a reef with low rates of carbonate production and/or high coral mortality, increased rates of bioerosion synergize the acceleration of the reef structural degradation (Perry and Harborne 2016).

4.6.2 Endolithic Bioerosion

Endoliths refer to a wide range of organisms colonizing inside any kinds of rocks, reef structure, animal shells, etc., and they can be categorized into three groups: (1) chasmoendoliths, those that inhabit crevices and cracks in a rock; (2) cryptoendoliths, those that inhabit in cavities within porous rocks, including holes or spaces created by euendoliths; and (3) euendoliths, those that create holes or spaces that match the shape of their body; they can be alternatively called as rock-boring organisms, e.g., sponges, polychaetes, bivalves, sipunculid worms, foraminifera, decapods, cirripeds, cyanobacteria, chlorophytes, rhodophytes, and fungi (Golubic et al. 1981; Hutchings 1986; Bromley 1994). Coral reef bioerosion is mainly influenced by the activities of various euendolithic organisms and epilithic organisms that are those growing partly on the surface of hard substrates (Perry and Harborne 2016). Endolith consists of two sub-groups, namely, (1) macroborers are the borers that produce boreholes with diameters of more than 1 mm through chemical dissolution and mechanical abrasion processes, and (2) microendolithic borers are the borers widely found within carbonate substrates in the marine environment and produce boreholes with a diameter range of ~1 to 100 μm through a chemical etching process (Golubic et al. 1975).

Sponges are the major infaunal bioeroders, comprising about 75–90% of the macroborers (Goreau and Hartman 1963; MacGeachy and Stearn 1976; Highsmith 1981; Highsmith et al. 1983; Perry and Harborne 2016). Sponges that have been identified as bioeroding species are membered in the orders Hadromerida (Clionaidae, Spirastrellidae, and Alectonidae), Poecilosclerida (Arcarnidae), Halichondrida (Halichondriidae), and Haplosclerida (Phloeodictyidae) (Hutchings 2011). Sponges tend to colonize on dead basal and cryptic surfaces of corals, possibly resulting in weakening and breakage of reef structure due to a chemical etching process and the mechanical deterioration of coral skeleton. Coral tissue contacting sponge is chemically corroded and then removed mechanically, leaving behind scallop-shaped excavations. The bioerosion is resulted by sponges significantly contributing to both coral reef erosion and the production of carbonate sediment (Perry and Harborne 2016). Sponge larvae can colonize both live and dead substrates. Several studies reported boring rates by sponges from experimental coral substrate deployed at reef sites in the Indo-Pacific region; the boring rates in the Great Barrier Reef were 0.01–0.3 kg $CaCO_3/m^2$-year (Osorno et al. 2005) and in French Polynesia was 0.1–0.9 kg $CaCO_3/m^2$-year (Pari et al. 1998). The response of bioeroding sponge *Cliona orientalis*, a photosymbiotic sponge with dinoflagellates of the genus *Symbiodinium*, to different ocean warming and acidification scenarios was simulated by Fang et al. (2018), revealing there were lateral tissue extension, bleaching, and reduction on respiration and photosynthesis under the scenarios of combined ocean acidification and ocean warming. They found that the mortality of the photosymbiotic sponge was probably seen due to the combined ocean acidification and ocean warming, reducing its ability to erode coral reefs. This reflects that the bioerosion caused by *C. orientalis* may occur temporarily or permanently depending on the future viability of the sponge.

Some mollusks belonging to six families are considered as coral borers; some species in the families Mytilidae and Lithophaginae bore into live corals. All species in the families Petricolidae, Pholadidae, Clavagellidae, and Gastrochaenidae bore only into the dead coral substrate. Two species of gastropod, *Leptoconchus* sp. and *Magilopsis* sp., are also recognized as live coral borers (Soliman 1969;

MacGeachy and Stearn 1976; Highsmith et al. 1980; Moretzsohn and Tsuchiya 1993; Hutchings 2011). After settlement, the mollusks have mechanical and chemical mechanisms to bore inside the basal parts of coral colonies and erode the structure of coral reefs. Some mollusks use their shells for mechanical boring, and they use the chemical dissolution process by secreting some substances on live corals (Kleeman 1990; Moretzsohn and Tsuchiya 1993). The boring rates of mollusks on experimental coral substrates deployed at reef sites in the Indo-Pacific region are 0.01–0.5 kg $CaCO_3/m^2$-year (Osorno et al. 2005) and 0.12–1.2 kg $CaCO_3/m^2$-year in the Great Barrier Reef (Tribollet and Golubic 2005). In French Polynesia, the total macroboring was 0.01–0.05 kg $CaCO_3/m^2$-year which bivalves were the major contributor (Pari et al. 1998).

Several polychaetes in the families Cirratulidae, Eunicidae, Sabellidae, and Spionidae are endolithic bioeroders in coral reef ecosystem (Hutchings 2011). Inhabiting on within both live and dead corals, polychaetes still prefer living on dead corals, and they are early colonists (Hutchings and Peyrot-Clausade 2002). Species composition of the polychaetes varies in accordance with the substrate colonization; in a mature substrate, early colonizers that are generally short-lived species are replaced by longer-lived species. Most of them produce chemicals to develop boreholes; however, the use of mechanical abrasion can be also found for some species. Boring polychaetes may significantly contribute to overall bioerosion rates by modifying substrate and facilitating other borers, even though they relatively extract small amount of $CaCO_3$ compared with sponges and bivalves (Bak 1976; MacGeachy and Stearn 1976; Highsmith 1981; Hutchings et al. 1992). Several taxa of sipunculan worms, e.g., Aspidosiphon, Lithacrosiphon, Paraspidosiphon, and Phascolosoma, are infaunal borers (Rice and Macintyre 1982; Hutchings 2011). They are commonly found in dead coral substrates, but rare in well-eroded substrates (Rice and Macintyre 1982). Cirripeds, endolithic barnacles, are also locally important an endolithic bioeroder in some coral reefs (Bromley 1978). Estimated boring rates for polychaete and sipunculan worms at some reef sites in the Indo-Pacific were 0.1–0.3 kg $CaCO_3/m^2$-year (Osorno et al. 2005). In the Great Barrier Reef, the total macroboring after 1 year was 0.01–0.13 kg $CaCO_3/m^2$-year, which was mainly contributed by sipunculans and polychaetes (Tribollet and Golubic 2005). The total macroboring reported in the Reunion (0.05–0.4 kg $CaCO_3/m^2$-year) and French Polynesia (0.01–0.07 kg $CaCO_3/m^2$-year) were mainly contributed by polychaetes (Chazottes et al. 2002; Pari et al. 1998).

The activities of photosynthetic cyanobacteria, chlorophytes and rhodophytes, and heterotrophic fungi and bacteria can also degrade carbonate substrate in coral reefs by producing boreholes with a diameter range of ~1 to 100 μm (Golubic et al. 1975). These species may be used as palaeobathymetric and ecological indicators because they inhabit special ecological niches (Radtke and Golubic 2005). Microborers can create networks of tunnels in carbon substrate using biochemical dissolution. Light level and depth are important limiting factors, influencing the spatial and temporal variations of microbioerosion rates (Ehrlich 1990). In Reunion, the erosion rate of shallow reefs ranged from 0.04 to 0.07 kg $CaCO_3/m^2$-year, and the highest rate was found at the sites with higher nutrients (Chazottes et al. 2002). The higher rates tended to be found at the Great Barrier Reef Shelf with the range of 0.13–1.35 kg $CaCO_3/m^2$-year. Studies on experimental substrates illustrate that microbioerosion rates tended to decrease through time (Kobluk and Risk 1977; Tribollet and Golubic 2005). Colonies of microborers can be found on both live and dead coral substrates, forming a clear green banding below the coral tissue surface of corals, for example, the band of *Ostreobium* sp. found in the skeleton of *Porites lutea* (Fig. 4.2; Sangsawang et al. 2017). Some phototrophic species rapidly colonize in a dead coral substrate. They are later occupied by low light-tolerant species and by heterotrophic fungi when the substrate is overgrown with either turfs or algae. Green alga *Ostreobium quekettii* is generally found as a dominant on a coral substrate with high cover of crustose coralline algae, increasing the microboring rates of the substrate (Perry and Harborne 2016; Sangsawang et al. 2017).

Composition, boring pattern, and activity of microboring organisms can be different between live and dead coralline crusts. Tribollet and Payri (2001) reported that the cyanobacteria *Plectonema terebrans* (83%) were a dominant colonizer, followed by the alga *Ostreobium quekettii* (7%), inhabiting in the crusts of live coralline alga *Hydrolithon onkodes*. They tended to grow and produce branched filaments from the inside to the crust's surface with the bioerosion of 0.12 g $CaCO_3{\cdot}cm^{-3}$. The skeletons of dead coralline alga were bored inward by some cyanobacteria, e.g., *Hyella caespitosa*, *Mastigocoleus testarum*, and *P. terebrans*, and various chlorophytes, with the carbonate removal rate of 0.49 $gCaCO_3.cm^{-3}$. The higher rate of bioerosion in the dead crust was due to a change in species composition of bioeroders, larger filament diameters, and deeper penetration depth of endoliths. The bioerosion rate was also synergized by exposing to grazing activities of fish, sea urchins, and mollusks (Tribollet and Payri 2001). Carbonate dissolution by microborers can be magnified under ocean acidification as illustrated by Tribollet et al. (2019), who studied the effects of seawater alkalinity and the activity of natural microboring communities, dominated by the chlorophyte *Ostreobium* sp., on carbonate budget of the Larégnère reef, New Caledonia, Oceania. They found that the dissolution was higher at night, but it can still occur via photosynthetic activity. The dissolution process was also enhanced with an increased acidic condition where an acidity

Fig. 4.2 Endolithic community (green layer) in the skeleton of *Porites lutea* (Source: Sangsawang et al. 2017)

threshold reached the partial pressure of carbon dioxide (pCO_2) of $\geq$ 920 μatm, indicating that microboring activities and ocean acidification can play a significant role in reef carbonate dissolution.

4.6.3 External Bioerosion

Algal grazing, particularly by parrotfishes and urchins, is a critical process to maintain coral-dominated communities and control the growth of macroalgae (Mumby et al. 2006a, b). Coral reefs overgrown with macroalgae are prone to partial coral mortality, limitation on coral settlement, and coral diseases (Nugues et al. 2004; Nugues and Bak 2006; Box and Mumby 2007; Birrell et al. 2008a, b). Direct predation on live corals by fishes and urchins can cause bioerosion, which its rate varies according to their densities and bites rates. The bioerosion rate caused by such species is generally higher than that caused by endolithic bioeroders (Rotjan and Lewis 2006; Hoey and Bellwood 2008; Perry and Harborne 2016).

Sea urchins, such as genera *Diadema* and *Echinometra*, are membered in a major group, strongly influencing reef bioerosion (Glynn 1997; Ruengsawang and Yeemin 2000). They use their Aristotle's lantern for grazing on carbonate substrate, while calcium carbonate particles and other pellets, e.g., coralline algae, calcareous macroalgae, etc., are excreted (Hutchings 1986). Some graze on entire coral recruits leading to damage of the coral skeletons (Bak and van Eys 1975; Sammarco 1980; Carpenter 1981; Sammarco 1982). Bioerosion at the base of corals can weaken coral skeletons, making them vulnerable to storms (Bak 1994). Bioerosion rates by sea urchins vary considerably depending on the body size and species (Bak 1994; Carreiro-Silva and McClanahan 2001). Estimated bioerosion rates caused by *Diadema setosum* ranged from 0.31 to 1.8 g $CaCO_3$/ind-d (Mokady et al. 1996; Ruengsawang and Yeemin 2000; Carreiro-Silva and McClanahan 2001; Muthiga and McClanahan 2007). The bioerosion rates caused by *Echinometra mathaei* were relatively low with a range of 0.11–0.14 g $CaCO_3$/ind-d for (Russo 1980; Bak 1990; Mokady et al. 1996). *D. setosum* is mostly found on shallow coral reefs, and it is rare below 10 m deep. The abundances of *D. setosum* tend to increase with increasing sediment sizes and decreasing coral and macroalgal cover (Mokady et al. 1996; Coppard and Campbell 2005; Dumas et al. 2007; Muthiga and McClanahan 2007; Ruengsawang and Yeemin 2000). *Echinometra mathaei* is adaptable to inhabit in an exposed coastal habitat where wave energy is relatively high. In Fiji, *E. mathaei* is generally found in various habitats ranging from the forereef to seagrass beds; the highest abundance has been observed in the mid-back reef zone (Coppard and Campbell 2005). Total sea urchin bioerosion of 4.5 kg/m^2-year was estimated in the reefs of Moorea-Maiao, French Polynesia (Bak 1990). In the Gulf of Thailand, the bioerosion rates caused by *D. setosum* ranged from 0.34 to 1.43 g$CaCO_3$/individuals/day or 1.64–5.5 Kg $CaCO_3$/m^2/year. The shallowest zones with high population density exhibited the highest bioerosion rates. The increased population density of *D. setosum* and the bioerosion rates were also promoted by the first severe coral bleaching event took place in the Gulf of Thailand in 1998 (Ruengsawang and Yeemin 2000).

Parrotfishes have a special dental morphology and a biting mechanism that are possible to remove both carbonate substratum and live corals through grazing (Rotjan and Lewis 2006; Almany et al. 2009). The parrotfish species *Cetoscarus bicolor*, *Bolbometopon muricatum*, and *Chlorurus sordidus* are generally found in the Pacific (Bellwood and Choat 1990). Some parrotfishes, e.g., *Scarus ghobban* and *S. globiceps*, that have weak bite and thin teeth are known as scrappers, and they mostly bite flat microhabitats. Croppers are another group of parrotfishes that remove only algae and do not leave bite scars (Bellwood and Choat 1990). Bites caused by parrotfishes can erode the reefs at a rate of 5.6 kg/m^2-year (Bellwood 1995). At a reef with a large population of *B. muricatum*, the bioerosion rate can be as high as 32.3 kg/m^2-year, because such fish mainly feed on live corals (Bellwood and Choat 1990; Bellwood et al. 2003; Hoey and Bellwood 2008). On the other hand, parrotfish grazing can help increase light penetration and clear more areas for boring sponges (Cebrian 2010). The gross sediment production rate produced by *Chlorurus gibbus* was estimated to be 1043 kg/year per individual, supplying interstitial sediment and sands to the coral reef ecosystem and others such as beaches (Bellwood 1995; Perry et al. 2015). The species-specific bioerosion depends on species distribution which is generally influenced by physical factors such as depth, topography, and reef zone. Studies of species distributions on the Great

Barrier Reef (GBR) exhibited clear differences in bioerosion rates among habitats. Hoey and Bellwood (2008) found that there were significant differences in the densities of four parrotfishes, i.e., *Bolbometopon muricatum*, *Chlorurus microrhinos*, *Chlorurus* spp., and *Scarus* spp., throughout the reef profiles (back reefs, reef flats, reef crests, and reef slopes) of the GBR. Inshore reefs tended to have high parrotfish densities of smaller parrotfishes with high rates of sediment reworking, while outer reefs had low densities of larger parrotfishes, making the rates of bioerosion and coral predation in this zone higher (Hoey and Bellwood 2008). Additionally, herbivore assemblages on the GBR between deep outer-slope zones and shallower habitats were also significantly different, according to Russ (1984). Overfishing affects the abundance of parrotfishes, consequently decreasing bioerosion. Bellwood et al. (2003) reported that green humphead parrotfish *Bolbometopon muricatum* had been heavily harvested across the Indo-Pacific. This may affect bioerosion processes on outer shelf reefs where this fish plays an important role in such a process. It is important to conserve reef fishes, particularly herbivorous, to maintain natural bioerosion in the coral reef ecosystem. Many areas have been designated as marine protected areas to conserve reef fishes. Parrotfishes are one of the main fish groups, as they are a key component for the coral reef ecosystem (Stockwell et al. 2009).

Other fishes and other marine organisms also have indirect roles in bioerosion and reef sediment systems. Surgeonfishes are important in sediment transport; about 18% of inorganic sediment in the Pacific reef crests was related to the ingestion and defecation of surgeonfishes (Krone et al. 2011). The territorial behavior of damselfishes may cause a small-scale spatial distribution of bioerosion since they prevent other fishes as well as sea urchins from feeding on within their territories (Sammarco and Williams 1982; Sammarco et al. 1986). Without fish grazing, bioerosion in such areas may occur due to boring organisms (Risk and Sammarco 1982; Sammarco et al. 1987). Some gastropods can also be bioeroders; for example, the gastropod *Drupella* that feeds on living coral tissue can potentially cause coral mortality. Furthermore, the dead coral substrate can be eroded by sea urchins or other bioeroders that prefer colonizing on it (Lam and Shin 2007). Chitons are capable of eroding carbonate substrate; for example, the chiton *Acanthopleura gemmata* on the Great Barrier Reef had an erosion rate of 0.16 kg $CaCO_3$/individual/year; however, they are mostly found on the rock rather than actual reef substrata (Barbosa et al. 2008). Other mollusks such as limpets and littorinas are also a bioeroder (Tribollet and Golubic 2011).

4.6.4 Environmental Impacts on Bioerosion

Natural and anthropogenic disturbances can change the diversity and assemblage of benthic communities and may influence the bioeroding organisms, consequently the rates of carbonate production and erosion in the coral reef ecosystem. For instance, higher productivity due to eutrophication can promote the growth and activities of some filter feeders such as endolithic bivalves and sponges (Fabricius 2005), leading to the higher bioerosion (Holmes et al. 2000). The higher nutrient levels can increase algal biomass, which is further associated with grazers and endolithic bioeroding communities (Perry and Harborne 2016). In Tahiti, sea urchins were a dominant bioeroder in high-nutrient sites where the high macroalgal cover was high, but the bioerosion in low-nutrient sites was mainly caused by endolithic sponges (Paris et al. 2002). Rice et al. (2020) examined the influence of nutrient supply on the dynamics between internal and external bioeroders and the interaction between a boring bivalve, *Lithophaga* spp., and parrotfish bioerosion on massive *Porites* corals on the fringing reefs around Moorea, French Polynesia. They found a positive correlation between *Lithophaga* densities and nitrogen levels. Massive *Porites* were more colonized by *Lithophaga* and had more chances to be bitten by parrotfishes, reflecting that increased nutrient levels may strengthen the relationship between internal and external bioeroders, yielding higher bioerosion rates.

Sedimentation can potentially influence bioerosion. A number of studies on cross-shelf gradients in bioerosion have been conducted across the Indo-Pacific, mostly on the Great Barrier Reef, by comparing the bioerosion along with the reef profile from the inshore (high sedimentation and high turbidity) to offshore environments (clear water). These studies illustrate that the lower rates of bioerosion, associated mostly with sponge boring and low grazing, are found on inshore reef sites compared to offshore reef sites, where they are dominated by grazers and endoliths. Corals in the inshore environment do not show any signs of internal bioerosion, which is their response to high sedimentation conditions, making the residence time of dead coral substrate low (Perry and Harborne 2016).

Climate change has generated direct and indirect impacts on the coral reef ecosystem, causing several changes such as reduction in live coral cover, reef biodiversity, and structure. These changes may associate with reef bioerosion and the community of bioeroding organisms (Perry and Harborne 2016). High rates of bioerosion were observed on the reefs that have experienced with coral bleaching and mortality, mainly caused by elevated sea surface temperature (SST), as well as coral diseases. The bioerosion rates of dead corals following bleaching events may be higher due to the activities of external grazers. Overgrowth of skeletons can also attract more herbivorous organisms to feed on, increasing the bioerosion caused by such grazing activities (Pratchett et al. 2008). Additionally, ocean acidification may also increase the level of *Lithophaga* sp. bioerosion, and it may possibly occur in this region by 2100 (Barkley et al. 2015).

4.7 Coral Reef Refugia Under Global Change

4.7.1 Coral Reef Refugia Concepts

Refugia are defined as "habitats that components of biodiversity retreat to, persist in and can potentially expand from under changing environmental conditions" (Keppel et al. 2012). Coral reefs refugia should be able to provide a long-term buffering and to retain suitable conditions for coral growth and reproduction and reef-associated species from the extensive stressors under climate change, particularly elevated seawater temperature and ocean acidification (Dobrowski 2010; Keppel and Wardell-Johnson 2012; Kavousi and Keppel 2018). However, the concept of coral reef refugia is still unclear and confusing since many studies related to climate change refugia for coral reefs refer to different phenomena, for example, refuges, pristine habitats, and higher tolerance to environmental stress, which are distinct from the concept of coral reef refugia under climate change (Kavousi and Keppel 2018). Refuges and refugia are clearly distinct based on their time scale. While refuges provide temporarily suitable habitats, refugia are considered as long-term habitats over decades or centuries or several generations (Keppel and Wardell-Johnson 2012). For example, storms and cloud cover can help reduce seawater temperature and decrease coral bleaching, but this is not long-term protection. Thus, they should be as refuges, rather than refugia. Pristine habitats and marine protected areas are not considered as coral reef refugia as they do not provide long-term protection from climate change, e.g., coral bleaching events (Riegl and Piller 2003; Darling et al. 2010; Gilmour et al. 2013; Hughes et al. 2017a, b). A reef that has tolerant coral species to extreme climatic conditions cannot be identified as refugia because the reef does not provide more favorable or stable environments. Importantly, the long-term ability of location/area to mitigate major climate change stressors is the key functionality to be considered to identify coral reef refugia (Kavousi and Keppel 2018).

Previously, Glynn (1996) suggested some characteristics of the areas that can be potentially refugia for global warming, including high latitudes, moderate depths, isolated reefs with vigorous currents, and any reefs with lower coral bleaching/mortality than surrounding reefs. Riegl and Piller (2003) later proposed additional criteria for identifying potential refugia: the presence of healthier coral reefs where cold currents can reduce the thermal stress and health status of offshore coral reefs. However, health status may not reflect long-term environmental stability (Gilmour et al. 2013; Hughes et al. 2017a, b). The areas with slower local climate change and historically most stressed areas may also be potential refugia (Riegl 2003). Several studies have used coarse-scaled (>4 km) climate models to predict remarkable losses of coral reefs over entire regions by the end of the century, to help locate some potential large-scale refugia (van Hooidonk et al. 2014; Freeman 2015). Recently, Kavousi and Keppel (2018) suggested six factors identifying the capacity of refugia, including long-term buffering, multi-stressor protection, accessibility, microclimatic heterogeneity, size of refugia, and low exposure to other disturbances. Of these factors, long-term buffering and protection from multiple climatic stressors are essential for effective coral reef refugia from the impacts of anthropogenic climate change.

4.7.2 Coral Reef Refugia from Thermal Stress

Temperature-induced severe bleaching events have been considered as climate change impacts on coral reefs, spatially occurred across tropical regions. Furthermore, prolonged exposure to elevated seawater temperature can also cause coral mortality; however, exposure to bleaching conditions varies spatially at larger scales. van Hooidonk et al. (2013) applied IPCC AR5 models to construct the maps of global bleaching conditions at different Representative Concentration Pathways (RCPs), including RCP 4.5, 6.0, and 8.5. Annual bleaching is expected to start at the GHG concentration of 510 ppm CO_2 equivalent. At the RCP 8.5, bleaching conditions may occur for all locations in 2040 (median year). Reducing GHG emissions from RCP 8.5 and 6.0 can also delay annual bleaching for more than two decades in 23% of simulated reefs. Based on their study, they recommended that the reefs in the western Indian Ocean, Thailand, the southern Great Barrier Reef, and central French Polynesia can be potentially temporary refugia for climate change (van Hooidonk et al. 2013). Cacciapaglia and van Woesik (2015) identified climate change thermal stress refugia for reef corals in the Indian and Pacific Oceans using a species distribution modeling approach in which 12 coral species that have a different local response to thermal stress were incorporated. Based on their projection, by the year 2100, 9 of the 12 coral species studied may fail to occupy 24–50% of their current habitat, mainly occurring at a latitude range of 5°–15° in the north and south hemispheres. Two common species, *Acropora hyacinthus* and *A. digitifera*, will be adaptable to 1 °C elevated temperature and possible to maintain their current habitat, while *Porites lobata*, a heat-tolerant coral species, will increase its current distribution by 14%. They proposed five areas in the Indian Ocean, i.e., southwestern Madagascar, the Maldives, the Chagos Archipelago, Western

Australia, and Seychelles, and seven areas in the Pacific Ocean, i.e., northern Indonesia, Micronesia, the northern Marshall Islands, the southern Great Barrier Reef, the Solomon Islands, Vanuatu, and French Polynesia, to be conserved as coral reef refugia under climate change.

High-latitude coral reef communities have been discussed as their potential to be climate change refuges for vulnerable tropical coral reef species, making them more ecologically important and leading to conservation priority. Coral reef communities in high-latitude regions are influenced by marginal environmental conditions, and they have unique characteristics such as the specific biogeographical overlap of taxa, endemic species, and seasonal variation in species composition (Beger et al. 2014). Being threatened by elevated seawater temperatures, reef-building corals tend to distribute poleward. Thus, high-latitude regions may serve as refugia under climate change. Management interventions, both active and passive strategies, should be applied on high-latitude coral communities that have potential for climate change refuge sites to prevent local threats and enhance ecosystem resilience, being ready for the migration and relocation of coral populations (Beger et al. 2014). Genetic diversity and connectivity can also explain the possibility of the northward migration of some coral populations. Nakabayashi et al. (2019) observed the connectivity among three cryptic lineages of *Acropora hyacinthus* along the Kuroshio Current and found that only one was distributed in temperate regions, indicating that the current might act as a larval dispersal barrier between temperate and subtropical regions. Furthermore, the level of genetic diversity gradually declined toward the edge of the species distribution. Marginal populations may be vulnerable to climate changes as their genetic diversity tended to decrease (Nakabayashi et al. 2019).

It has been hypothesized that deeper coral reefs have less exposure to heat stress than shallow ones, hoping that deep coral reefs may be potential deep reef refugia, protecting corals from bleaching. Several studies reflect some possibilities that deep coral reefs can be thermal refuges; for example, Baird et al. (2018) reported a curvilinear decline in the percentage of colonies bleached with depth on the shelf of the northern Great Barrier Reef. Frade et al. (2018) found that bleaching impacts on the deep reefs had less severity severe than that at shallower reefs because the heat stress at the deeper reefs is reduced by upwelling. However, this hypothesis still needs verification due to the inconsistent results among studies. Venegas et al. (2019) argued that deep reef refugia should not be assumed as a broad ecosystem-wide, according to their study examining the depth refuge over 457 reef sites among 49 islands in the western and central Pacific Ocean using satellite and in situ temperature data. Overall, they found that no capability on deep reef refugia was found to the depth of 38 meters, indicating that many deeper coral reefs in that deep range are as vulnerable to heat stress as shallower reefs. However, there are some spatial and temporal variations on heat stress along depth gradient depending on various factors, particularly the vertically stratified conditions, light exposure, oceanic currents, internal wave activities, etc. (Venegas et al. 2019).

Dongsha Atoll or Pratas Island is located in the South China Sea and characterized by two physical phenomena: elevated sea surface temperature and the upwelling of cold deep waters induced by the world's strongest internal waves influencing the outer slope of the atoll, making the coral species composition and structure between the lagoon and forereef clearly distinct. Heat-tolerant corals, particularly massive *Porites*, foliaceous *Echinopora*, *Pavona*, and *Turbinaria*, were mainly found in the lagoon, while thermally susceptible scleractinian corals like *Acropora*, *Pocillopora*, and *Montipora* were dominated in the forereef. The forereef exhibited higher coral cover and species richness and low mortality rate compared to the lagoon. Dongsha Atoll could potentially be a thermal refuge for reef-building corals in the northern South China Sea (Tkachenko and Soong 2017). In the Andaman Sea, internal waves play an important role in diminishing the impacts of coral bleaching events. The large-amplitude internal waves (LAIW) generate frequent upslope intrusions of cold sub-pycnocline waters that helped reduce the impacts of the 2010 bleaching event on shallow coral reefs. Reefs that are influenced by LAIW can be local refugia for bleaching-susceptible corals (Wall et al. 2015).

4.7.3 Coral Reef Refugia from Ocean Acidification

Ocean acidification (OA) or global decline in seawater pH has been considered as important threat in marine ecosystem due to the concerns of the possible increase in calcification rate of marine organisms, particularly marine calcifiers (Manzello et al. 2012; Comeau et al. 2014; Kapsenberg and Cyronak 2019). Research previously conducted focused on using comparable partial pressure of CO_2 (pCO_2) ranges to determine the effect of OA on coral reef calcifiers. Natural variability in seawater carbon dioxide provides safe zones, called ocean acidification refugia, for various marine species from ocean acidification. Comeau et al. (2014) compared the impacts of OA on two corals (*Pocillopora damicornis* and *Porites*) and calcified algae (*Porolithon onkodes* and *Halimeda macroloba*) in Hawaii, Moorea, and Okinawa, under three different pCO_2 levels (400, 700, and 1000 matm). No clear effects of OA were found on those, except for *P. onkodes*. The OA effects *on P. onkodes* were location-specific, revealing the depression caused by high pCO_2 only in Moorea and Hawaii, indicating that the reefs in Okinawa might have some potentials for ocean acidification refugia.

Kapsenberg and Cyronak (2019) proposed the definition of ocean acidification refugia as “Areas of the coastal or open ocean that exhibit persistent environmental conditions such that a species’ vulnerability to anthropogenic ocean acidification is reduced, where vulnerability is the combination of sensitivity, exposure, and adaptive capacity.” They also developed the framework and criteria for identifying potential areas as ocean acidification refugia. The framework focuses on two main aspects (reducing exposure and enhancing adaptive capacity) to mitigate the impacts of ocean acidification on coral reefs.

4.8 Marine Protected Area Networks (MPA Networks)

4.8.1 MPA Network Design Principles

Marine protected areas (MPAs) are defined as any marine area dedicated to the protection and maintenance of biodiversity as well as associated cultural resources and managed through legal or other effective means (Dudley 2008; IUCN-WCPA 2008). There are various types of marine protected areas, most of which rely on regulations, for example, marine reserves, which can be either no-take areas or the areas whereby some activities are restricted, the areas with different governing systems or special regulations/agreements. A collection of individual areas that are ecologically connected and synergized at various spatial scales are recognized as a marine protected area network (Dudley 2008; IUCN-WCPA 2008). MPA networks can obtain the benefits of well-managed individual marine protected areas with less operational costs. Furthermore, MPA networks are essential for enhancing coral recovery among MPAs after experiencing disturbances (Marshall and Schuttenberg 2006). MPA networks can be designed to be flexible and adaptive to address multiple objectives and suitable to local contexts (IUCN-WCPA. 2008; FAO 2011). The concept of MPAs, particularly marine reserves, have been applied across the world as a management tool, aiming to achieve ecosystem conservation and utilization, specifically marine fisheries (Russ 2002; Mumby et al. 2006a, b; Lester et al. 2009; Stockwell et al. 2009; Gaines et al. 2010). Several studies have reported that MPAs helped maintain the species diversity, abundance, and biomass and increase the reproduction of many marine species, particularly economically important fisheries species (Russ 2002; Halpern and Warner 2003; Palumbi 2004; Lester et al. 2009; Babcock et al. 2010). Moreover, MPAs can also contribute various benefits as a supply of eggs, larvae, and adults to other areas (Russ 2002; Gell and Roberts 2003; Gaines et al. 2010; Harrison et al. 2012; Sutthacheep et al. 2016).

To achieve effectiveness, MPAs should be as a part of a border framework, for example, ecosystem-based management (NRC 2001; Ehler and Douvere. 2009; Agardy 2010; Agardy et al. 2011; Alino et al. 2011). MPAs have been widely integrated within the ecosystem-based management in which ecosystem and human aspects are holistically considered, aiming to enhance ecosystem health and resilience while maintaining the provision of ecosystem services (Christie et al. 2009; Link 2010; Yeemin et al. 2018). Well-designed and effective MPAs and their networks can become a key component contributing to the success of ecosystem-based management. Additionally, lessons learned and effective strategies for achieving sustainable utilization, biodiversity conservation, and climate change objectives can also be obtained from the implementation (FAO 2003, 2011; Green et al. 2013). Design principles have been comprehensively outlined, providing various considerations to achieve desirable objectives. Two design principles, i.e., biophysical and socioeconomic, have been extensively applied among field managers and practitioners. Basically, biophysical principles consider a biological and physical process to achieve biological objectives, while socioeconomic principles emphasize maximizing societal benefits along with minimizing costs, achieving sustainability (Fernandes et al. 2012; Green et al. 2009; Wilson et al. 2011; Sutthacheep et al. 2018a, b). Both principles should be harmoniously integrated in MPA design process, to ensure that the strategies and implementation cover biological and socioeconomic objectives, as well as align with local legal, political, and institutional needs (Green et al. 2013).

As the impacts of global warming have increased, the design of MPA networks tended to focus on biodiversity protection from climate change (IUCN-WCPA 2008; McLeod et al. 2009; Green et al. 2009; Wilson et al. 2011). Three major objectives related to biodiversity, fisheries, and climate change are generally mentioned during the design process of MPAs and MPA networks. Fisheries issues have been discussed in terms of avoiding conflicting uses within MPAs, particularly marine reserves or no-take areas. It is important to highlight the benefits of MPAs, which enhance fisheries production in fished areas, and it should be incorporated in the design process. Although biophysical design principles tended to emphasize biodiversity protection, they can also enhance sustainable fisheries and reef resilience to climate change (Fernandes et al. 2012; Halpern and Warner 2003; McLeod et al. 2009; Gaines et al. 2010). Some conflicting suggestions may arise from different existing principles with different objectives, the integration of these principles is highly recommended to concurrently achieve all objectives. Green et al. (2013) recommended 15 principles for integrating fisheries, biodiversity, and climate change objectives into MPA network design, as the following: (1) prohibiting/limiting destructive activities;

(2) designating 20–40% of each habitat as marine reserves; (3) replicating protection of habitats within marine reserves; (4) ensuring critical habitats are in marine reserves; (5) ensuring MPAs are permanently or long-term operated (20–40 years); (6) designing a multiple-use marine protected area; (7) designing minimum and variable sizes to MPAs; (8) separating marine reserves by 1–20 km; (9) including an additional 15% of key habitats in shorter-term marine reserves; (10) locating MPA boundaries both within habitats and at habitat edges; (11) having MPAs in more square or circular shapes; (12) controlling and minimizing local anthropogenic threats; (13) including resilient sites in marine reserves; (14) including special or unique sites in marine reserves; and (15) locating more protection upstream.

It is highly recommended that MPAs and MPA networks should be designed and implemented in accordance with adequate scientific information such as spawning, feeding and nursery areas, and ecological connectivity of juvenile fish/corals among locations. In the case of urgency with the data-sparse situation, the combination of best available scientific information, expert opinions, and local knowledge can also be applied. Research and monitoring are still required for the improvement of future MPA implementation and expansion of MPAs and MPA networks. The scientific information is also important for the evaluation of MPA management effectiveness. Practically, the scientific information should be available and digested into simple form for local MPA managers and practitioners (Ministry of Environment of Japan 2010). The planning design needs to be conformed with local context and data availability. Available global databases can be applied with local knowledge to support site selection. For example, the design framework of MPAs in Southern Negros Marine Key Biodiversity Area in the Philippines incorporated several datasets such as the accounting of marine resources, identification of the important areas for biodiversity conservation and fisheries, and identification of land- and sea-based activities threatening marine biodiversity and utilization. Importantly, local communities and municipalities were engaged throughout the MPA networking processes (Cabral et al. 2015).

Although each marine protected area (MPA) has been designated on a specific case, at a larger scale of MPA networks, particularly regional and global, the overall objectives on biodiversity at all levels, i.e., populations, species, and communities, should be emphasized. As the proportion of marine areas being protected is extremely low, it is important to expand MPA networks to cover ecologically critical areas. For instance, only 2% of the marine areas in the Coral Triangle (CT), one of the global biodiversity hotspots, are currently protected in any form of MPA. Asaad et al. (2018) highlighted the importance of MPAs for biodiversity conservation in the CT by analyzing both biodiversity features (i.e., habitats, species richness, species of special conservation concern, restricted-range species, and essential areas for sea turtles) and the likelihood of threats. They illustrated that the current MPA system is able to protect about 5% representation of biodiversity features. Approximately 37% and 65% of the biodiversity features will be more protected if the MPA coverage is increased to 10% and 30% of the total areas of the CT, respectively. They recommended some marine areas that should be designed as MPAs, as the following: the Halmahera Sea, the outer island arc of the Banda Sea, the Sulu Archipelago, the Bismarck Archipelago, and the Malaita Islands. It is also beneficial to expand existing MPAs covering adjacent areas, for example, the Birds Head of Papua, Indonesia; the northwestern part of the Sibuyan Sea, the Philippines; the northern part of Sabah, Malaysia; Milne Bay Province, Papua New Guinea; and Santa Isabel Island in the Solomon Islands (Asaad et al. 2018).

Some studies illustrate that MPA networks can help increase the resilience and recovery of coral reefs after bleaching events. It has been projected that coral reefs in Micronesia could possibly face bleaching events annually by 2040. Regarding that, the Government of Palau has planned to integrate ecological connectivity information, particularly population genetic structure and dispersal patterns, into MPA network design to strengthen reef resilience and recovery after the bleaching events. Cros et al. (2017) revealed that the ecological connectivity of *A. hyacinthus* among the 25 reefs around Palau remained low and there was self-seeding within the reef. The population of *A. hyacinthus* were mainly resulted from self-seeding within reef sites. Knowing this helps construct MPA designs to protect coral reefs under climate change.

4.8.2 Spatial Variations in MPA Networks

Management effectiveness of MPAs and MPA networks varies considerably depending on localities and management practices. For example, China is one of the countries that have long experience of MPA management with more than 250 MPAs designated, but the overall management effectiveness is still below desired expectation due to some major problems regarding systematic and scientific approaches, laws and regulations, governance system, conflicts between conservation and exploitation, financial supports, and monitoring programs (Li and Fluharty 2017). In that regard, Li and Fluharty (2017) proposed the need for improving MPA practices in China, focusing on the improvement of the governance system by strengthening collaboration and connection among MPAs to be functioned as a social, institutional, and learning network, enabling the coherent collaboration/work among MPAs. To achieve conservation objectives, marine protected area networks with appropriate layout, types, and scale are needed to maintain ecological connectivity among MPAs and adjacent areas, sustaining ecosystem functions and services of marine resources in China (Wang 2018).

At the regional scale, the Coral Triangle Initiative (CTI) is an international partnership of six countries (Indonesia, Malaysia, the Philippines, Papua New Guinea, the Solomon Islands, Timor-Leste), aiming to develop a large marine protected area system that consists of comprehensive, ecologically representative, and well-managed MPAs and MPA networks. The project focuses on three principles: ecological, social, and governance. The MPA implementations among CTI countries revealed five common success factors as the following: (1) engagement of multi-stakeholders and intersectoral collaboration; (2) integration of scientific information and local knowledge as well as local participation; (3) enhancement of local capacity; (4) designing multiple-use zones to reduce conflicts; and (5) availability of effective learning and governance networks in which all stakeholders have participated. These key considerations can be applied for the future expansion and establishment of the MPAs and MPA network within the CIT region and other locations of the world (Weeks et al. 2014).

MPA performance can be possibly failed due to conflicts among stakeholders, but engaging local stakeholders in all important decision-making during MPA design, particularly the size, boundary, and location of MPAs, can support conflict resolution and also enhance understandings and knowledge of local people. Krueck et al. (2019) provided an interesting case illustration regarding applying participatory MPA design on Selayar Island, Indonesia, and revealed how to overcome the local disagreement between ecological and social preference on MPA designs. Initially, the disagreement arose when local people supported having four small reserves (0.5–1 km wide) located in the south, while the ecologically optimal MPA design needs one or two large reserves (4–6 km wide) located in the north. The participatory MPA design enabled local people, scientists, and other stakeholders to negotiate altogether, coming up with the alternative MPA design of two reserves with the size of 1.5–2 km wide, located at agreed locations. These MPAs were believed to conserve key fisheries species along with the increase of local fisheries resources as well as the effective management of the MPAs (Krueck et al. 2019).

4.8.3 Fisheries in MPA Networks

Fisheries management is one of the important objectives for the establishment of marine protected areas (MPA) and MPA networks across the world, along with coral reef conservation. In the case of MPAs in the Philippines, some MPAs seemed ineffective because the sizes of MPAs are generally small with high fishing pressures. Several studies highlight the importance of information on reef fish abundance and diversity that can be beneficial to the monitoring and evaluation of MPA effectiveness. Based on the study of Muallil et al. (2015), as many as 114 species belonging to 7 families (Acanthuridae, Scarinae, Lutjanidae, Epinephelinae, Mullidae, Haemulidae, and Lethrinidae) of reef fishes were found inside and outside MPAs in 37 coastal municipalities in the Philippines. The abundance, diversity, and species richness of reef fishes inside the MPAs were higher than those outside the MPAs. Interestingly, fishes with a total length of more than 25 cm were relatively abundant inside the MPAs. The authors suggest that more MPA effort should be emphasized to effectively protect various species of important reef fishes (Muallil et al. 2015). Recently, Muallil et al. (2019) observed fish biomass inside and outside 57 locally managed marine protected areas (MPAs) within the nationally protected Tubbataha Reef National Marine Park (TRNMP), covering 20 provinces in the Philippines. The biomass of seven major reef fish families was observed, including Acanthuridae, Labridae (subfamily Scarinae), Lutjanidae, Serranidae (subfamily Epinephelinae), Mullidae, Haemulidae, and Lethrinidae. They found that 68% of the MPAs had their fish biomass level lower than the maximum sustainable yield for multi-species coral reef fisheries (B_{MMSY}), indicating that these MPAs are overfished. The situation became worse outside the MPAs with the higher proportion of overfished MPAs (86%). Average fish biomass inside the MPAs remains low, with about 20.4% of the unfished level and 10.9% for the biomass outside the MPAs. The fish biomass does not depend on the size and age of MPAs. The authors also argue that although the MPAs are not effective enough for coral reef fisheries management, there are some higher conservation outcomes compared to having no MPA (Muallil et al. 2019).

Fish community structure can be highly dynamic due to the changes of coral reefs after disturbances, e.g., a decline in live coral cover and loss of habitat complexity. Some fish species, called winners, may become abundant in deteriorated reefs, while the abundance of most species, called losers, decline. Thus, knowing the dynamics of fish community structure is helpful to determine the coral reef ecosystem health after experiencing disturbances. Lowe et al. (2019) provide a long-term study on the impacts of benthic habitat changes on wrasse abundance on fringing coral reefs in the Great Barrier Reef, Australia. They revealed that low abundances of several wrasses, i.e., *Hemigymnus melapterus*, *H. fasciatus*, *Cheilinus fasciatus*, *Labroides* spp., *Oxycheilinus digramma*, and *Thalassoma* spp., may be resulted from the reduction of live coral cover and/or loss of habitat complexity following disturbances. On the other hand, there was a positive correlation between the densities of *Halichoeres* spp. and covers of sand and rubble. The wrasse densities on the inshore Great Barrier Reef were influenced by taxa-specific benthic habitat associations rather than NTMR effects and variable top-down predator effects (Lowe et al. 2019).

4.8.4 Assessment and Conservation in MPA Networks

Assessing the effectiveness of conservation strategies is required to maintain biodiversity and ecosystem function and services. Several sets of indicators have been proposed for assessing marine protected areas, but the assessment requires certain information that may not readily available in some MPAs, affecting the assessment accuracy and validity. To overcome such problems, Venegas-Lia et al. (2016) proposed an alternative assessment method using MPA centroid buffers as proxies to indicate their effectiveness. They applied 612 existing MPA boundaries and created centroids and circular buffers of area equal to that of the MPAs' original polygons. A bias of the buffer was calculated from the errors in the estimated area of protected coral reefs. They revealed that the percentage of bias was not influenced by the size of MPA when MPAs are smaller than 100 and 1000 km^2 at a national and a regional level, respectively. To avoid large underestimation, the countries with large MPAs, e.g., Indonesia, should use buffers as MPA boundaries proxies to infer the conservation results of coral reef protection in the MPAs.

MPA maps and mapping systems are a crucial component for managers and practitioners as well as researchers to manage and conduct research on MPAs and MPA networks. An atlas of the Coral Triangle region has been developed and available through the online platform http://www.marine.auckland.ac.nz/CTMAPS, consisting of three major components. The first component provides biodiversity features on marine protected areas, environmental data, and threats. The second one offers spatial information on the areas that have high biodiversity conservation values. The last component illustrates priority areas to be expanded for the Coral Triangle MPA network. The atlas is an interactive online atlas where relevant datasets aggregated and organized systematically from various sources are composed of, supporting a wide range of users and encouraging the capacity building on biodiversity conservation and ecosystem-based management for the Coral Triangle region (Asaad et al. 2019).

A theory of change incorporating research synthesis can be used for evaluating the efficiency of MPAs. Frasera et al. (2019) developed the method to evaluate the efficacy of no-take zones in the Great Barrier Reef Marine Park using 48 studies with 782 measures of impact. They used six principles to assess impacts on biodiversity, including (1) understanding context; (2) identifying the theory of change and causal pathway; (3) anticipating heterogeneity; (4) selecting appropriate methods; (5) identifying a credible counterfactual; and (6) clarifying and interrogating the assumptions required to make causal inferences. They found that the impacts on biodiversity in no-take zones were neutral (57%) or positive (33%). The positive impacts were likely to increase with time from the establishment of no-take zones. The majority of positive impacts were due to fish species for consumption. The authors also mentioned that the impact evaluation techniques could facilitate causal inferences of the impact of marine protected areas (Frasera et al. 2019).

Extensive studies reveal the importance of governance influencing the effectiveness of MPA management. Interesting lessons learned from the implementation of 123 designated MPAs across the South China Sea coast and Hong Kong have recently been suggested by McCook et al. (2019). Limited resources, insufficient enforcement, and coastal development are still the key challenges to conserving ecosystem goods and services in the MPAs. Fortunately, the recent national policy of China tends to balance environmental management and economic development under the strategy known as eco-civilization. This will contribute a great benefit to the marine environment in China and a global environment. The authors also proposed recommendations to improve the MPA performance, covering six themes: (1) maintaining and enhancing marine capacity; (2) promoting economic valuations of ecosystem goods and services and natural capital; (3) improving legal mechanism and enforcement; (4) reducing pollution, particularly water pollution; (5) integrating marine management boundaries in some areas; and (6) enhancing local participation and education (McCook et al. 2019).

4.9 Passive and Active Restoration of Degraded Coral Reefs

The concept of passive and active restoration is adapted from restoration practices for forests (Bradshaw 1996). Passive restoration is the effort to enhance natural recovery and improve ecological functions by reducing and/or eliminating anthropogenic impacts, but active restoration takes human interventions to directly help ecosystems recover to their healthy state (Bradshaw 1996; Holl and Aide 2011; Rinkevich 2019). Several activities are known as active restoration, such as direct coral transplantation, coral gardening, substratum addition (artificial reefs), substratum stabilization and enhancement, and coral larval enhancement.

4.9.1 Passive Coral Restoration

Passive restoration strategies have been applied across the world with various interventions, mainly as a part of environmental programs such as water quality improvement, limiting destructive fishing, limiting the number of tourists, temporary closure, etc. In the case of Thailand, passive restoration strategies have been established as the first priority in the Thailand's Coral Reef Restoration Plan (4 strategies and 15 measures), focusing on reducing major threats to coral reefs, i.e., tourism impacts, water pollution, sedimentation, and fishery impacts as described below (Suraswadi and Yeemin 2013).

The strategy on reducing major threats from tourism has four measures, including (1) minimizing diving impacts (e.g., controlling and monitoring impacts caused by divers, protecting risky and fragile reef area and zoning, enhancing on-board waste management, providing enough mooring buoys, promoting the use of snorkeling trail); (2) raising awareness and knowledge (e.g., establishing tourist center, providing trainings for relevant agencies including tourists and local people, promoting coral reef conservation through various media); (3) enhancing co-management and collaboration (e.g., applying carrying capacity concept, initiating networking among stakeholders, setting up specific committee, legislating relevant regulations, and enforcing tourist operators to use mooring buoy and to have proper waste management); and (4) formulating monitoring plan for tourism activity (e.g., monitoring tourism impacts and status of coral reefs at tourism sites, encouraging local participation in monitoring plan, improving monitoring techniques).

There are five measures to reduce water pollution: (1) assessing water quality in coral reef area; (2) controlling water quality (e.g., providing proper waste water treatment system for households and fish piers, supporting wetland conservation around coral reef area, supporting availability of waste tank installed on boats, prohibiting discharge of ballast water near coral reefs, supporting the use of eco-friendly sun protection lotion, promoting closed aquaculture system); (3) raising awareness and local knowledge (e.g., providing knowledge about impact of water pollution on coral reefs, promoting water conservation campaigns through local media, setting up youth water conservation group, showing water quality information in tourism sites); (4) enhancing co-management and collaboration by practicing and publishing guidelines about mitigation water pollution incident; and (5) formulating monitoring plan for water quality management around coral reef area (e.g., monitoring water quality, installing real-time water quality measurement instrument, monitoring water discharge from local communities).

The following measures have been proposed to reduce threats from sedimentation: (1) applying integrated coastal zone management (e.g., minimizing deforestation and promoting reforestation in coastal areas, promoting sustainable agriculture to reduce soil erosion, engaging local communities into environmental impact assessment and mitigation, legislating local regulations to control coastal development and construction, providing training on coastal zone management for local staff and stakeholder) and (2) reducing threats from coastal development (e.g., using vetiver glass to prevent soil erosion, limiting construction activities during the rainy season, controlling underwater mining, monitoring suspended solid and sedimentation in coral reefs).

Last but not least, four measures reducing fishing impacts on coral reefs were suggested with the following activities: (1) minimizing fishing impacts (e.g., prohibiting the use of destructive fishing gear, provide illegal fishers with training on sustainable fishing practices, preventing waste dumping from boats, providing artificial reefs to prevent the destruction of large-scale fisheries on coral reefs, promoting aquaculture of ornamental fishes, campaigning reef clean-up initiatives); (2) raising awareness, local knowledge, and capacity by providing officials and fishers with training on coral conservation and promoting coral conservation through various media; (3) encouraging integrated fishery management by establishing fisheries networks and fisheries coordination center as well as appropriate fishing zones; and (4) formulating a monitoring plan for reef fisheries (e.g., monitoring reef fisheries, setting up participatory patrol network, improving monitoring techniques). Once the natural condition becomes suitable for corals to grow, active restoration strategies may be subsequently applied with appropriate coral reef propagation techniques (Suraswadi and Yeemin 2013).

Local participation is significant throughout the processes of coral reef restoration projects, from planning to evaluation processes. It has a strong influence on the success of the projects. The other benefit is that local participation can also contribute to awareness-raising and knowledge enhancement. Several studies showed the roles of local communities synergizing coral reef restoration efforts across Southeast Asian countries. In Vietnam, local communities were educated through several training during the coral restoration projects, and they also supported the project implementation. Likewise, in Indonesia, many coral restoration projects were designed to strengthen local community participation in all aspects of reef management via training them to be realized the importance of biological information as a baseline data such as live coral cover, the diversity of reef fishes, and benthic organisms. Local project managers play important roles in helping to develop community-based management frameworks, focusing on seeking alternative income generation and fostering the engagement of local communities throughout the projects from selecting until monitoring the MPAs (Chou et al. 2009).

Passive restoration strategies have been found in various coral restoration plans across the world. In Japan, the Action Plan to Conserve Coral Reef Ecosystems 2016–2020 had been initiated and maximized its effectiveness by focusing priority issues for conserving the coral reef ecosystem, consisting of (1) mitigating land-based pollution, particularly red soil sediment and nutrient salts; (2) promoting sustainable tourism in coral reef ecosystems; and (3) creating the relationship between local livelihoods and coral reef ecosystems. The main goal of this plan was to address the three priority issues by 2020, aiming to achieve its goals on both the conservation of the coral reef ecosystem and the effectiveness of the Action Plan to Conserve Coral Reef Ecosystems in Japan. The survey and monitoring have been heavily emphasized to promote the enhancement of marine protected area management and scientific information and knowledge (Ministry of the Environment of Japan 2016). Passive restoration can also be found in the National Oceanic and Atmospheric Administration (NOAA)'s Coral Reef Conservation Program Strategic Plan. The plan consists of several strategies to increase reef resilience to climate change, sustainable utilization, and habitat restoration, including (1) supporting a resilience-based management approach; (2) improving fisheries sustainability (data enhancement and capacity building for coral reef fisheries management); (3) reducing land-based sources (effective watershed management plans and local capacity for watershed management); and (4) restoring coral populations by improving habitat quality for supporting coral recruitment (National Oceanic and Atmospheric Administration 2018).

4.9.2 Direct Coral Transplantation

Direct coral transplantation projects have been applied in many locations. Yeemin et al. (2006) have highlighted some key considerations learned from the coral reef restoration projects in Thailand, including:

1. Preventing coral reef degradation is more important than implementing coral reef restoration projects.
2. The operation cost of coral reef restoration projects is generally high, and it is difficult to conduct in a large scale.
3. Governments and communities should work together to prevent damage to coral reefs, and the governments should also provide enough facilities for coral prevention.
4. In the areas with enough supply of coral larvae but insufficient available substrate, providing hard substrata may be appropriate. Coral transplantation can be applied at areas where natural recruitment is limited.
5. The projects should be implemented in appropriate scale to ensure that areas are effectively controlled and managed, achieving the benefits on ecosystem restoration, education, research, and ecotourism.
6. Long-term objective should be also established, and the project should be carefully designed, particularly the selection of appropriate transplanted coral species and project sites, to foster their resilience to future environmental changes and to contribute to sustainable uses.
7. It is extremely significant to engage local communities into all stages of the projects from planning, implementation, and evaluating and monitoring to elevate their awareness and to ensure the proper use of direct and indirect benefits derived from the project.
8. Restoration techniques and methods should be simple and cheap but practical in locality, for example, using materials available in local areas can minimize project operation cost.
9. Natural coral fragments should be considered to enhance to increase the survival of those natural coral fragments that are likely to be buried.
10. Using natural planula larvae in restoring coral reefs should be developed, e.g., providing more artificial substrates to enhance coral settlement, cultivating corals, rearing coral planula, etc.; however, these techniques may not be cost-effective in some situations and locations.
11. Scientific information on coral biology and ecology, e.g., coral fragment, reproduction, settlement, recruitment, and partial mortality of coral colonies, should be continuously developed as they are highly important for the success of coral reef restoration projects, particularly in the planning process, e.g., selection of sites and methods (Yeemin et al. 2006).

In the South China Sea, direct coral transplantation can be found with the use of either entire colonies or fragments (Chou et al. 2009). Transplantation of whole coral colonies has been extensively reported in many locations across the region, conducted by various agencies. Yap (2003) mentioned that the success of coral reef restoration projects depends on the long-term survival and adaptability of transplants. In Peninsular Malaysia, a hundred of branching coral colonies were collected from natural reefs and transplanted onto an area of 200 square meters, located about 30 meters from the original site. The coral fragment was fixed to maintain an upright position using wire mesh placed at the bottom of the fragment. Approximately 70% of the survival rate was observed within 6 months. Malaysia's marine parks authority has applied this technique for restoring small shallow reefs (less than 6 meters) damaged by boat grounding or anchoring. There are some efforts to increase the survival rate by elevating the transplanted fragments for 50 centimeters above the seafloor (Chou et al. 2009). In the inner Gulf of Thailand, a transplantation program was carried out to restore damaged reefs at Kham Island, in Sattahip Bay. Eleven genera of hard corals (i.e., *Platygyra* spp., *Montastraea* spp., *Porites lutea*, *Favia* spp., *Symphyllia radians*, *Galaxea fascicularis*, *Montipora* spp., *Favites abdita*, *Pavona frondifera*, *Diploastrea heliopora*, and *Acropora* spp.) and two general of soft corals (i.e., *Sinularia* sp. and *Xenia* sp.) were transplanted by using underwater cement to rapidly attach the coral branches and "heads" onto concrete plates. Under this program, a total of 303 coral colonies (260 massive and 40 branching colonies of hard corals and 3 colonies of soft corals) were relocated from original sites, where the sedimentation rate is high, to the transplantation site by navy vessels. All coral colonies were submerged in aerated seawater during the relocation process. The monitoring on growth rate and survival from 1995 to 1997 exhibited that about 92% of the total transplanted corals were still alive after 6 months of the transplantation. Collaboration among relevant sectors, including the Thai Royal Navy, local communities, students, diving clubs, and private sectors, was an important factor contributing to the project's success (Yeemin et al. 2006). In Singapore, the land reclamation project in the early 1990s destroyed coral communities. Thus, the Nature Society of Singapore, in collaboration with volunteer divers, initiated a coral relocation program for such corals to the new location, and it became one of the world's largest coral transplantation programs. The monitoring conducted by the researchers of the National University of Singapore reported that less than 11% of the transplanted corals survived because of lacking efforts to ensure that transplanted colonies were firmly attached to the substratum (Chou and Tun 1997).

Direct transplantation of coral fragments seems to be extensively applied across Southeast Asian countries. The first coral restoration using coral fragments in Thailand was implemented by cementing the fragments onto concrete blocks. *Porites lutea* showed the highest survival rates of 95%, followed by *Acropora* sp. (83%) and *Pocillopora damicornis* (42%). Although epoxy-cement mixture showed the best adhesion, it is expensive, making it difficult to be applied at the large-scale restoration project. Thus, the mixture of cement, gypsum plaster, and sand was then alternatively used. Later in 1993, a transplantation effort was made at the degraded reef in the west of Krok Island using 30 cement blocks with *Acropora* fragments. The transplantation covered about 30 square meters. After 2 months, 88.24% of them were still alive. The transplanted corals grew at the rate of 6–10 centimeters per year even after 12 months (Sirirattanachai 1994; Sirirattanachai et al. 1994).

Coral fragments resulting from intensive grazing or boring or even from physical breakages caused by storms can also be used for transplantation. Some coral restoration projects in Thailand used the fragment transplantation technique, for example, the restoration project at Khang Khao Island in the inner Gulf of Thailand where fragments of several types of corals, i.e., *Acropora* and *Goniopora*, *Porites lutea*, and faviid corals from a non-reef coral community, attached onto hard substrata with underwater cement. Lessons learned from the project revealed that survivability depends on the size and type of coral fragments as well as the habitat condition and this technique can be further applied in other areas to restore coral community. In 1995, a collaborative project on coral restoration was implemented in Chonburi, the inner Gulf of Thailand, engaging a local university, school, and the Thai Royal Navy. This was a part of the activities under the school's Marine Science Club that aims to raise students' awareness of marine conservation. The students fixed 58 *Acropora* fragments into specially designed PVC pipe frames within the coral nursery area. The transplanted fragments were expected to increase to 500 fragments by 2001 and expected to achieve as many as 10,000 fragments which are the project target. The overall survival rate in the nursery area ranged between 90% and 95%. The fragments with a length of 3 cm or above exhibited the highest survival rate. This project not only elevated the students' awareness of coral reef conservation but also encouraged their learning through experimental activities (Yeemin et al. 2006).

In Vietnam, coral fragments used for coral restoration projects are taken from healthy natural reefs and are attached to several types of structures such as dead coral, concrete blocks, concrete tubs, or steel rods. The first coral restoration project was implemented in 2000 at Con Dao reefs, which had been damaged by typhoon Lynda. Later in 2002 and 2005, the coral restoration projects were applied at the coral reefs in Van Phong and Nha Trang. An extensive coral restoration was initiated to restore and manage coral reefs in south Qui Nhon Bay, Binh Dinh Province. The coral reefs had been degraded because of coral mining and destructive fishing practices. Based on the monitoring data from 2002 to 2004, it revealed that *Acropora nobilis*, *A. yongei*, and *A. microphthalma* were the fast-growing corals. *Porites nigrescens* was well adaptable to seasonal change. It was found that foliose corals (i.e., *Montipora*, *Echinopora*, *Pachyseris*, *Echinopora*), branching *Acropora*, and *Porites* were beneficial for coral restoration. The coral restoration was also applied for the reefs in Phu Quoc archipelago under the UNEP/GEF Project "Reversing Environmental Degradation Trends in the South China Sea and the Gulf of Thailand." The transplantation used more than 700 fragments from 8 species, i.e., *Acropora nobilis*, *A. microphthalma*, *A. millepora*, *A. copiosa*, *A. microclados*, *A. digitifera*, *Pocillopora damicornis*, and *Porites cylindrica*. About 80% and 70% of the total transplanted fragments were alive after 6 and 12 months, respectively. The highest survival rate was found for *Porites cylindrica*; however, it had the slowest growth rate (Vo et al. 2005).

4.9.3 Coral Gardening

Adapted from the concepts used in silviculture, coral gardening has been recognized as the most effective technique for active coral reef restoration, compared with the former direct transplantation of coral colonies from natural reefs onto damaged reefs (Epstein et al. 2001; Epstein et al. 2003; Rinkevich 1995, 2006, 2019). Generally, coral gardening consists of two main processes, nursery and transplantation. Nursery refers to the process of growing large stocks of coral colonies in mid-water floating nurseries, while transplantation is the process of transplanting nursery-farmed coral colonies onto degraded reef areas. The general requirements for coral gardening include (1) a mid-water garden should consist of a large number of coral species with massive, branching, and encrusting forms; (2) establishing unlimited stocks of coral colonies in underwater nurseries; (3) the successful transplantation of farmed coral colonies onto degraded reefs; and (4) the cost of nursery and transplantation process is inexpensive (Rinkevich 2014, 2015). Coral gardening aims to grow coral colonies until they are able to survive, reducing their mortality at transplantation sites. Maintaining coral nurseries at mid-water provides some benefits, i.e., reduced competition for substrate and light, fewer predation pressures, less sedimentation, and better seawater quality (Shafir and Rinkevich 2008; Shafir and Rinkevich 2010). To ensure that it can be applied in other areas, restoration techniques should be low cost and simple while maximizing survival and productivity (Rinkevich 1995, 2000, 2005, 2006; Lirman and Schopmeyer 2016).

Rinkevich (2019) reviewed and illustrated that coral gardening had been developed and improved on various aspects including (1) nursery types (such as the regular bed nursery, the rope nursery, the depth-adjustable nursery, the nursery housing stock of large colonies, and the larval dispersion hub nursery); (2) increasing efficiency for nursery maintenance, sustainability, and productivity; (3) spat feeding in ex situ nurseries for enhanced growth/survival; (4) enhancing growth/survival; (5) the use of eco-friendly antifouling for nursery maintenance; (6) the use of coral fragments that lack polyps; (7) the increasing stocks of larvae from brooding coral species; and (8) techniques to increase the survival rate of coral propagules. Some methods for coral transplantation process have been developed as the following: (1) attachment procedures; (2) coral self-attachment to substrates; (3) clustering transplants for better outcomes; (4) substrates and coating materials; (5) seeding approaches for enhanced settlement and early post-settlement survival; (6) new seeding methodologies; (7) nutritional enhancement to accelerate the growth and survival of corals after transplantation; and (8) maintaining/enhancing genotypic diversity. The development of coral gardening protocols can both promote growth and survival at the nursery stage and contribute additional long-term impacts such as their growth and survival rates as well as the reproduction of transplanted corals (Horoszowski-Fridman et al. 2011, 2015; Horoszowski-Fridman and Rinkevich 2017).

Ecological engineering can support the concept of coral gardening and ecosystem restoration, benefiting both human society and the natural environment. Ecological engineering is important to help to restore degraded coral reefs caused by anthropogenic impacts and global climate change, along with using scientific knowledge to maintain/enhance ecological functions and services of coral reefs (Mitsch 2014; Horoszowski-Fridman and Rinkevich 2017). Active coral gardening has been recognized as a part of an ecological engineering platform for coral reef restoration. Some characteristics are similar to the concept and tools of ecological engineering (Raymundo and Maypa 2004; Horoszowski-Fridman et al. 2011, 2015; Horoszowski-Fridman and Rinkevich 2017). Some marine species can be allogenic and autogenic ecosystem engineers, for example, reef-building corals. They might be impacted by climate change, degrading their engineering capacity. Thus, the understanding of engineering capacity and their ecological functions are vital for supporting coral reef restoration (Wild et al. 2011). Applying the concept of ecological engineering into ecological restoration synergizes the desirable outcomes. Ecological engineering provides predictable outcomes with higher functionalities related to expected ecosystem services, while ecological restoration generates biodiversity-related outcomes that promote the long-term recovery of lost services. The integration of both concepts is considered a valuable method for coral gardening, and it may diminish the restoration impacts on coral reef biodiversity (Aronson et al. 2016; Rinkevich 2019).

Various issues of coral gardening were learned from extensive use of ecological engineering approaches. Herbivorous organisms, particularly fishes and invertebrates, such as sea urchins and gastropods, are an important biological controller for the fouling of macroalgae in coral nurseries. Their grazing activities help control coral-algal dynamics and increase coral growth and recruitment as well as overall coral health (Shafir et al. 2004, 2006; Shafir and Rinkevich 2008). Ecological engineering has been applied for reproductive and planula larvae purposes to construct larval supply through transplantation of nursery-farmed gravid colonies, larval dispersion hubs, or artificial spawning hotspots and to increase larval survival and growth (Amar and Rinkevich 2007; Horoszowski-Fridman et al. 2011; Linden and Rinkevich 2011, 2017; Rinkevich 2014, 2015; Horoszowski-Fridman and Rinkevich 2017; Linden et al. 2019; Zayasu and Suzuki

2019). The methods of ecological engineering applied to restore reefs varied in different locations and purposes. The ecological engineering generally focuses on (1) selection of coral species together with considering their autogenic/allogenic engineering characteristics; (2) serially positioning nurseries to enhance larval recruitment; and (3) growing large coral colonies from ex situ settled sexual recruits (Raymundo and Maypa 2004; Rinkevich 2014; Forsman et al. 2015; Horoszowski-Fridman et al. 2015; Rachmilovitz and Rinkevich 2017; Page et al. 2018). Rinkevich (2019) suggested some useful tools for successful active coral reef restoration, consisting of improvement of coral gardening methods, application of ecological engineering, promotion of migration or colonization, genetics/evolution, microbiome, coral epigenetics, and coral chimerism.

Baums et al. (2019) highlighted the importance of genetic advancement to help reestablish coral populations that are capable of sexual recruitment and genetic exchange to enhance their adaptive capacity under the changing environment. It considers the adaptive genetic variants existing in coral populations for outplanting and monitoring to enhance effective restoration practices. Several genets should be obtained from diverse local reefs. During the propagation, the genet performance (e.g., partial mortality, wound healing rate, skeletal growth rate, bleaching and infectious disease traits, sexual reproductive output) should be monitored and assessed before outplanting to enhance sexual reproduction. Some techniques included routine genotyping of propagated stock, trait-based assessment of genet performance, jump-starting genetic admixture by producing the first-generation offspring for outplanting, and promoting long-range genetic exchange (assisted gene flow, AGF). This information is useful for managers to propagate genets that have desirable characteristics, for example, low partial mortality, wound healing ability, high growth rate, resistance to bleaching and diseases, and high sexual reproductive ability.

4.9.4 Substratum Addition (Artificial Reefs)

The addition of artificial substrate may be important in the area where the substrate is damaged or unstable, making coral larvae difficult to recruit and survive. This method should be used only when the substratum is damaged or insufficient. Artificial substrates range from simple to complex structures, made from a variety of materials, such as PVC tubes, concrete, and fiberglass. In Malaysia, the selection of materials used for artificial reefs is based on three criteria: convenience in mobilization, low cost, and non-labor-intensive. In Singapore, the reefs are generally impacted by high sedimentation, so hemispherical domes made of fiberglass have been used to enhance natural coral recruits and the growth of fragment transplants. Fiberglass artificial substrate can be easily deployed by divers because its weight is generally light. Importantly, artificial substrates should be firmly attached at location, and they do not generate any impacts on local live corals (Loh et al. 2006). In Vietnam, steel poles were used to fix coral fragments to dead coral substratum to increase stability. Concrete tubs were used in the area with limited available substrate, and they increase stability and sediment rejection slopes (Chou et al. 2009).

In Thailand, artificial substrates were deployed in Phuket, the Andaman coast of Thailand, with the objectives of fish recruitment. The initial implementation used a total of 225 triangular concrete modules with the dimension of 50 × 50 × 50 cm. These modules were designed to have three levels of complexity, low, medium, and high complexity, consisting of three, six, and ten units of 50-cm-long concrete pipes of 20, 15, or 10 cm internal diameters, respectively, cemented together into triangular prisms. A total of 25 modules of each type were deployed on three-replicate 5 m × 5 m sandy areas at 4 m depth, covering a total area of 225 m^2. Later, additional 1055 concrete modules with different structures were later deployed, including 50-cm-high concrete domes (with or without netting coats), double-domes, hollow concrete construction blocks, and additional triangular concrete prisms. A total of 1280 modules were finally established, covering an area of about 1280 m^2. Based on the monitoring information, the density of coral recruits observed on triangular prism modules was about 20–40 times greater than that on the natural reef. Furthermore, holes and cavities in the modules became an important shelter for fish and other organisms. Seven years after deployment, 16 genera of corals had settled on the modules, dominated by *Porites lutea*, *Millepora* sp., *Acropora* spp., and *Pocillopora damicornis*, and about 53–60% of the module surfaces were covered live corals. No differences in the growth forms or species of coral were detected among the three levels of complexity. The dome modules had the least efficiency. Rapid co-colonization of fishes was observed within the first 4 months, probably migrating from nearby coral communities. As many as 88 species in 23 genera consisting of migratory, seasonal visitors and resident species were found in the deployment site. No difference of fish assemblages was found among module types and between deployment site and natural reefs. After 7 and 9 years, corymbose *Acropora* colonies were observed with a great abundance of damselfish species. The fishes *Pomacentrus moluccensis* and *P. adelus* were observed with a density of 22–25 per 25 m^2. Twelve years after the deployment, the modules were mostly covered by live corals. This method is useful for restoring coral reefs in areas with insufficient stable substrates, but the environmental condition is suitable for coral growth (Thongtham and Chansang 2009; Edwards 2010).

At Parker Point in the industrial port of Dampier, Western Australia, where coral reefs were impacted by land reclamation, provision of artificial substrates was initiated in 2006 using local rock and recycled concrete sleepers, covering a total area of about 0.6 hectares. Although the environmental condition in this area was not much suitable for corals, coral colonization can still be observed. The coral density observed on the tills exhibited a range of 113–909 recruits per m^2. However, the coral density observed in the quadrats gradually increased from 6.0 recruits per m^2 at 8 months to 24.0 recruits per m^2 at 62 months after deployment. The composition of coral taxa found on the artificial reef was similar to nearby natural reefs, but the proportions were different. Three corals, i.e., *Pseudosiderastrea tayami*, *Mycedium elephantotus*, and *Leptastrea purpurea*, were abundant on the artificial reef. A rapid increase in coral cover was observed at 62 months after the deployment. This study highlights that even in the area experiencing natural and anthropogenic disturbances, the provision of artificial substrates can still be beneficial for promoting coral recruitment and coral recovery (Blakeway et al. 2013).

4.9.5 Substratum Stabilization and Enhancement

Unstabilizing or loosen substratum obstructs coral recruitment and reduces coral survival rates, leading to the slow or limited recovery of coral reefs. Unstabilizing or loosen substratum occurs on the substrate with coral rubble which is caused by physical damages from storms, ship groundings, illegal dynamite fishing, etc. (Boström-Einarsson et al. 2018, 2020). The methods used for substratum stabilization and enhancement vary among locations. In the coral reef rehabilitation project in Komodo National Park (KNP), Indonesia, different low-cost methods using rock piles, cement slabs, and netting pinned to the rubble were compared at a scale of 1 × 1 m. They found that higher densities of corals were observed on rock, followed by cement, netting, and untreated rubble. Later, the plots of rock piles (10 × 10 m) were established in 2000. Three years after the establishment, an increase in the cover of scleractinian corals was found on the rocks. Regardless of larval supply adequacy, rocks seemed to be a great option for substratum stabilization and enhancement as their cost is relatively low and it is possible for a large-scale rehabilitation (Fox et al. 2005). Rubble fields were also found in the Philippines due to blast fishing. Efforts to stabilize a 20-year-old rubble field in the Philippines were implemented using plastic mesh and rock piles with the seize plot of 17.5 m^2, aiming to increase topographic complexity and restore fish habitat. Within 3 years, fish abundance and body size in the restored areas were similar to those observed in nearby natural reefs. Coral recruitment and coverage increased over time. The survival of coral recruit observed on restored areas (63.5%) was much higher than that on rubble (6%). The cost of this method is also low for stabilizing rubble fields to enhance natural coral recovery (Raymundo et al. 2007). Giant clam shells can also be used for stabilizing soft bottoms, according to the implementation in the Philippines. Live coral colonies can grow on the shells of live clams and shells of dead clams also a calcium carbonate substrate used for coral transplantation (Chou et al. 2009).

4.9.6 Coral Larval Enhancement

The coral larval enhancement approach is also known as larval propagation, sexual propagation, or larval re-seeding. The overall objective is to increase the rates of larval production and to enhance the success of coral recruitment. Several methods have been developed to deal with natural limitations, including (1) limited coral fertilization rates due to low coral cover and asynchronous spawning, and (2) coral embryos and larvae can be moved away from reefs and settle on an area with unfavorable conditions (Harrison and Wallace 1990; Richmond 1993; Jones et al. 2009; Boström-Einarsson et al. 2018). Most methods focused on promoting coral settlement and recruitment at reef sites where coral recruitment is abnormally declined. Several studies recommend that sexual reproduction methods are beneficial for restoring the coral population as they increase genetic diversity, leading to the improvement of adaptation and resilience (van Oppen et al. 2017). Generally, two approaches to coral larval enhancement have been recommended to enhance coral recruitment.

1. Collecting or rearing embryos and larvae to settle on artificial structures and later relocating on natural reefs. Some studies illustrated that the culture of spawned coral gametes could produce a large number of embryos and larvae, some of them settled on settlement surfaces that can be further relocated to coral reefs (Omori 2005, 2019; Omori et al. 2008; Iwao et al. 2010). The success of transplantation of settled juvenile corals, derived from ex situ culture, onto natural coral reefs was also reported in the Philippines. The survival rates depend on the size and age of recruits; the larger size and older age classes had higher survivability (Raymundo and Maypa 2004; Villanueva et al. 2012; Baria et al. 2012; Guest et al. 2014). A study in Palau illustrates that the larvae of *Acropora digitifera* were ex situ reared and they settled on concrete pallet balls and settlement tiles in an enclosed tent (Edwards et al. 2015).
2. Developing larval enhancement techniques, for example, collecting coral gametes during spawning and rearing embryos and larvae in tanks or on the coral reef, and

then releasing them directly onto the reef (Heyward et al. 2002, Suzuki et al. 2012; dela Cruz and Harrison 2017). An experiment conducted at Ningaloo Reef, Western Australia, revealed the success of larval enhancement by collecting spawned and rearing the embryos and larvae in a floating pond for 6 days before releasing them to natural reefs. They also found that recruitment rates on tiles in the larval enhancement plots observed after 6 weeks were approximately 100 times compared to control sites (Heyward et al. 2002).

Achievement of long-term larval enhancement and recruitment has been found on degraded reef areas in Northern Luzon, Philippines (Harrison et al. 2016; dela Cruz and Harrison 2017). dela Cruz and Harrison (2017) found that recruitment and reestablishment of a breeding population of *A. tenuis* colonies were observed after 3 years, resulting from mass larval settlement. They collected spawned gametes from 30 gravid colonies and then reared the embryos and larvae in ex situ tanks for 4 days. They were then transferred and retained in low-cost fine mesh larval enclosures for 5 days. They also found higher rates of larval settlement tiles, while none of the settlement was observed on control tiles. The highest mortality rates of settled corals were observed within the 5 months after settlement, and then the mortality rates became low (dela Cruz and Harrison 2017). The rapid growth of these settled corals in the larval enhancement plots spawned annually over the past 3 years, and they became the essential sources of larval production on these reefs. The larval enhancement of *Acropora* species and some brain corals in the Philippines provided similar patterns of settlement, recruitment, and growth. Larval enhancement which was conducted on large-scale reef patches (100 m^2) in the southern Great Barrier Reef provided desirable outcomes (Boström-Einarsson et al. 2018).

Suzuki et al. (2020) designed an integrated in situ collector system to collect spawned gametes and culture them until they settled on artificial substrates. A cylindrical larval cradle was designed covering with a nylon mesh, having a total volume of 9 m^3, positioning vertically toward the seafloor. They recommended three considerations to maximize the efficiency of the larval cradle: (1) availability of an open area of the sea surface and the use of fine mesh size (<100 μm) yielded high fertilization and survival rate (>90%); (2) a special skirt-shaped net (3 m in diameter), connected with bundle storage by a connection hose, helped collect more gametes from colonies over a wide area; and (3) availability of short square tube pieces (square hollow sections, SHS) can facilitate larval settlement and survival. This system helped collect a number of million eggs and enhance several thousand settled juvenile corals, leading to higher survival rates during early life stages.

Cryopreservation of larvae has been suggested to use for preserving coral sperm under ultra-low temperature to conserve genetic diversity. However, cryopreservation of larvae is still impractical due to various reasons such as large volume, membrane complexity, and chilling injury.

Technically, cryopreservation can be applied with coral larvae by vitrificating them in a 3.5 M cryoprotectant solution (10% v/v propylene glycol, 5% v/v dimethyl sulfoxide, and 1 M trehalose in phosphate buffered saline). To resume them, they are warmed at a rate of approximately 4,500,000 °C/min with an infrared laser, showing about 43% survival rate, in the case of *Fungia scutaria* larvae. About 12 h after laser warming, surviving larvae were able to swim and continue to develop. This is important for the biodiversity preservation of coral larvae; however, research and development is still required to overcome such limitations and support the future application (Daly et al. 2018).

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Biogeochemical Dynamics of Coral Reef Systems

5

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Abstract

Biogeochemistry of chemical elements plays a critical role in the evolution of coral reefs with significant impacts on the relationship between corals and symbiotic algae, new vs recycled productions, and the biodiversity of coral ecosystem. In this chapter, we review the major driving forces and pathways of chemical elements in coral reefs and assess the effects of biogeochemical cycles on the autotrophic and heterotrophic processes as well as the calcification of corals in the Western Pacific Ocean. Using a modeling approach, we estimate the influence of hydrographic properties and nutrients on the dynamic nature (e.g., production, respiration, and calcification) of coral systems. This study is essentially based on the research results from the Western Pacific Region, but the experiences and lessons learned can be beneficial to the other areas of the world.

Keywords

Coral reefs · Biogeochemical cycling · Nutrients and trace elements · Modeling approach

Notations[1]

Symbols	Meaning and Units
Ω_{ar}	Degree of saturation for aragonite in seawater, which is a function of temperature and salinity
CH_2O	A simplified form representing photosynthetic organic matter
DIC	Dissolved inorganic carbon (μmol/l or μM)
DIN	Dissolved inorganic nitrogen (μmol/l or μM)
DIP	Dissolved inorganic phosphorus (μmol/l or μM)
DOC	Dissolved organic carbon (μmol/l or μM)
DSi	Dissolved silicate (μmol/l or μM)
Forgc	Organic matter ingestion in numeric simulation
G	Calcification rate of corals in numeric simulation
GE	Temperature-dependent zooxanthellae growth efficiency in numeric simulation
pCO_2	Partial pressure of CO_2 in water and/or atmosphere, unit in μatm and/or ppm (v/v)
Pg	Gross photosynthesis rate of coral reefs in numeric simulation
POC	Particulate organic carbon (μmol/l or μM and/or % of total suspended matter)
R	Respiration rate of coral–zooxanthellae symbiosis in numeric simulation
NEP	Net ecosystem production (mmol C/m^2/day)
NEC	Net ecosystem calcification (mmol/m^2/day of $CaCO_3$)
TA	Total alkalinity (μmol/l or μM)

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[1] Summary of abbreviations and symbols with their units used in the text of this chapter

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5.1 Introduction

Coral reefs (CRs) are widely distributed in tropical and subtropical areas of the Western Pacific–Indian Ocean and Caribbean Sea between 40 °N and 40 °S and have an indispensable role in the economics of most maritime countries in these regions, such as food supply, tourism operation, and shore protection. Coral reefs in the Western Pacific Ocean, like those in other tropical waters, can be classified as fringing reefs and individual reefs that make atolls and/or coral islands in the open water, as well as the Great Barrier Reefs (GBR) that covers an area of 250×10^3 km^2. The fringing reefs in coastal environment are connected to the land mass and/or islands through back flats (i.e., reef flat) and/or seagrass beds; hence, they are affected by the freshwater discharges from land sources, including fresh water, dissolved chemicals, and total suspended matter. On the other side, atolls are usually located in the area far from the direct impact of land-sourced materials (e.g., plumes from river) where the concentration of dissolved nutrients can be low. The dichotomy of coral ecosystems in oligotrophic waters has been debated in the literature and concerns the fact that coral reefs are in the environment of very low nutrient levels but display a highly productive nature, reaching up to 5–10 g C/m^2/day in comparison to the world ocean average of 0.4 g C/m^2/day (D'Elia and Wiebe 1990; Atkinson and Falter 2003; Atkinson 2011). Like the other parts of this planet, however, coral reefs in the Western Pacific Region can be considered as over-stressed ecosystems under the perturbations of natural as well as anthropogenic forcings and suffer from declines in most coastal areas from the molecular to the system levels, including health, diversity, various functions, and services (Wilkinson, 2008, Chap. 2).

Biogeochemical cycles play a key role in maintaining productive coral reefs in the marine environment, because high production requires to feed coral with organic matter and calcium in sufficient quantities and these materials are supplied through complex interactions and cycling loops between land, ocean, and atmosphere. The availability and stoichiometric ratio of nutrient species have a dramatic influence in determining the primary production, biodiversity, and structure of phytoplankton community, which in turn impacts the entire coral ecosystem through changes in food relationship (i.e., bottom–up effect). The role played by the microbial loop in the ecosystem function is also determined by the availability of some of micronutrients (e.g., trace elements). From the law of conservation of mass, the sustainability of coral reefs relies on the relationship of external and recycled macro- (i.e., N, P, and Si) and micronutrients, such as Cd, Co, Cu, Fe, Mn, and Zn. While the recycled nutrients maintain the basic metabolic processes of reef system, the supply of external supply of nutrients and trace elements determines the amount and quality of new or net production and hence food supply to human society. Moreover, the biogeochemical cycles can be linked to the energy flow of the ecosystem through the measurement of metabolic organic matter (e.g., heat change) and law of conservation of energy.

In this chapter, we examine the interactions of biogeochemistry and coral ecosystem at the functional level. First, we identify the external forcings that provide the macro- and micronutrients to the coral reefs. Then the major sources of chemical elements are compared to understand the collective impacts of the various driving forces on the coral ecosystem. The major pathways of element cycle are coupled with the metabolic processes that link the different components of the coral symbiotic community with corals, as well as other pelagic and benthic organisms in the reef system. Based on an overview of the biogeochemistry of coral reefs, we analyze the potential impacts of climate change and human activities with the prospect of global warming and coastal economic booms in the twenty-first century. Finally, model approach is adopted as a tool to understand the critical role of biogeochemistry in coral reefs, with applications of scenario analysis. Although this work is focused on the studies of coral reefs in the tropical and subtropical environments of the Western Pacific Region, results from other world oceans are incorporated when comparison and synthesis are undertaken.

5.2 External Driving Forces of Coral Reefs

The biogeochemistry of coral reefs is under the combined driving forces (i.e., multi-stressors) that regulate the nature of the flow of chemical materials through water exchange. The driving forces also include natural processes as well as the external impacts related to human activities, summarized in Table 5.1 with brief discussion as below.

5.2.1 Solar Radiation

In surface oceans, solar photon flux reaching the sea surface can be as high as ca. 250 W/m^2 in tropical and subtropical waters. A reduction of radiation with water depth follows an exponential and/or power law and is affected by the surface photon flux and turbidity of the water column. The euphotic water depth adjacent to coral reefs can be up to 50–100 m. With the solar radiation, an increase in temperature can change the density of the upper part of water column and create the thermocline.

Although the solar energy is indispensable to the photosynthesis of coral ecosystems, strong radiations in a low-latitude aquatic environment can cause damage to

Table 5.1 Important driving forces in the biogeochemical cycles of coral reefs

Driving forces	Temporal and spatial dimensions	Measurements requested
Solar radiation	Daily and seasonal nature, with changes due to cloud cover and across low latitudes	Photon flux at surface, UV, and photosynthetically active radiation (PAR) in the water column
Ocean circulation	Seasonal and inter-annual character, with nature linked to climate variability like ENSO and the Pacific Decadal Oscillation (PDO), having an impact on basin-wide scale	Velocity, salinity, temperature, epifluorescence, and turbidity
Tides (e.g., M_2, S_2, K_1, and O_1)	Semi-diurnal, daily, monthly, and seasonal variations, particularly in the coastal zone with strong effect of mixing and transportation	Time series for water level and current (i.e., direction and speed)
Ekman pumping and suction	Related to the wind-induced circulation and interactions with benthic topography in low latitude region, with strong seasonal and the mesoscale nature	Temperature and salinity, nutrient concentration, DO, and dissolved inorganic carbon
Riverine influx and groundwater discharge	Daily and seasonal variations and linked to human beings on land, with changes in fluxes of water, sediment, and pollutants (e.g., nutrients)	Salinity/conductivity and temperature, turbidity, and nutrient concentrations
Atmospheric depositions	Including wet and dry fluxes either from land sector or from the seaside, with daily and seasonal variation and fingerprints of human emission	Aerosol, gas, and rainfall collections for chemical composition analysis and air mass trajectory determination
Eutrophication	Phenomena related to the over-enrichment of nutrients from land sources, with impacts most likely at mesoscale in coastal environments	Hydrographic parameters (e.g., S and T) and nutrients, phytoplankton taxonomy, and pigments
Oxygen depletion and hypoxia	Either local or basin-wide scale with seasonal and/or annual persistence, having negative impact to the food webs	Hydrographic parameters and dissolved oxygen
Reclamation	Human activity in coastal areas, leading to loss of habitats because of changes in land use for the purpose of economics	Change in coastal line and bathymetry, mapping of surface areas
Fishery	Harvest of organisms through food web, with negative effect of by-catch	Composition and quantity of harvested biomass
Coastal engineering	Events related to the economic activities, including the construction of harbors, oil platforms, and sediment dredging	Mapping of impacted areas and bathymetry
Climate change and variability	Surface water warming, ocean acidification, and sea level rise	Time series for pH, carbonate system (e.g., $p\mathrm{CO}_2$ and TA), temperature, and sea surface variability at gauge stations

photosynthetic cells, particularly the shortwave radiation with wavelength of <400 nm (e.g., UVA and UVB). The tropical oceans are subject to the low solar zenith angle, the natural thinness of the stratospheric ozone layer, and the high transparency of the water column (Banaszak and Lesser 2009). In the tropical ocean, solar radiation can penetrate to a considerable depth and favors expulsion of symbiotic algae and other more resilient coral reef turf algae (Fricke et al. 2014; Zhou et al. 2017).

5.2.2 Tide and Waves

In coastal areas, tidal energy plays an important role in the mixing, transport, and dispersion of water, planktonic cells (e.g., phytoplankton and zooplankton), and sediments. Tidal currents can be 1–2 m/s, and excursion can extend to 10–20 km or even more in a typical semi-diurnal tidal circle. Wave energy and tidal-induced waves can stimulate strong horizontal and vertical mixing. In shallow water environments, vertical distribution of wave energy can structure the benthic boundary layers and even destroy the sea bottom morphology and result in the resuspension of deposited sediments. These resuspended sediments can be carried upward along with vertical mixing by waves. Internal waves generated from the ocean interior may also up-slope to the coral reef to bring cold and nutrient-rich deep ocean water and create strong mixing and subsequently affect the coral biology.

In the tidal-affected areas, a difference of water level between flood and ebb tides, e.g., 2 m, may expose coral reefs to the air and/or close to the sea surface during low tide period. Aerial exposure can be a great stress for corals, if they are close to the sea surface.

5.2.3 Winds and Monsoon

Transfer of energy and momentum from atmosphere to the ocean can be through wind, which usually is an important driving mechanism for surface water movement that affects coral reefs, particularly fringing systems (Li et al. 2013). In tropical and subtropical oceans, winds stir the sea surface and induce currents that disperse the pollutants in a range of mesoscales (e.g., 50–100 km) and create a vertically well-mixed water layer of dozens of meters (e.g., 10–20 m). In extreme cases, such as during the typhoons and/or tropical cyclones, this strong vertical mixed layer can reach up to 50–100 m.

The monsoon is another important phenomenon of tropical and subtropical oceans, which not only can create the dry and rainy periods of a year but also results in different patterns of surface water circulation and hydrography, such as the temperature structure, salinity gradient, current/flow field, depth of vertical mixing, and waves with different periods.

5.2.4 Water Circulation and Currents

Here circulation refers to a net and consistent water flow pattern in a relatively open area with typical rates of 10–50 cm/s that directly affects the hydrographic structure (e.g., salinity and temperature) of the water body in the sub-basin scale, with profound significance for material transport (e.g., coral larvae) and connectivity between individual reef systems. Usually water movement patterns between the foreside and backside of coral reefs are different, and hydrographic and chemical (e.g., nutrients) gradients can be generated across the reef crest. In the case of fringing reefs and atolls, the reef flat and lagoon behind the reef edge/crest have a relatively limited water exchange with the open ocean, and hence extended residence and/or flushing times may occur.

5.2.5 Land-Sourced Influxes

Rivers play an important role in the delivery of land-sourced materials to the ocean, including fresh water and terrestrial sediments, which impact particularly on fringing reef systems (McCulloch et al. 2003). Influx of fresh water can create buoyancy plume with dramatic effect on salinity distribution near the surface, generating a halocline. Terrestrial sediments carried by river increase the turbidity of the water column with a negative effect on photosynthesis. The deposition of suspended sediments may cover the surface of corals and affect the metabolic processes there.

Another important pathway of terrestrial dissolved solutes into the coastal area is through submarine groundwater discharge (SGD). Here SGD includes the direct inflow from aquifers (e.g., fresh water) as well as the seepage of recycled seawaters. Recently, it has been recognized that SGD plays a non-negligible role in the delivery of chemical materials from land to the ocean, including coral reefs (Street et al. 2008; Moore 2010; Amato et al. 2016).

5.3 Sources of Chemical Elements in Coral Reef Systems

The delivery of chemical materials to coral reefs, such as nutrients and pollutants, consists of various pathways, as illustrated in Fig. 5.1. Collectively, these sources carry the chemical materials that determine the upper limit of new production if the material is referred to as limiting nutrients or create damage to the coral reefs when referring to pollutants and/or toxins, taking into consideration the utilization efficiency of the ecosystem.

5.3.1 Terrestrial Material Inputs

River and SGD can deliver nutrients and trace elements directly to the coral reefs through dispersal of fresh water plumes and seepage from the sea bottom, which can induce degradation of coral systems in the adjacent marine environment (Roder et al. 2013). In the case of SGD, the flux also includes chemical elements remobilized from the seabed and carried by the recycled seawater. Relative to seawater, the solutes discharged by rivers and SGD sources usually have much higher concentrations of nutrients, organic carbon, and trace elements. The stoichiometry of nutrient species from land sources, such as DIN/DIP and DSi/DIP, can be elevated compared to the Redfield ratio (e.g., N: P = 10–20) in the ocean, where DIN refers to dissolved inorganic nitrogen ($DIN = NO_3^- + NO_2^- + NH_4^+$). The DIP refers to dissolved inorganic phosphorus and is similar to soluble reactive phosphorus (SRP) in practice, and DSi refers to the concentration of dissolved silicate, respectively.

However, if the SGD is dominated by recycled seawater, the salinity and/or conductivity of seepage solutes can be high, and nutrient concentrations are relatively low, approaching those of seawater. In this case, ratios of DIN/DIP and DSi/DIP can be similar to or even lower than the so-called Redfield ratio.

Generally, concentrations of nutrients, trace elements, plant pigments (e.g., Chl-*a*), and suspended sediments are higher in the nearshore compared to offshore waters across the coastal environment. Thus, nearshore corals and benthic communities must adapt to higher variations in light availability and gradients of hydrographic as well as chemical variables than those on reefs more distant from the coast, although the processes contributing to such declines in properties change from place to place (Cooper et al. 2007).

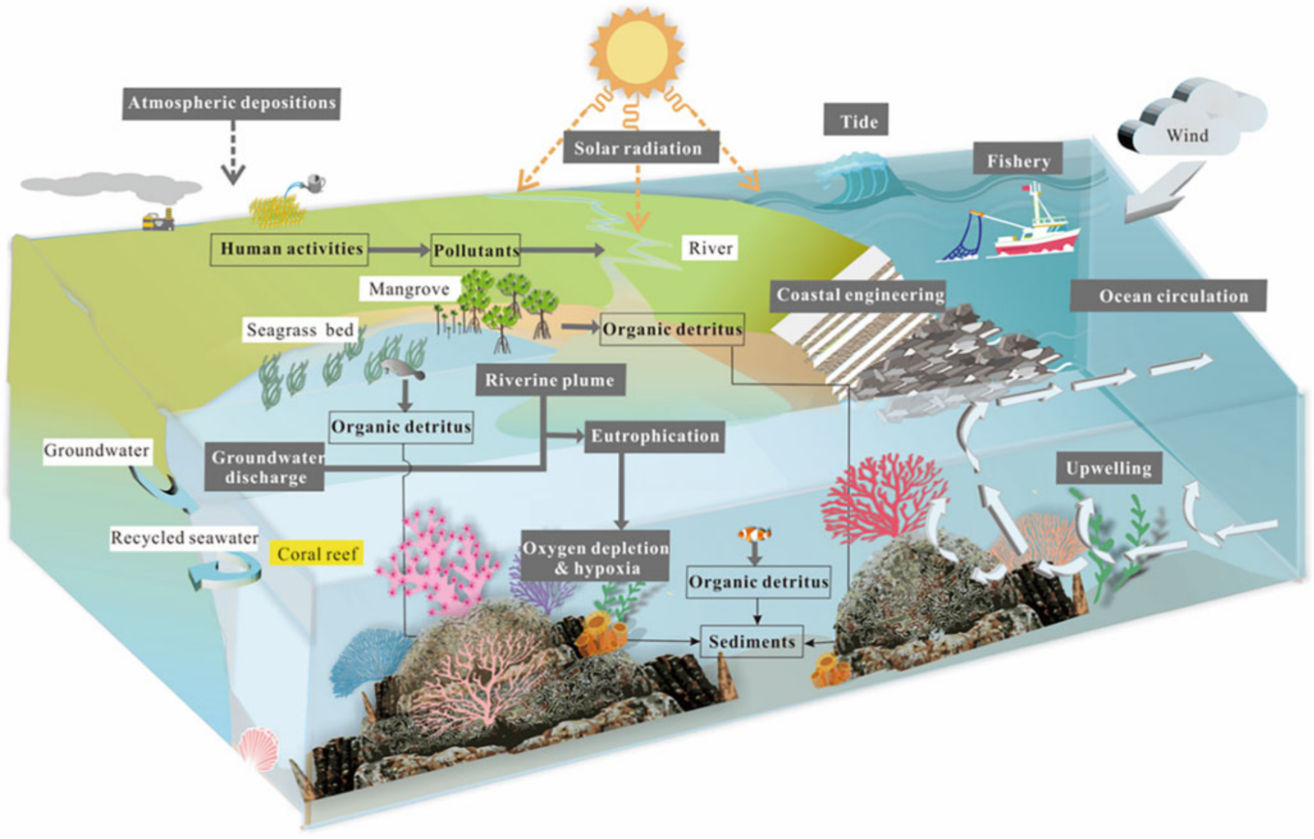


Fig. 5.1 Cartoon illustration of major driving forces that regulate cycles of chemical species (i.e., nutrients, trace elements, and other pollutants) in the coral reefs and adjacent marine waters, with their nature and potential impacts presented in Table 5.1

5.3.2 Atmospheric Depositions

Atmospheric flux to the sea surface consists of components such as wet (i.e., rainfall) and dry depositions, the latter including aerosols and gas species for some of chemical elements (e.g., NO_x). Although riverine input is usually considered important on the biogeochemistry of the adjacent marine environment, this impact decreases in the ocean along with increase of distance from the coast as river flow rapidly loses its inertia and/or identity, such as changes in salinity and temperature of surface plumes. Hence, atmospheric depositions of chemical elements can become the dominant external source of nutrients and other pollutants to the remote areas, particularly offshore coral reefs and oceanic atolls (Ren et al. 2017).

The composition and variability of atmospheric depositions can be related to the wind field and nature of the source region, which can be identified with the help of techniques, such as air mass back trajectory simulation. Usually, the air mass from urban and suburban areas have higher concentrations of nutrients and other pollutants than the remote regions. For example, concentration of nutrients in marine aerosols is lower than those from the land sector. Again, when compared to surface seawater, continental aerosols have higher DIN/DIP values than the Redfield ratio. Different from phosphorus, gas species of nitrogen can make a significant contribution to the total atmospheric deposition flux. Similar to the watersheds of the river, however, human activities from up-wind area can have an important influence on the composition of atmospheric depositions to the surface ocean. The NH_4^+/NO_3^- ratio of air masses from areas affected by agriculture can be twice as high as those from urbanized regions because of loss via evaporation of chemical fertilizers (e.g., ammonia).

5.3.3 Coastal Upwelling

Coastal upwelling occurs because of geostrophic effect (i.e., Coriolis forcing) on circulation and also because of interactions between wind-induced currents and topography of coast and/or sea bottom. In the tropical and subtropical oceans, wind-driven circulation is usually accompanied by upwelling in coral reef areas. The impact of upwelling on the surface seawaters is related to the depth from where water mass is upwelled and the chemical composition of the in situ water body. Generally, the upwelled water has lower temperature, pH and dissolved oxygen but higher concentration of nutrients and dissolved inorganic carbon (i.e., $p\mathrm{CO}_2$) relative to the surface water. Those upwelled nutrients promote the primary productivity in euphotic zone, while high CO_2, low temperature and pH, and low dissolved oxygen may have negative effects on the metabolism of organisms (e.g., coral cells). The persistent upwelling can cause the damage to the coral systems as well because of exposure to low temperature and to depletion of dissolved oxygen.

5.3.4 Recycling Within the System

In coral reefs, a large amount of macro- and micronutrients can be recycled because of heterotrophic processes. Microorganisms decompose the organic materials and provide inorganic nutrients to autotrophs via mineralization, which is referred to as the microbial loop. Different from externally supplied macro- and micronutrients, the recycling can be considered as "internal source" of nutrients to the autotrophic organisms, e.g., zooxanthellae, for coral reefs. Here the so-called internal source of nutrients also includes the supply of nutrients through sediment–water exchange in coral reefs. The recycling of nutrients within the system plays a critical role in maintaining the balance of anabolic and catabolic processes at the basic metabolic level without export of net products from the ecosystem.

Suzuki and Casareto (2011) reported the molecular size distribution of DOC and DON in coral reefs and indicated that a low molecular weight fraction (i.e., <1000 dalton) represents more than 30%–40% of total DOC and DON (Fig. 5.2). Apparently, the high molecular weight dissolved organic matter (DOM) is generated within the coral reefs (e.g., internal cycling), while a large amount of low molecular weight fraction can be carried into the coral reefs through exchange with offshore waters (i.e., external sources). Dissolved organic matter includes a wide range of components, such as urea, amino acids, carbohydrates, and humic and fulvic substances. As shown by Suzuki and Casareto (2011), dissolve organic matter released by nitrogen fixers make up a significant amount of DON in coral reef waters, and N_2 fixation can contribute up to another 30%–40% of community primary production.

5.4 Major Pathways of Biogeochemical Cycles

Biogeochemical cycles consist of a number of pathways that decipher the chemical reactions at the molecular level and determine the direction and rate of material flow in coral reef systems. Some of the major pathways that compose the loop of biogeochemical cycles for coral reefs are shown in Fig. 5.3. In this section, we analyze the major pathways of material flow in the biogeochemical cycles and examine their inter-relationships, which allows understanding of cycles for nutrients and trace elements in the coral reefs based on knowledge of the food web. A comparison among different biogeochemical pathways requires the integration of research data from various reef systems and in different hydrographic conditions.

5.4.1 Autotrophic Production and Symbiosis

Probably the most marvelous feature of coral reefs is the symbiotic relationship between zooxanthellae, a type of dinoflagellates and coral polyps. In such a symbiotic system, zooxanthellae serve as autotrophs that absorbs solar energy and takes up the macro- and micronutrients in a proportional way to synthesize the organic molecules of reduced carbon, given that dissolved inorganic carbon (DIC) is not limiting. The chemical reaction of photosynthesis can be simplified as:

$$\mathrm{CO}_2 + \mathrm{H}_2\mathrm{O} + \text{Nutrients} \xrightarrow{\text{hv}} \text{Organic matter} + \mathrm{O}_2, \quad (5.1)$$

The primary production of coral reefs can be determined through measurements of synthesized organic matter on C-14 and/or C-13 labeled DIC after incubation experiments. In fact, photosynthesis is composed of a series of anabolic reactions and the produced organic molecules, such as amino acids, fatty acids, sugar, and other carbohydrates, which have different metabolic functions depending upon the species of interest and available macro- and micronutrients. It should be recognized that photosynthesis by zooxanthellae is a powerful engine that drives the energy flow and biogeochemical cycles of coral systems.

The photosynthesized organic matter is used to maintain the metabolic requirements (e.g., respiration, growth, and reproduction) of primary producers, and another part of the organic material is translocated to feed corals and hence drives the main chain of the food web. The dead cells can be released into water as particulate organic matter (POM) and then heterotrophically decomposed by microorganisms including fungi (e.g., microbial loop). Synthesized organic matter can also be released into water via excretion in dissolved forms (i.e., DOM).

Coral polyps can use the energy of translocated organic matter from zooxanthellae to satisfy their metabolic requirements. The exudation of wastes (e.g., mucus) from corals includes organic forms of nutrients, which upon remineralization produce inorganic nutrient species (e.g., DIN and DIP) that again can be used by zooxanthellae to fuel photosynthesis, which is considered as a type of recycled production.

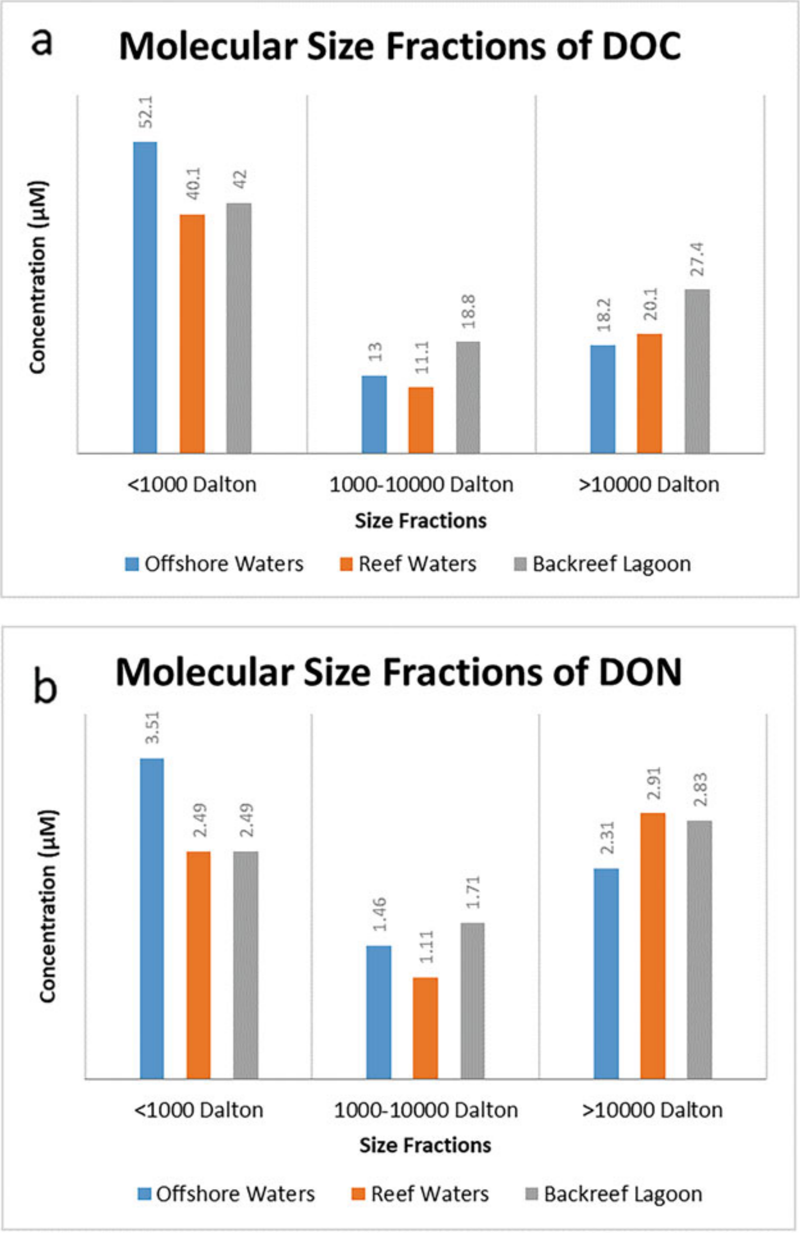


Fig. 5.2 Concentration (µM) and molecular weight size distribution (i.e., Daltons) of coral reef waters at the Okinawa, (**a**) for DOC and (**b**) for DON; data are from Suzuki and Casareto (2011)

In coral reefs, the ratio of new and recycled productions can be very different between different coral species, depending on the availability and proportion of external and recycled nutrients. In the case of nitrogen limitation and if we assume that external source of DIN is in the form of nitrate and recycled inorganic nitrogen in the form of ammonium, the proportion (i.e., "*f* ratio") of new versus total productions can be estimated by:

$$f = \frac{NO_3^-}{NO_3^- + NH_4^+}, \tag{5.2}$$

where $NO_3{}^-$ and $NH_4{}^+$ represent new and recycled productions, respectively, sustained by nitrogen (Sarmiento and Gruber 2006). The new and recycled productions can be determined by mesocosm experiments (e.g., incubations) using N-15 labeled nitrate and/or ammonium and then measure the N-15 to N-14 ratios of end products of photosynthesis.

Community productions and respiration of coral reefs vary over a wide range depending upon the place and with strong daily and seasonal variabilities in the Western Pacific Region (Table 5.2), in comparison to other places in the broad Indo-Pacific Rim (e.g., Andaman Sea), Caribbean Region, and the Red Sea, respectively (Yates and Halley 2003; Silverman et al. 2007a, b, 2014; Jantzen et al. 2013; Naumann et al. 2013; Tac-An et al. 2013). However, the comparison indicates that coral reefs can be an important

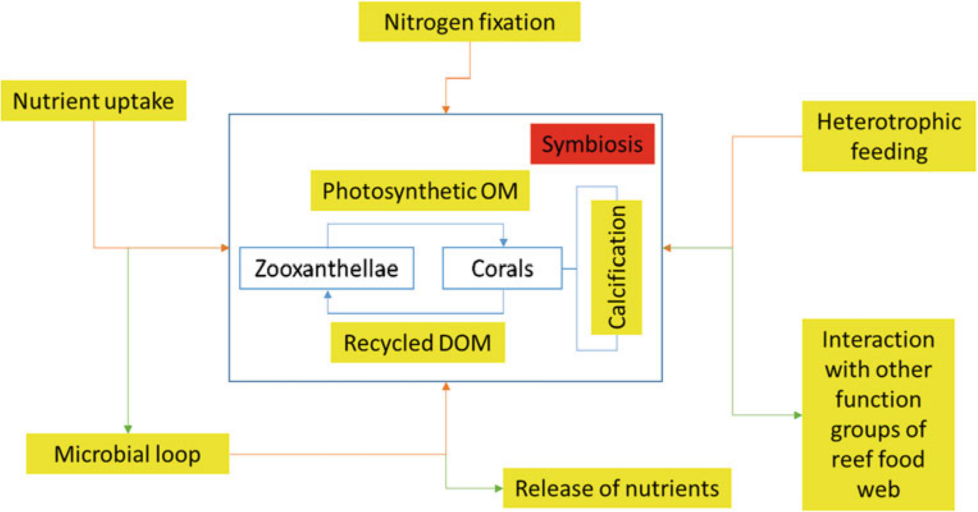


Fig. 5.3 Illustration of major pathways of biogeochemical cycles that is related to the processes of energy and material transfer for the coral reefs. Symbiosis of corals and zooxanthellae cells are illustrated in the box. Arrows in brown color indicate driving forces, those in green show the feed-backs and/or interactions

export source of nutrients and organic matter to the adjacent offshore environment and hence the supporter of ecosystem stability in a much larger spatial scale (Sheppard et al. 2009).

5.4.2 Heterotrophic Processes

Beside the zooxanthellae and coral symbiosis, coral cells can sustain metabolism, growth, and reproduction via heterotrophic pathways (Fig. 5.4). It has been reported that corals can use dissolved organic materials in the water column, organic detritus, and even organic materials attached to suspended particulate matter (SPM) in their life cycles (Houlbreque and Ferrier-Pages 2009). Also, heterotrophy can be an important mechanism of energy gain for corals living in radiation-limited conditions, through which corals shift to rely on heterotrophic food supply compensating for low photosynthetic carbon gain to meet their energetic requirements (Anthony and Fabricius 2000). Undoubtedly, the heterotrophic strategy of physiology for growth and reproduction is of benefit to coral ecosystems, which makes coral cells become more adaptive to the changes in water quality, and recovery can be more rapid after the damage, such as bleaching and diseases.

However, the triggers of switch between autotrophy and heterotrophy are not yet well understood for the systems of zooxanthellae and coral host. In terms of nutrient cycles, it is possible that both autotrophic and heterotrophic pathways can depend upon the stress of availability of external sources (e.g., nutrient limitation). Apparently, the zooxanthellae and coral host that can function via the heterotrophic pathway have advantage in competition for limited nutrients and dissolved organic matter and hence demonstrate a better adaptability to the unfavorable conditions than those that rely exclusively on the autotrophic metabolism.

Using a molecular assessment approach, Levy et al. (2016) compared light and heterotrophy effects on the auto-ecology of reef-building corals. The results indicate that feeding with plankton nauplii can allow corals to resist the light stress by supplying anti-oxidants and energy-rich molecules (e.g., vitamin E in unsaturated fatty acids) that protect against and/or repair photo-oxidative damages (i.e., bleaching), as well as maintain metabolism. In addition to photo-damage, unfed corals suffer from disruption of Ca^{2+} homeostasis and loss of endosymbionts that can be linked to the depressed calcification (e.g., calcium pump), and hence heterotrophic capacity can be a selective evolution strategy in climate change (Levy et al. 2016).

In summary, coral heterotrophy includes a wide diversity of food sources, which account for a large part of energy budget of corals and compensate for the shortage of nutrients and other elements that is not translocated by the photosynthesis of symbionts. There is increasing evidence that light/photosynthesis and feeding interact to determine the tissue compositions, including lipids, fatty acids, sterols, and alcohols (Ferrier-Pages et al. 2011). Feeding is also thought to provide the symbiosis with some essential amino acids because animals are unable to synthesize them de novo. Heterotrophy can increase resilience of coral colonies to bleaching through the enhancement of lipid stocks for host, which provides nutritional supply to prevent photo-damage to symbiotic algae and/or reduce the demand of host for photosynthetic products, so that symbionts can use the reserved energy for recovery (Ferrier-Pages et al. 2011). Finally, heterotrophy can stimulate the calcification through the tissue growth-enhanced supply of dissolved inorganic carbon, construction of organic matrix can be stimulated by providing necessary amino acids, and in this case, organic matrix synthesis and calcification are tightly coupled (Ferrier-Pages et al. 2011).

Table 5.2 Comparison of primary productions (unit: g C/m^2/day), community respiration (unit: g C m^2/day) and calcification (unit: g CaCO$_3$ m^2/day) rates of coral reefs from the Western Pacific Region. Coral reef situations and/or measurement time/season (e.g., MM/YY) are given in the brackets

Location/types	References	Net community calcification (±sd)	Net community production (±sd)	Community gross primary production (±sd)	Community respiration (±sd)
Reef flat (Heron Reef), Great Barrier Reef	Albright et al. (2015)	18.74 (daytime)	6.28 (daytime)		
		2.16 (night)	−6.42 (night)		
		10.57 (daily)	−0.086 (daily)		
Lagoon (Heron Reef), Great Barrier Reef	McMahon et al. (2013)	20.42 (daytime)	11.06 (daytime)		
		−8.89 (night)	−7.89 (night)		
		5.77 (daily)	0.066 (daily)		
Reef flat (Davies Reef in summer), Great Barrier Reef	Albright et al. (2013)	26.42 ± 9.61 (daytime)	0.43 ± 0.23 (daytime)		
		4.80 ± 9.61 (night)	−6.34 ± 5.76 (night)		
		15.61 (daily)			
Reef flat (Davies Reef in winter), Great Barrier Reef	Albright et al. (2013)	19.22 ± 7.21 (daytime)	0.40 ± 0.16 (daytime)		
		2.40 ± 7.21 (night)	−1 ± 1.72 (night)		
		8.41 (daily)			
Coconut Island, Hawaii	Andersson et al. (2009)	7.93 ± 1.2 (daily)			
Dongsha Atoll, South China Sea	DeCarlo et al. (2017)	39.04 ± 9.01	1.20 ± 3.60		
Ningaloo Reef, Australia	Falter et al. (2012)	19.02 ± 4.00 (summer)		16.8 ± 0.84 (summer)	
		20.02 ± 1.00 (winter)		12.60 ± 0.72 (winter)	
Moorea Island, French Polynesia	Gattuso et al. (1993)	24.30		7.7–9.0	7.1–7.7
Ofu Island, American Samoa	Koweek et al. (2015)	21.62	9.79		
Ishigaki Island, Japan	Kayanne et al. (2005)	12.7 (bleaching)		7.58 (bleaching)	7.15 (bleaching)
		12.11 (degraded)		5.57 (degraded)	4.42 (degraded)
		7.00 (recovering)		4.74 (recovering)	3.58 (recovering)
		11.21 (recovering)		6.3 (recovering)	4.73 (recovering)
Palau Islands	Kayanne et al. (2005)	13.01 (living)		7.36 (living)	6.19 (living)
		7.41 (dead)		3.16 (dead)	2.86 (dead)
Bora Bay, Japan	Kraines et al. (1997)	12.51 (10/1993)	0.30 (10/1993)		
		16.68 (10/1993)	5.11 (10/1993)		
		5.84 (03/1994)	−2.40 (03/1994)		
		31.70 (07/1994)	12.90 (07/1994)		
One Tree Island, Australia	Kwiatkowski et al. (2016)	12.28 ± 2.64 (daytime)	3.66 ± 1.64 (daytime)		
		−4.56 ± 1.44 (night)	−2.94 ± 1.76 (night)		
		3.63 ± 0.95 (daily)	0.50 ± 0.26 (daily)		
Kaiona Beach Park, Hawaii	Lantz et al. (2014)	18.62 ± 4.60		11.65 ± 3.41	11.30 ± 2.94
Makapu'u Beach Park, Hawaii	Lantz et al. (2014)	14.51 ± 3.40		4.79 ± 2.24	3.86 ± 1.27
Kaneohe Bay, Hawaii	Shamberger et al. (2011)	23.54 (summer)	−1.90 (summer)		
		29.31 (winter)	−0.66 (winter)		
Vietnam coasts, South China Sea	Tac-An et al. (2013)			7.85–17.10	

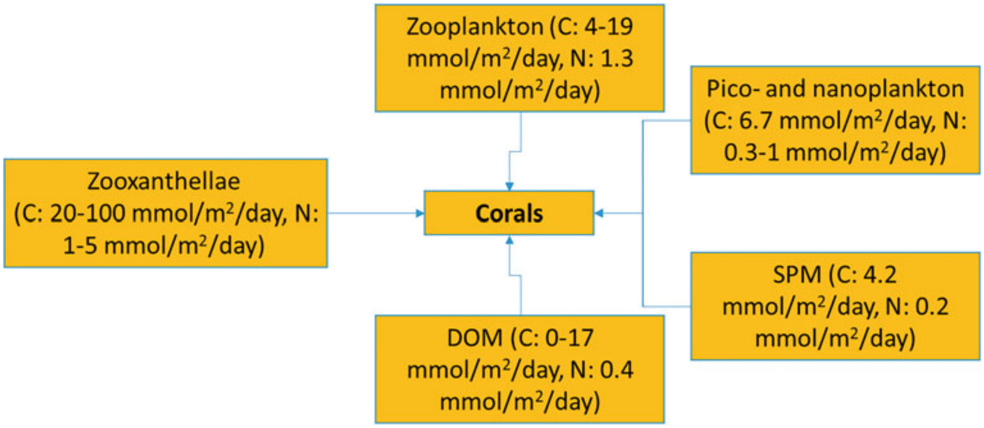


Fig. 5.4 Comparison between autotrophic and heterotrophic acquisition of organic matter (i.e., C and N) in coral and zooxanthellae symbiosis (unit: mmol/m^2/day), using *Stylophora pistillata* with polyps density of 0.5×10^6 individuals/m^2; data are from Houlbreque and Ferrier-Pages (2009) and Ferrier-Pages et al. (2011)

5.4.3 Coupling Between Pelagic and Benthic Sub-systems

Owing to the nature of shallow water depth and active hydrodynamics of coral reefs, the cycle of macronutrients and trace elements in the pelagic zone (i.e., water column) can be closely linked to the processes of benthic organisms. For example, solar radiation can reach to the sea bottom and fuel the photosynthesis of benthic algae and/or seagrass, which consumes the macronutrients and trace elements and alters the inventory of chemical elements in the water column. On the other side, deposited organic materials in bottom sediments fuel the heterotrophic decomposition that results in the accumulation of inorganic nutrients (i.e., mineralization) in pore waters. Hence, sediment–water exchange flux of solutes can make an important contribution to the level of nutrients and trace elements in the above water body. In this case, the sediment–water exchange flux (F_x) can be described as (Lerman 1978):

$$F_x = -\varphi D_x \frac{\partial C}{\partial X}, \tag{5.3}$$

where φ is porosity of bottom sediments, D_x stands for the diffusion rate, and $\frac{\partial C}{\partial X}$ represents the measured gradient of solute concentrations (C) across the sediment–water interfaces.

5.4.4 Food Web Dynamics

The food web of coral reefs consists of zooxanthellae and coral symbiosis as well as other organisms, such as phytoplankton and other algae, zooplankton, swimmers (e.g., fish) and benthos (e.g., crustaceans and clams), and microorganisms and fungi (Fig. 5.5).

Interactions between prey and predators and among different functional groups at the same trophic level drive the flow of materials and energy in the food web. Because the biogeochemical cycle is closely related to the material flow in the food web, and the organic matter and energy are linked through the law of transformation (i.e., 1 calorie = 4.18 J), food web dynamics regulate the fate of chemical elements through trophic relationship as well as the interaction between the main food chain and the microbial loop of ecosystem. This will eventually impose an impact on the mass/inventory of chemical elements in the water body.

Briefly, external nutrients and trace elements are imported to the coral reefs through water exchange and used by photosynthesis of phytoplankton and zooxanthellae symbiotic with corals. The synthesized organic matter is then transferred upward higher trophic levels through food relationship. The excretion and exudation of organic matter can fuel the fungi and microbial activities that regenerate the inorganic form of chemical elements through mineralization. The organic detritus deposited to the sea bottom can be decomposed via heterotrophic degradation, and the solutes produced can then be fed back to the water column through the sediment–water interface fluxes. The chemical elements can also be exported to the open waters through tide and circulation.

Dinsdale and Rohwer (2011) indicate that apex predators are the main consumers of system primary production via trophic transfers, and removal of macroorganisms (i.e., top–down effect) disrupts the ecosystem but does not necessarily result in a predation release that allows biomass of lower trophic levels to increase (e.g., to boom) and consume more algae. Instead, the remaining herbivores can be less effective in harvesting algae, which causes a reduction in the amount of organic matter that is drawn up the food web. The excess organic matter in the low trophic levels is then available for the microbial loop. An increase in microbial activity directly threatens corals by creating diseases. In fact, overfishing can be synergistic with the effect of eutrophication (i.e., bottom–up effect) on coral reefs, and eutrophication by itself can lead to phytoplankton blooms that damage coral reefs as well (Abram et al. 2003).

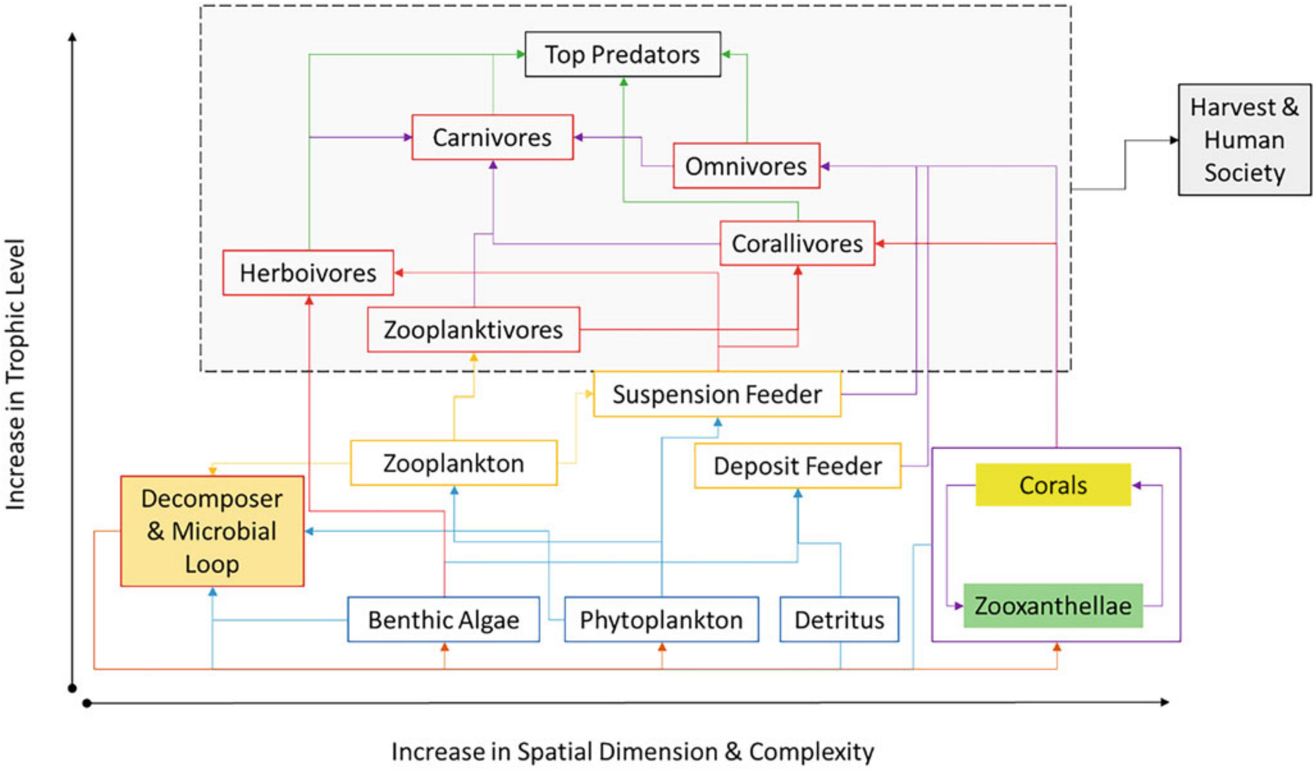


Fig. 5.5 A simplification of food web relationship for coral reefs, illustrating the food and energy relationships between different trophic levels. The figure is based on the modification of Glynn (2004) but emphasizes on the links of food web with human society and the significance of microbial loop

5.5 Interactions Between Biogeochemistry and Coral Reef Ecosystems

Coral reefs are found worldwide in warm, high salinity, and low turbidity tropical and subtropical environments. In a review by D'Elia and Wiebe (1990), concentrations of nutrients for worldwide coral reefs were reported as ranging 0.1–5 μM for DIN, 0.02–1 μM for DIP, and 1–10 μM for DSi, respectively, values that are comparable to the oligotrophic offshore open seawaters. Similar to other marine ecosystems, these low concentrations of nutrients and trace elements sustain a considerable biomass of coral reefs and are actively involved in almost all known pathways of carbon metabolism, such as mass transfer, productivity, coral growth, as well as biogeochemical cycles in aerobic and/or anaerobic conditions (Atkinson and Falter 2003; Atkinson 2011).

5.5.1 Impact of Nutrients on the Coral Ecosystems

As shown in Table 5.3, concentrations of macronutrients in coral reef waters from the Western Pacific Ocean are relatively low but with a wide range of DIN/DIP ratios; these numbers are, however, similar to other world-ocean coral reefs reported in the literature, e.g., 0.01–3.3 μM for NO_3^- (Silverman et al. 2007a).

Koop et al. (2001) summarize the results of a nutrient enrichment (i.e., N and P) experiment (i.e., ENCORE Project from 1993 to 1996) on an offshore reef of One Tree Island in the Great Barrier Reef. It was found that ^{15}N uptake rates of zooxanthellae vary in a wide range of 3.6–32 mmol N/m^2/day and nitrogenase activity can be promoted by the addition of DIP into the reef systems, which can be twice as high as the control. A significant reduction of alkaline phosphatase activity was observed in the P-addition experiments (Koop et al. 2001). The reported nitrogen uptake rate from One Tree Island was generally comparable to other coral reefs, but in the higher rank (Atkinson and Falter 2003). At Ningaloo Reef in the Western Australia affected by the Leeuwin Current, the uptake rate was 5–15 mmol N/m^2/day for NO_x and 0.1–2 mmol P/m^2/day for PO_4^{3-}, respectively, at the reef flat, while values of 0.2–3 mmol N/m^2/day for nitrogen fixation and/or uptake were reported in the literature (Grover et al. 2003; Holmes and Johnstone 2010; Falter et al. 2012; Wyatt et al. 2012). Moreover, following the addition of external nutrients (i.e., N and P), the rate of sediment denitrification was doubled (Koop et al. 2001), most likely because of an

Table 5.3 Summary of average concentration (±sd) of nutrients (μM) and chlorophyll a (Chl-*a*: μg/L) in the water column from selected coral reef sites of the Western Pacific Ocean. For the purposes of comparison, published results after the mid-1990s were selected; the range of reported concentrations is in brackets

Reef systems	Area	$NO_3^- + NO_2^-$	NH_4^+	PO_4^{3-}	DSi	Chl-*a*	References
Kamala Bay	Hawaii	0.72	0.10	0.08		0.17	Grigg (1995)
One Tree Island	Great Barrier Reef	2.94	0.65 ± 0.69	0.20 ± 0.06		0.16–0.21	Koop et al. (2001)
Wet tropics	Great Barrier Reef	0.18	0.08	0.11		0.33	Uthicke et al. (2014)
Burdekin	Great Barrier Reef	0.18	0.10	0.09		0.38	Uthicke et al. (2014)
Whitsundays	Great Barrier Reef	0.21	0.13	0.12		0.48	Uthicke et al. (2014)
Fitzroy	Great Barrier Reef	0.15	0.07	0.12		0.47	Uthicke et al. (2014)
Sandy Bay	Western Australia	0.71	0.18	0.10	0.35	0.4	Wyatt et al. (2012)
Sanya Bay	South China Sea	2.3 (0–10.3)	13.4 (4.8–42.7)	0.09 (0–0.58)	3.7 (1.6–10.3)	1.23 (0.32–3.53)	Li et al. (2016)
Wenchang	South China Sea	4.56 (3.45–11.26)	8.24 (2.77–32.28)	0.28 (0.19–0.38)	4.14 (2.28–10)		Li et al. (2015)
Zhubi Reef	South China Sea	0.21–1.42	0.72–1.86	0.08–0.55	1.2–9.0	0.062–0.43	Shen et al. (2010)
Zhaoshu Island	South China Sea	0.68 (0.36–2.25)	0.97 (0.43–1.79)	0.07 (0.03–0.29)		0.03 (0.02–0.06)	Wu et al. (2017)

increase in depositional flux of organic detritus to the sea bottom that stimulates heterotrophic decomposition. There is no evidence, however, that phytoplankton biomass was increased, as well as the primary production rate, at One Tree Island when compared to open offshore waters. This is presumably related to the nature of rapid water flushing, hence a rather short residence time of nutrients in reef systems.

Direct evidence on the relationship between nutrient enrichments and coral growth seems still limited. However, enrichment of nutrients can affect the coral reefs through switch between the autotrophic and heterotrophic pathways of metabolism. In the ENCORE Project, coral growth (e.g., linear extension) rate increases with the addition of DIP, but reduces in the case of ammonium amendment (Koop et al. 2001), which is in contrast to the previous studies and indicates that response of coral growth depends on the species of interest. At the One Tree Island, the effect of nutrient addition on calcification is both species and nutrient specific, and calcification of corals in nutrient amendment experiments showed a strong seasonality, which suggests that in addition to nutrients, other factors play an important role too. Changes in micro-density of corals indicate the modification at scale of crystal architecture (Koop et al. 2001). In the case of nutrient amendments, mortality of small sub-colonies (i.e., nubbins) is higher than large coral colonies, and DIP was found to have a more negative effect than ammonium for unknown reasons (Koop et al. 2001). Photo-physiology of coral and zooxanthellae symbiosis can also be affected by the nutrient additions. For example, at the One Tree Island, it was found out that nutrient treatment significantly affected the compensation irradiance and initial slope of the maximum gross photosynthetic rate, which induces the observed changes in the ratio of photosynthetic production and respiration of corals (Koop et al. 2001).

The sexual reproduction of corals is also affected by the level of nutrients in the water column, but nitrogen and phosphorus may have different impacts on the reproduction of coral reefs. Exposure to elevated nitrogen and phosphorus affects the fertilization rates and/or reproductive capacity (e.g., number of eggs per polyp) and increases the number of irregular eggs and reduces the development and settlement rates (Koop et al. 2001). Moreover, it is observed that elevated nitrogen can reduce the amount of lipids in the tissues of coral, while exposure to high phosphorus increases the lipid concentration (Koop et al. 2001). Hence, the change in nutrient concentration and DIN/DIP ratio of water body can both have large effects on the composition and energy storage (e.g., fatty acids and esters) of synthesized organic matter of corals.

Obviously, the most direct influence of external nutrients and trace elements to the coral reefs is on the autotrophs, which is a fundamental question to understand the interactions of biogeochemistry and coral reefs. The multi- and mutualistic correlations between zooxanthellae and corals, as well as with other animals (e.g., clams) of reef systems, guide the energy and material flow from driving forces (e.g., input of nutrients and trace elements) to the marine food web. Apparently, coral species, colony size, water motion, and the loading of nutrients and trace elements determine collectively the character of response of autotrophs of coral symbiosis. Addition of nitrogen and phosphorus can

Table 5.4 Summary of inorganic carbon parameters (±sd) for the selected coral reefs sites from the Western Pacific Ocean. Range of reported concentrations is also shown

Reef systems	Area	TA (μmol/kg)	DIC (μmol/kg)	$p\mathrm{CO}_2$ (μatm)	References
Wet tropics	Great Barrier Reef	2231 ± 60	1957 ± 53	437 ± 42	Uthicke et al. (2014)
Burdekin	Great Barrier Reef	2272 ± 38	1990 ± 44	433 ± 36	Uthicke et al. (2014)
Whitsundays	Great Barrier Reef	2273 ± 28	1995 ± 25	425 ± 25	Uthicke et al. (2014)
Fitzroy	Great Barrier Reef	2283 ± 65	2005 ± 61	412 ± 45	Uthicke et al. (2014)
Sattahip Bay	Gulf of Thailand	2148 ± 45	1880 ± 39	480 ± 40	Viyakarn et al. (2015)
Kaneohe Bay	Hawaii	2160–2280		431–622	Shamberger et al. (2011)
Sandy Bay	Western Australia	2272–2284	1907–1973	287–359	Falter et al. (2012)
Sanya Bay	South China Sea	2300–2327		373–420	Zhang et al. (2013)
Yongxing Island	South China Sea	2421 ± 142		456 ± 249	Yan et al. (2011)
Yongshu Reef	South China Sea	2240 ± 56		395 ± 25	Yan et al. (2011)

dramatically increase the population density of zooxanthellae resident in coral colonies, followed by an increase of Chl-*a* per unit surface area (i.e., number), while the pigment's (e.g., Chl-*a*) content per zooxanthellae cell is not affected (Koop et al. 2001). This is inconsistent and/or in contrast with previous observations on corals and other animals (Hoegh-Guldberg and Smith 1989; Dubinsky et al. 1990; Stambler et al. 1991; Belda et al. 1993; Muller-Parker et al. 1994). Furthermore, after the amendment of nutrients, the material storage (e.g., starch) of zooxanthellae chloroplast of reef animals (i.e., giant clams) is altered, and it has been suggested that under enriched nitrogen conditions, zooxanthellae can remobilize the storage of starch to synthesize amino acids (Ambariyanto and Hoegh-Guldberg 1996; Koop et al. 2001).

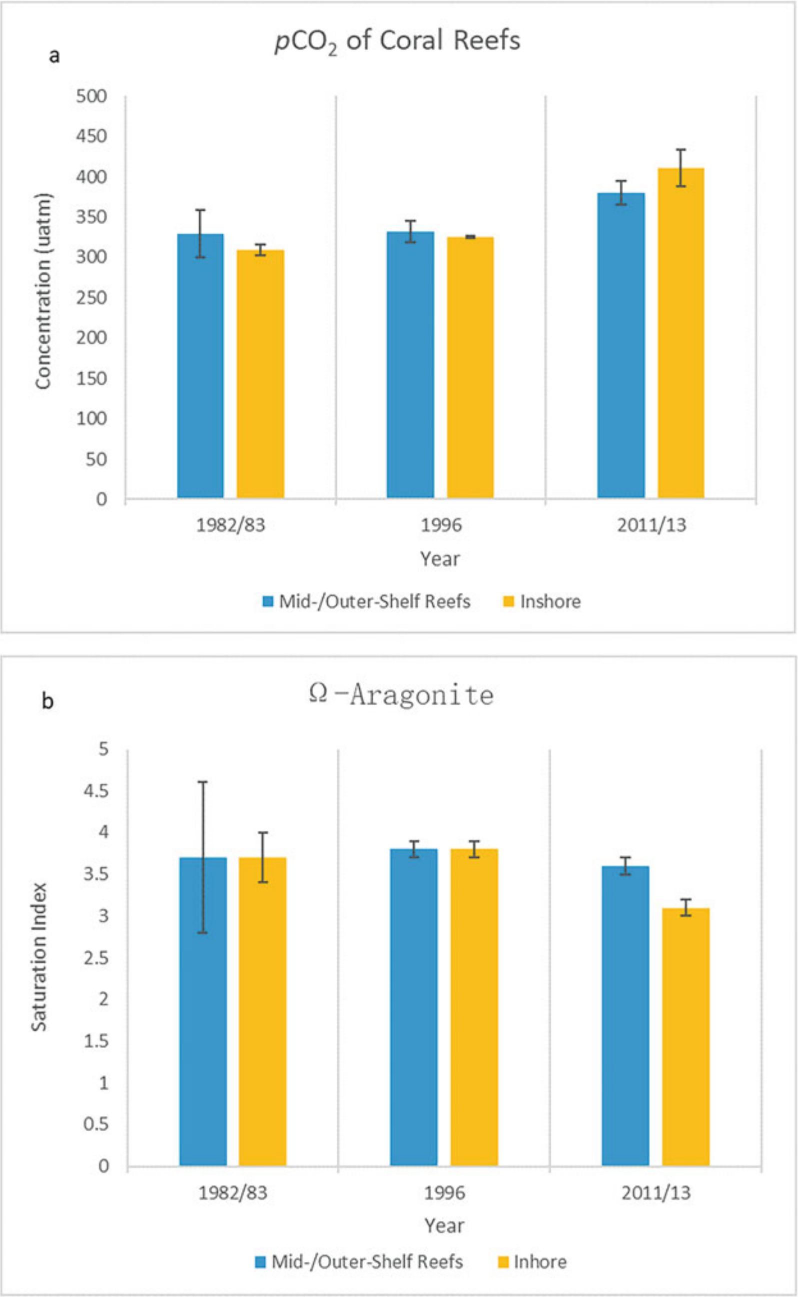
5.5.2 Carbon Chemistry and Calcification

Knowledge of calcification of corals is critical to understand the biogeochemistry of carbon as well as other chemical elements for a given reef system and spatial and temporal scales of variability of air–sea interface processes. Calcification can be linked to the basic function of ecosystems, such as the photosynthesis and respiration for coral reefs (Al-Horani et al. 2003). Coral reefs are characterized by the dominance of autotrophic processes (i.e., increasing pH and thus decreasing $p\mathrm{CO}_2$) during the day and of respiration (i.e., reduction of pH with high $p\mathrm{CO}_2$) at night. This can lead to considerable diurnal fluctuations of pH, dissolved inorganic carbon (DIC) and $p\mathrm{CO}_2$, and saturation index (e.g., Ω for aragonite) of calcium carbonates in the water column, as well as the differences between various coral reef systems (Table 5.4). The nature of net-autotrophic coral reefs raises water pH and therefore increases their buffering capacity against ocean acidification, because of changes in $p\mathrm{CO}_2$ (Kleypas et al. 2011). The ratio of primary productivity and respiration (p/r) is often lower for nearshore reefs than those at offshore areas further from the coast, because of increased solar radiation penetration depth associated with reduction of turbidity under direct terrestrial influence (Fabricius and De'ath 2008; Nobes et al. 2008). This leads to the argument that inshore reefs may be less able to buffer rising dissolved inorganic carbon through photosynthesis (Uthicke et al. 2014). Another possibility is that the p/r ratios are smaller in nearshore than offshore waters, indicating that autotrophic processes become important in offshore environment. At the daily scale, the net calcification rate accounts for 10%–20% of energy consumption relative to the community gross primary productions with a global average of 110 mmol CaCO_3/m^2/day, and the calcification can be decoupled from diurnal variation in light and from net production at seasonal scale (Falter et al. 2012).

The inshore reef data for $p\mathrm{CO}_2$ and Ω_{ar} from the Great Barrier Reef (Uthicke et al. 2014) are shown in Fig. 5.6. In the early 1980s, the average $p\mathrm{CO}_2$ and Ω_{ar} were 250–310 μatm and 3.7–4.1, respectively, which do not show significant differences between inshore and mid- and outer-shelf reefs and are also comparable to the measurements of the mid-1990s, that is, 325–332 μatm for $p\mathrm{CO}_2$ and 3.8 for Ω_{ar}, respectively (Fig. 5.6). In the period of 2011–2013, the $p\mathrm{CO}_2$ and Ω_{ar} from mid- and outer-shelf reefs remain 380 μatm and 3.6, respectively, though there is no systematic trend; the $p\mathrm{CO}_2$ of reef waters is lower than the atmospheric CO_2 pressure by ca. 4%. At inshore reefs, $p\mathrm{CO}_2$ of water body increases to 411 μatm–458 μatm with a fall of Ω_{ar} to 3.1–3.3; the $p\mathrm{CO}_2$ of inshore reef waters can be 17% higher than the atmospheric $p\mathrm{CO}_2$ (Fig. 5.6). Also, the Ω_{ar} from mid- and outer-shelf reefs can be 10%–20% higher than the inshore reefs. Over the last 30 years, the rate of increase for $p\mathrm{CO}_2$ at inshore reefs is 1.8–6.1 μatm/year, while the increasing rate for the atmospheric CO_2 is 1.6–2.0 μatm/year (Uthicke et al. 2014). It should be kept in mind, however, that the Ω_{ar} of the Western Pacific Ocean (e.g., Great Barrier Reef) is still comparable to the range of $\Omega_{\mathrm{ar}} = 3.3$–$4.1$ in a global distribution pattern (Silverman et al. 2007a).

Such a change in $p\mathrm{CO}_2$ and Ω_{ar} of coral reefs over the last 100 years should reflect the interactions of net ecosystem production (NEP) and calcification (NEC), which can be

Fig. 5.6 Comparison of (**a**) $p\mathrm{CO}_2$ in seawater and (**b**) aragonite saturation state (Ω_{ar}) from the Great Barrier Reef; data are from Uthicke et al. (2014)



estimated by examining the relationship of DIC and TA (Suzuki and Kawahata 2003). At the Great Barrier Reef, DIC and TA for the nearshore reefs are closely correlated, and both show strong correlations with salinity. There is a trend of DIC and TA for nearshore reefs of the Great Barrier Reef, that is, DIC and TA tend to increase from the north to the south, and $p\mathrm{CO}_2$ data show an elevation in wet season compared to dry season (Uthicke et al. 2014). Correspondingly, the NEP/NEC ratio decreases from 1.2 to 7.3 in nearshore waters to 0.4 for offshore reef systems, suggesting a spatial trend of decrease in the importance of calcification in regulating the carbon cycle from nearshore to offshore and also an increase of influence from primary production to respiration ratio (Uthicke et al. 2014). With regard to aragonite saturation, the observed Ω_{ar} in the wet season is increased albeit with higher $p\mathrm{CO}_2$ and lower pH, relative to dry season, which is explained by the higher water temperature, resulting in a reduction of carbonate solubility in the wet season (Uthicke et al. 2014). Furthermore, it is suggested that over an annual scale, the $p\mathrm{CO}_2$ dynamics for the nearshore reefs from the northern part of the Great Barrier Reef is primarily regulated by biological processes, while in the south and for offshore reefs, seasonal $p\mathrm{CO_2}$ changes are most likely affected by temperature based on the method of Takahashi et al. (2002).

In the Great Barrier Reef, shifting of the *p*/*r* ratio is sensitive to the influence of terrestrial runoff that is characterized by elevated chlorophyll and nutrients and increased turbidity, because approximately 20% of reefs lie within 10 km of the coast and are under direct terrestrial (river) influence from surface runoff and SGD (Uthicke et al. 2014). This, at present, results in nearshore reefs being subject to higher $p\mathrm{CO_2}$ and lower Ω_{ar} than on the outer-shelf; both have strong variability between day- and nighttimes, i.e., diurnal cycle (Uthicke et al. 2014).

For comparison, in the Gulf of Eilat (i.e., Aqaba) of the Red Sea, it was found that the coral reef net community calcification rate is from -4 ± 7 to 108 ± 10 mmol/m^2/day for $\mathrm{CaCO_3}$ over a period of 5 years (1997–2002), with averages of 60 ± 20 mmol/m^2/day of $\mathrm{CaCO_3}$ in summer and 30 ± 20 mmol/m^2/day for $\mathrm{CaCO_3}$ in winter seasons, respectively (Silverman et al. 2007b). The observed net community calcification rate is positively correlated with the change in water temperature (22 °C–28 °C) as well as Ω_{ar} (3.7–4.4); note that the latter is also a function of temperature (Silverman et al. 2007b). For a given temperature and at the same Ω_{ar}, the influence of nutrients on calcification is negative for Aqaba coral reefs, i.e., high nitrate data show lower rates of calcification compared to low nitrate levels, which is similar to the previously published results (Marubini and Davies 1996; Langdon and Atkinson 2005). However, the effect of nutrients on the carbonate calcification can be polyfunctional and in many different aspects. For example, exposure to high nutrient levels will cause excess production over respiration, which induces increases in pH and $\mathrm{CO_3}^{2-}$ concentrations, beneficial to the high Ω_{ar}. However, increase of respiration and heterotrophic rates in coral reefs induces accumulation of $p\mathrm{CO_2}$ that has a negative effect on calcification. Moreover, Glynn (1997) indicated that coral infestation with boring animals is increased in eutrophic environment, hence inducing higher opportunities of bio-erosion, which is another forcing that regulates the carbon cycle of the system.

In the Kaneohe Bay of the Hawaii close to the Subtropical Gyre of the North Pacific Ocean, TA and $p\mathrm{CO_2}$ illustrated a nature of strong diurnal variability, with 2120–2280 μmol/kg for TA and 250–700 μatm for $p\mathrm{CO_2}$ in the period of 2008–2010 (Shamberger et al. 2011). In 2008–2010, nighttime TA was found 5–6% higher than in daytime, but $p\mathrm{CO_2}$ could differ by a factor of 2 (Shamberger et al. 2011). The daily NEC for $\mathrm{CaCO_3}$ based on ΔTA/ΔDIC calculations ranged from 166 to 372 mmol/m^2/day of $\mathrm{CaCO_3}$, which is comparable to values of 174–331 mmol/m^2/day from box model estimates (Shamberger et al. 2011). Coral reefs are net photosynthetic in daytime and net respiring at night, with NEP varying from −330 to 103 mmol C/m^2/day from ΔTA/ΔDIC calculations and −378 to 80 mmol C/m^2/day from box model estimates, respectively (Shamberger et al. 2011). NEP is the most important factor in regulating the daily cycle of $p\mathrm{CO_2}$ in the coral reefs, which in turn controls the variability of Ω_{ar} between day and night. In the Kaneohe Bay, the calcification rates are highest during the day when solar radiation, temperature, and Ω_{ar} are all high, and low rates of calcification occur at night when light, temperature, and Ω_{ar} are low, and the system is net calcifying on a daily basis (Shamberger et al. 2011). Hence, photosynthesis in daytime draws down water $p\mathrm{CO_2}$ and increases Ω_{ar} that motivates the high rate of calcification of corals.

The observed NEC from Hawaii is similar to those measured on other coral reefs, such as Moorea, French Polynesia, and the Great Barrier Reef (Gattuso et al. 1996). Note that the coral calcification can also be affected by heterotrophic processes. It has been shown that heterotrophic feeding of corals can enhance the calcification rates in both light and dark conditions and hence provide another source (mechanism) of calcification during the time of stress, e.g., high $p\mathrm{CO_2}$ but low nutrients in the water column (Cohen and Holcomb 2009; Houlbreque and Ferrier-Pages 2009). Through heterotrophic feeding, corals are able to calcify at a relatively high rate albeit under stress of comparatively low Ω_{ar} at night. It should also be noted that the algal population of coral reefs could be source of organic matter that drives respiration of the whole system. Respiration measurements indicate that particulate organic carbon and nitrogen could also be available for coral feeding (Houlbreque and Ferrier-Pages 2009; Wyatt et al. 2010). Moreover, similar to the NEP, the daily NEC of coral reefs can also be correlated with residence/flushing time of water bodies, emphasizing the significance of hydrodynamics in reef systems.

Finally, based on the linear relationship between NEC and $p\mathrm{CO_2}$ as well as between NEC and Ω_{ar}, it can be predicted that NEC will equal to dissolution (i.e., NEC = 0 at daily scale), that is, the "threshold" for calcification, at $p\mathrm{CO_2} = 886.4$ μatm, $\Omega_{\mathrm{ar}} = 1.65$, and/or $[\mathrm{CO_3}^{2-}] = 106.7$ μmol/kg at the Kaneohe Bay, which is different from the "critical value" (i.e., threshold estimate) for coral reefs from other world oceans and even other areas of Hawaii (Shamberger et al. 2011). This makes the authors to argue that the relationship between NEC and Ω_{ar} from one reef will not be applicable to predict calcification rates from other coral systems. Hence, it can be expected that some coral reefs may be more sensitive than the others to the increase in $p\mathrm{CO_2}$ caused by ocean acidification.

5.5.3 Mass Flow and Relationship with Energy Budgets

In the zooxanthellae and coral symbiosis, carbon fixation by photosynthesis is one of several important sources of organic matter to the host (i.e., coral polyps). Hence, the translocation of organic matter from symbiotic zooxanthellae to the host coral animals becomes one of the crucial pathways of energy and materials to maintain the metabolic requirement of coral colonies (Muscatine and Weis 1992). As reviewed by Falkowski et al. (1984), there are other possible carbon sources, including predation on zooplankton and microorganisms, uptaking of particulate and dissolved organic matter, feeding on mucus and organisms attached to detritus, etc. It has been shown that coral colonies growing at high light can obtain all the reduced carbon needed for animal respiration from photosynthetic zooxanthellae, while those in shaded reef areas must acquire 30–60% of their reduced carbon heterotrophically (Muscatine et al. 1981; Falkowski et al. 1984). Indeed, 50–90% of the carbon fixed by zooxanthellae is translocated to the animal host with remarkable diurnal variability, since the carbon fixed in daytime can be translocated later at night. However, the assimilation efficiency of host can be low and variable. Presumably, the translocated products have skewed C:N ratio, e.g., nitrogen-poor organic matter (Muscatine et al. 1981; Falkowski et al. 1984). Fates of photosynthetically fixed organic matter include consumption also for the respiration, maintenance, and growth of zooxanthellae cells. The excretion is in the form of dissolved organic matter into the environment. The translocation of reduced carbon is used by the coral host for its maintenance of respiration, growth, reproduction (e.g., larvae), release of particulate and dissolved organic matter, such as mucus, as well as formation of organic matrix for carbonate skeleton (i.e., calcification) (Muscatine and Weis 1992). Also, the released organic matter (e.g., DOM) can fuel the microbial loop of food web.

Only a few studies have tried to link mass flow of coral food web with energy budgets. In fact, organic material sources and translocation pathways can also be deciphered by energy flow and budget through equivalence of heat measurements generated by combustion of reduced carbon. For example, formation of 1 mol of glucose requires 6 mol of oxygen with energy equivalent of 2817 kJ, while respiratory oxygen consumption can be converted to energy oxygen—Joule equivalent of 19.63 kJ/mol O_2 (Edmunds and Davies 1986).

Figure 5.7 shows the daily energy budgets for a zooxanthellae and coral symbiotic system based on the results from Davies (1984), Edmunds and Davies (1986), and Davies (1991). In the experiments, symbiotic zooxanthellae and coral systems show the daily (24-h) energy fixation of zooxanthellae and translocation to the coral host (Davies 1984, 1991; Edmunds and Davies 1986). In Fig. 5.7, a proportion of ca. 10–45% of photosynthesized energy participates in zooxanthellae respiration, <2% for cell growth, and about 50–90% of fixed energy is channeled to the host corals plus released into water (i.e., 15–30%). Furthermore, the energy channeled to coral host is used for animal respiration (35–75%) and coral growth (4–12%), and the rest of up to 60% is lost into adjacent waters, such as reproduction (e.g., larvae) and release of organic matter in the form of mucus, etc. (Fig. 5.7). It should be noted, however, that the abovementioned energy budget is based on the law of conservation and/or energy balance, and the loss term is estimated rather than directly measured and hence specified. For example, the loss term of zooxanthellae should also include energy consumption because of cell division and excretion (i.e., lysis) of organic matter, etc. It is known that corals can have heterotrophic feeding behavior as well, and the loss term of animals should also include exudation of organic wastes and in the form of debris. Davies (1991), for example, found that in the overcast weather, the coral respiration energy requirement is higher than the translocation from autotrophs and the animal energy budget can be "negative," indicating that heterotrophic feeding is an important supplementary mechanism.

The energy budgets for symbiotic zooxanthellae and coral systems mentioned above are confirmed by more recent experimental work and modeling approaches (Muller et al. 2009;

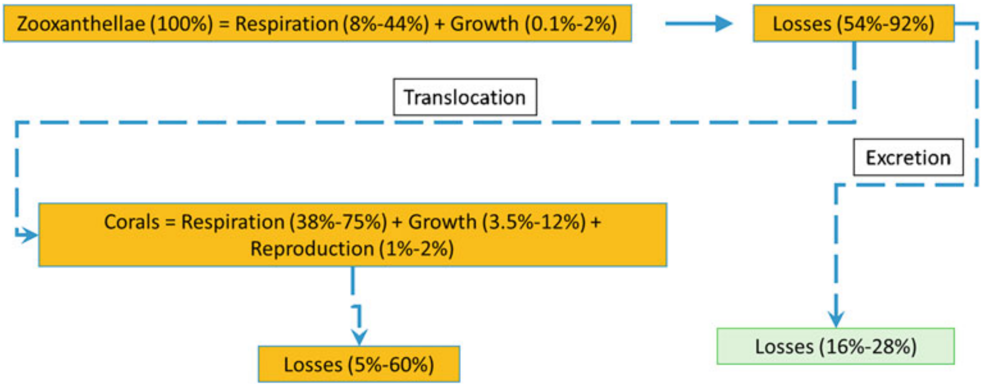


Fig. 5.7 Cartoon illustration of the energy budgets of zooxanthellae and coral symbiosis, summarized based on the data of Davies (1984), Edmunds and Davies (1986), and Davies (1991). Note in the figure that the "losses" term can be linked to the microbial loop of ecosystem

Table 5.5 Some of important pathways of carbon and other biologically important chemical elements in the ecosystem of coral reefs

Chemical reactions	Biogeochemical mechanisms
$CO_2 + H_2O \overset{hv}{\rightarrow}$ Organic matter $+ O_2$	Photosynthesis and primary production—that plant uses light as a source of energy and inorganic solutes (e.g., nutrients) to synthesize organic matter. The reverse process is referred to as respiration, with particular reference to breath
Organic matter $\rightarrow NH_4^+ + PO_4^{3-} + SiO_3^{2-}$	Remineralization, which describes the heterotrophic decomposition of organic matter by microbial organisms that regenerate simple forms of inorganic nutrients and trace elements
$N_2 \rightarrow$ Organic matter	Nitrogen fixation—some of microorganisms can synthesize organic nitrogen from N_2, similar to the legumes on land
$Ca^{2+} + 2HCO_3^- \rightarrow CaCO_3 + H_2O + CO_2$	Calcification—corals use calcium and DIC to build up their skeletons (i.e., aragonite), and other organisms can form calcite. The reserve of this reaction is dissolution of carbonates
$NH_4^+ + 2O_2 \rightarrow NO_3^- + H_2O + 2H^+$	Nitrification, in which ammonia is aerobically oxidized to nitrate
Organic matter $+ NO_3^- \rightarrow HCO_3^- + N_2$	Denitrification, in which nitrate is used as electron acceptor and hence reduced to gases nitrogen

Khalesi et al. 2011). For instance, Khalesi et al. (2011) reported that daily energy for the coral growth is 6–12% of total photosynthesis and up to 60–80% of total energy is used for host respiration, while energy losses amount to 10–50%.

It should be noted that before the 1990s, our understanding of the heterotrophic character of corals and its impact on biogeochemistry was rather limited and the feeding behavior of corals was poorly illustrated. Hence, in Fig. 5.7, the studies were focused on the autotrophic translocation of synthesized organic matter, whereas the contribution of heterotrophic feeding on the energy flow was not included and hence underestimated. Moreover, the energy distribution for calcification and reproduction were not well studied in the 1980s. We know that for the part of symbiotic zooxanthellae, the energy loss includes the excretion of photosynthesized organic matter that fuels the microbial loop and stimulates the recycling of nutrients and other trace elements. Calculation of the energy participation for corals from zooxanthellae (e.g., loss) needs to consider the requirements for calcification of host as well as the energy source from heterotrophic feedings, etc.

5.5.4 Discussion

From a biogeochemical point of view, stress of macro- and micronutrients on the coral reef ecosystem is most likely a "bottom–up" effect (Table 5.5). Changes in concentration and stoichiometric ratio among nutrient and trace element species, together with hydrodynamics (e.g., flushing time), regulate the uptake rates and community structure of primary producers. Through the trophic interactions and coupling between the main food chain and microbial loop, nutrients and trace elements can affect the entire ecosystem. At the same time, the species ratio (e.g., DIN/DIP), amount, and composition of export products can be altered.

Autotrophy starts from the solar energy, dissolved inorganic nutrients, and trace elements, while heterotrophy of reef corals is stimulated by the energy of decomposition of organic materials and organic form of chemical elements. The relationship of these two players regulates the switch of chemical element pathways in the ecosystem and the interactions of coral reefs with the adjacent environment and hence the chemistry and biogeochemical cycle. It seems that the outstanding feature of coral reefs is the very active productivity, coupled with complex food web structure and high biodiversity in a rather over-stressed condition (e.g., low nutrients and trace elements).

It has been argued in the scientific society that over-enrichment of nutrients causes coral degradation by stimulating the overwhelming growth of competitive algae. Indeed, laboratory and/or mesocosm experiments provide evidences that growth of other primary producers (e.g., algae) can take over the system in the situation of eutrophication. However, nutrient levels in such experimental setup can be orders of magnitude higher than in nature, and the work suffers the limitation of spatial dimension (e.g., effect of water flushing) and temporal (e.g., a few weeks to months) scales. In most of these experiments, the nature of hydrodynamics (e.g., flushing time) of coral reefs is not properly considered. Moreover, in nature, coral reefs prone to nutrient over-enrichments are usually exposed to combined anthropogenic (e.g., fishing pressure and turbidity) and oceanographic (e.g., temperature and salinity) stressors that can make reef systems more susceptible to nutrient effects or create symptoms similar to those expected to eutrophication following an increase in flux of nutrients into coastal waters (Szmant 2002). Such phenomena include, for example:

- Coral reefs affected by riverine input and SGD often suffer from high nutrients and DOC with low salinity and variable temperatures; the turbidity of coastal waters is usually high because of abundant total suspended matter from terrestrial sources. Together, these can cause damage through bleaching and coral diseases.
- In the area affected by upwelling waters, high nutrients and DIC can also be observed, while water temperature, pH, and DO are relatively low. The episodic upwelling

events of low temperature with a prolonged period can damage corals with the effect of bleaching, etc.

- In the scenario of climate warming, high nutrients may be accompanied by elevated temperature, decrease of pH because of ocean acidification, strong UV radiation, etc. The solubility of CO_2 also decreases with increase of water temperature.

In all the abovementioned scenarios and/or cases, primary production can be promoted and hence increase the food availability to the main food chain as well as fuel the heterotrophic decomposition of organic matter in the water column.

When compared to offshore reefs and atolls that are exposed to high oceanic energy and rapid flushing of water, the nearshore coral reefs are more likely to be affected by anthropogenic perturbations (e.g., nutrient loadings) from land and/or local human activities, such as aquaculture and waste drainage as well. It has been demonstrated that dominance of algal colonization can be a result of reduced herbivory predation because of overfishing and the increased coverage of macroalgae in turn leads to a more susceptible situation of coral colonies to algal overgrowth (Ostrander et al. 2000; Szmant 2002). Such phenomena can be misinterpreted as to what can be expected being a consequence of nutrient over-enrichment, although a shift of community structure may take place without any changes in nutrient conditions. Furthermore, decline of coral reefs can be induced by diseases and corallivores, which is somehow similar to the symptom of nutrient over-enrichments, including reduced growth and reproduction rates and increased susceptibility to bleaching and mortality (Szmant 2002).

At the ecosystem level, nutrient over-enrichment has been reported to cause a reduction of calcification and skeleton growth rates. Such negative effects are, however, species related. Some coral species are more sensitive to the nutrient over-enrichments, including a synergy effect of CO_2 for calcification (Marubini and Atkinson 1999).

Cycles of chemical elements in coral reefs are somehow similar to other coastal ecosystems. In terms of the nitrogen cycle, N-fixation and denitrification are important mechanisms to maintain the very active primary productivity but to avoid the build-up of nutrient concentrations, apart from physical dynamics, e.g., flushing rate (Koop et al. 2001; Zhang 2016). In the case of the ENCORE field experiments, the presence of normal grazing rates and moderate nutrient over-enrichments resulted in little change in biomass and community structure of algae; hence, the impact on the coral and algal competition is rather limited (Koop et al. 2001).

Another important factor affecting biogeochemistry is the nature and sources of dissolved and particulate organic matter, both allochthonous and autochthonous materials, in the coral reefs. It has been shown that small size particulate organic matter (POM) can be a significant nutrient supply to the coral reefs and the role of dissolved organic matter (DOM) as a prominent energy source is known although the liability and flux remain to be adequately quantified (Genin et al. 2009; Patten et al. 2011; Tanaka et al. 2011). In fact, the heterotrophic uptake of organic matter is an important mechanism of energy flow in the microbial loop and material supply for the main food chain, since the organic matter translocated from autotrophic zooxanthellae to corals is nitrogen-poor and has high carbon-to-nutrient ratio. Together with autotrophy, these two pathways of mass flow adjust the biogeochemical cycles within the system and exchange between reefs and open seawater. In the coral reefs of the Western Australia, the daily uptake rate of NO_x is five- to tenfold higher than for PO_4^{3-}, and the uptake rate of dissolved organic nitrogen (DON) can be as high as 100–150 mmol N/m^2/day, ca. one order of magnitude higher than NO_x (Wyatt et al. 2012). The authors also indicated that reef recycling can be highly variable over time, depending upon the pulses of organic matter concentration and transportation flux (Wyatt et al. 2010, 2012). Note that recycling of nutrients and other chemical elements in the coral reefs does rely on not only the rate of remineralization but also the re-assimilation of elements by the reef community, as well as the flushing time of coral reefs. In the Ningaloo coral reefs of the Australia, such remineralization of autochthonous organic matter (e.g., plankton detritus) is rapid with coherent changes in daily fluxes of both inorganic and organic nitrogen forms (Wyatt et al. 2012).

From Scheffers et al. (2004) and Wyatt et al. (2012), coral reefs can also be an important sink of dissolved silicate because of the metabolic role played by silica containing suspension to feed sponges (i.e., fungi). This is suggested to affect the remineralization of organic forms of nutrients, for example, N and P. Such a source of remineralized nutrients can support free-living and/or macroalgae as well as seagrass meadows of back reefs and even link to the aggregation of the fish community on the reef slope.

Corals are active heterotrophs in their feeding strategy, and the heterotrophy can account up to 70% of fixed carbon incorporated into skeletons, as well as nutrients and other trace elements that cannot be supplied from symbiotic algae (Fabricius et al. 1995; Grottoli and Wellington 1999; Palardy et al. 2006). Moreover, the heterotrophic pathway provides corals with a significant energy source when photosynthetic organic matter is limited, which has an advantage for survival in bleaching events and turbid coastal waters (Anthony 2006; Houlbreque and Ferrier-Pages 2009). As reviewed by Houlbreque and Ferrier-Pages (2009), the heterotrophic food source of coral species consists of a wide range of size fractions, including from nitrogen-rich dissolved organic matter (e.g., urea and free amino acids) up to mesoplankton at size of 500–1000 μm, such as ciliates, eggs and larvae, copepods, and zoeae. Recent studies showed that coral uptake rates ranged from 1.1 to 24 mmol N/m^2/day for dissolved amino acids that is even comparable to the nitrogen uptake rate of autotrophs in certain circumstances, indicating that DOM is an important energetic source for corals (Ferrier 1991; Grover et al. 2008). Furthermore, corals can ingest sediment and particles in suspension and use the organic matter attached to them with an assimilation efficiency of 50%–80% (Rosenfeld et al. 1999; Anthony 2000). It is possible that corals feed primarily in heterotrophic pathway during the night, and in daytime translocation of organic matter from symbiotic primary producers become dominant, and there is evidence that coral feeding increases with zooplankton abundance, water depth, as well as temperature (Palardy et al. 2005). Among the various possibilities of input, the ingestion of pico- and nano-plankton can bring three times more nitrogen than dissolved sources, including NH_4^+, NO_3^-, and amino acids (Houlbreque and Ferrier-Pages 2009). On the other side, heterotrophic behavior of corals can provide recycled nutrients to symbiotic algae, which supports the zooxanthellae recovery and mitotic cell division after bleaching events (Rodrigues and Grottoli 2007). It is thought that the switch between autotrophic and heterotrophic energy sources is species specific and apparently the corals with dual autotroph and heterotroph characters have advantage in life strategy and competition for limiting elements in terms of sustaining a positive energy balance in harsh conditions, e.g., recovery from bleaching (Houlbreque and Ferrier-Pages 2009). Other benefits of heterotrophic feeding of corals include increased energy storage through reduced organic carbon (e.g., protein, lipids, fatty acids, and sterols) in coral tissues, increasing concentration density of zooxanthellae as well as pigments Chl-*a* and Chl-c_2 in surface tissues, and higher calcification rate and skeleton growth through shifts of Ca^{2+}/H^+ pump (Houlbreque and Ferrier-Pages 2009).

In summary, the findings mentioned above from the Western Pacific Region have applications to other tropical and subtropical areas of global ocean; the results compare favorably to the data in the literature. Across the coral reef platform from Bermuda of the North Atlantic Ocean, the observed DIC, TA, pH, and Ω_{ar} all show strong seasonal as well international variations (Yeakel et al. 2015). However, the range of DIC (2000–2100 μmol/kg), pH (8.02–8.14), and Ω_{ar} (3.2–4.0) are comparable to values reported in Figs. 5.2 and 5.4. Moreover, it has been indicated that inter-annual changes in NEC and NEP of Bermuda coral reef platform are driven by the offshore processes, such as the water exchange and productivity (Yeakel et al. 2015). Therefore, the natural variability of coral reef biogeochemistry is ultimately regulated by the large-scale climate and oceanographic processes. In the trend of coral declines in global scale, Fowell et al. (2018) reconstructed the history of 100 years at the Mesoamerican Barrier Reef System of Belize, Caribbean Sea, using coupled $\delta^{11}B$–$\delta^{13}C$ measurements of reef-building coral samples (i.e., *Siderastrea siderea*). The results indicated that calcification of reef-building corals can be enhanced by moderate CO_2-induced reduction in seawater pH, presumably owing to CO_2 fertilization of symbiotic zooxanthellae. This underscores that evolution of carbonate system of coral reefs over the last century should not be controlled solely by anthropogenic CO_2 (Fowell et al. 2018).

Similar to other areas of the Western Pacific Ocean, Martias et al. (2018) observed a strong gradient of chemical materials (e.g., nutrients and Chl-*a*) across the coral reefs from the New Caledonia, which is induced by the erosion of ultramafic rocks from adjacent terrestrial source. Dominance of terrestrial organic matter occurred in the areas affected by the river effluents together with higher concentration for trace elements, such as Co, Cu, Mn, and Ni. In the area affected by the offshore waters, colored dissolved organic matter (C-DOM) turns to be the nature of photodegradation products. Statistical data analysis revealed the regulation of chemical gradients on the structure of pico- and nano-size plankton communities, including *Prochlorococcus*, *Synechococcus*, nano-eukaryotes, and different groups of bacteria (Martias et al. 2018).

In the Red Sea, Ellis et al. (2019) compared the coral reef status data over a period of four decades with in situ measurements in 2014–2015 and found out that hard corals and coralline algae are more sensitive relative to other species (e.g., turf, algae, and soft corals) to changing environmental conditions. Moreover, fishing pressure and eutrophication can exacerbate the impact of climate variability because of synergistic interactions. Given that coral reefs are in serious decline with an estimate 30% already severely damaged, reduction of hard corals will result in a reef environment dominated by macroalgae and turf communities, which is not necessarily taking place in the Red Sea but other coral reefs, such as in the Western Pacific Region (Ellis et al. 2019).

Radice et al. (2020) examined the bleaching (oceanic heat stress event) effects on the trophic status of coral reef environment from the Maldives of the Indian Ocean. Using data of $\delta^{13}C$–$\delta^{15}N$ isotope pairs of particulate organic matter, the author examined and compared before and after the 2016 mass coral bleaching event, and the results show the slow recovery of coral reefs based on the indication of water chemistry. Moreover, there is an increase in $\delta^{13}C$, $\delta^{15}N$, and C:N ratio for POM after the mass coral bleaching event, which underlines the changes in plankton community structure (Radice et al. 2020). The findings from Maldives highlight that the post-bleaching recovery of coral environment (i.e., reef trophic ecology) is regulated by the changes in oceanographic regimes related to ocean mixing and hence the regional circulation. Quite often, the recovery of coral reefs is a slow and sometimes irreversible process with respect to the relief of external forcings. There is usually a delay and/or lag relative to external pulses (driving forces), because of changing oceanographic regime, complex biogeochemical cycle, and the barriers of system connectivity in combination.

In the area of Gulf California (Mexico) from the Eastern Tropical Pacific Ocean, Norzagaray et al. (2020) found out that pH, aragonite saturation index (Ω_{ar}), and dissolved oxygen of fringe coral reefs are regulated by the proportional mixing of three different water masses. For example, the observed Ω_{ar} and pH increase with higher proportion of Gulf of California Water (GCW), while tropical surface water (TSW) is characterized by lower Ω_{ar} and pH. At seasonal scale, variability of Ω_{ar} and pH is controlled by water masses with different carbon chemistry, and transition between water masses related to mesoscale structures (e.g., eddies) results in water samples from coral reef with different biogeochemical signals (Norzagaray et al. 2020).

5.6 Prospect of Climate Change and Anthropogenic Perturbations

Increased $p\text{CO}_2$ can be beneficial to primary producers such as phytoplankton, benthic algae, and seagrass but might decrease coral calcification. There is also the potential for a phase/regime shift from coral reefs to algal-dominated ecosystems in high $p\text{CO}_2$ ocean. However, it should be kept in mind that at least to some extent, corals living in nearshore areas can grow under conditions previously predicted as detrimental for coral reef existence, for example, $p\text{CO}_2 > 450$ μatm and $\Omega_{ar} < 3.3$ (Hoegh-Guldberg et al. 2007; Veron et al. 2009).

In the global warming scenario, the coupling of higher water temperature and other stressors (e.g., ocean acidification) can make the coral reefs more prone to environmental changes. For example, elevated temperature during the hypoxic periods can exacerbate the stress impacts and susceptibility of corals to deoxygenation, with consequences of lowered diversity and shift in community structure (Altieri et al. 2017).

5.6.1 Global Warming and Ocean Acidification

It is believed that corals live in an environment that is very close to their upper limit (i.e., threshold) of thermal tolerance. Seawater temperature in many tropical areas has increased by 1–2 °C since the beginning of the Industrial Revolution because of accelerated human activities (e.g., emission of CO_2 and other pollutants) over the last several hundred years. It has been predicted that global warming will continue in the very near future and the seawater temperature will be increased by another 1–2 °C by the end of this century in response to greenhouse effect on average but with stronger inter-annual variabilities than ever before. This is likely to push corals beyond their thermal limits (i.e., threshold). Corals and their symbiotic zooxanthellae may not be able to acclimatize and/or adapt to such rapid and systematic temperature changes plus other sporadic thermal events. In the Western Pacific Ocean, the observed changes in sea surface temperature (SST) can be linked to the variability of Walker and Hadley Circulations (spatial effects) and to El Niño–Southern Oscillation (ENSO) (temporal-scale changes). The consequences of global changes on reef systems are not limited to corals alone in a warmer ocean, because ecosystem structure, function, and complexity created by coral reefs provide habitats, goods, and food for many other associated organisms, and millions of people rely on coral reefs for their livelihood.

The rate of warming in tropical oceans of the Western Pacific Region is 0.08 °C/decade for the period of 1950–2011, which is lower than the 0.12 °C/decade for the global average; in this period, SST of reef areas is in the range of 22–30 °C (Lough 2012). Over the last 30 years, SSTs of the tropical Western Pacific Ocean are systematically higher than in 1950–1980, with a maximum difference of ca. 0.5–1.0 °C, with an extension of the temporal period when corals are subjected to elevated temperature during the year (Lough 2012).

One of the direct consequences of global warming is the increase in SST. Increase in SST can push symbiotic algae (e.g., zooxanthellae) off from the corals and hence reduce the density of photosynthetic cells in surface tissues of the host, e.g., bleaching, which can be exacerbated by the changes in UV radiation that is another human impact on global climate (Lesser 1996). Dark reactions of photosynthesis are more sensitive than the light counterpart to the effects of thermal stress, and the damage caused by heat can be amplified by the radiation because high intensity of radiation leads to an overall reduction of light reaction and an increase in production of harmful chemicals such as free oxygen radicals (Jones et al. 1998). Moreover, increase in SST can change *p*/*r* ratio for reef systems because respiration increases more rapidly with temperature, resulting in corals becoming more prone to other stressors (e.g., diseases). The potential change in *p*/*r* ratio for coral reefs under thermal stress has a direct consequence of new vs recycled productions and a shift of relative importance of cycle pathways for chemical elements in the ecosystem, including nutrients.

In the twentieth century, large-scale, strong, and massive coral bleaching episodes usually coincide with periods of high SST and are related to the ENSO, such as 1982–1983, 1987–1988, 1991–1992, 1994–1995, and 1997–1998, although it has been reported that bleaching can also take place during La Niña events (Hoegh-Guldberg 1999).

However, “bleaching” is not a straightforward consequence of thermal stress (i.e., increase in SST), and it has been reported that corals with high symbiont cell density—a ratio of the total number of symbionts to the total number of host cells—are more vulnerable to thermal stress and hence become more prone to the damage created by the climate-induced bleaching events (Cunning and Baker 2013). In addition to bleaching, higher temperature can have negative effects on the development of individuals and on the reproduction capacity of coral populations, with negative consequences on exchange of chemical elements between reef corals and water bodies through reduced maturation, fertilization, and calcification.

Change in water pH has different temporal scales. Daily pH variability takes place, e.g., high in daytime induced by photosynthesis but low at night because of dominance of respiration. Episodic and substantial reduction of pH can occur in coastal environments that is related to deoxygenation of water body because of hypoxia and/or even anoxia, as well as associated with upwellings. In the global change scenario, slow but continuous reduction of surface water pH induced by so-called ocean acidification is taking place that is related to the anthropogenic emission of CO_2 and other greenhouse gas species (e.g., CH_4 and N_2O). Reduction of surface water pH has a number of effects on the biogeochemistry of coral reefs, such as direct impact on calcification and indirect effects including change of speciation, bioavailability of chemical elements, etc.

Over the last 200 years, surface ocean pH has been reduced by 0.1–0.2, while daily variability of coastal waters and some seasonal hypoxic systems can have pH ranges higher than this value (i.e., 0.1–0.2). This indicates that coral reefs in coastal environment can develop a better ability for adaptation than oceanic reef atolls toward the impact of ocean acidification.

Seawater pH has important effects on the development coral organisms at the life history level. For example, Viyakarn et al. (2015) showed that at a pH range of 7.6–7.9, the coral larvae settlement declines relative to normal pH = 8.1 and the metamorphosis/life cycle is considerably delayed, which has a dramatic and negative effect on the system recruitment.

Nevertheless, the experimental work on the effects of ocean acidification in the literature is undertaken within limited space and time, and hence the reported results may suffer from the constraints of spatial and temporal scales. The reason is that organisms may adapt the change in pH if the biological evolution is fast relative to the rate of pH reduction (i.e., ocean acidification). Model simulations of dinoflagellates and sponge symbiosis of the Indo-Pacific Region show that in a scenario of +1.97 °C and +184.1 μatm of pCO_2, animal hosts benefit from a greater supply of photosynthetic products for growth, while in the scenario of +3.46 °C and +586.5 μatm of pCO_2, animal hosts experience the highest metabolic demand but carbon acquired is insufficient as indicated by a negative energy budget (Fang et al. 2014).

5.6.2 Impacts of Sea Level Rise

Collectively, thermal expansion of surface waters and reduction of continental glaciers result in the slow but continuous sea level rise since the Industrial Revolution started from Europe more than 200 years ago. In the Holocene, the development of coral reefs was diversified by wave-affected fore reefs and less disturbed or calm back reefs with a depressed topography in the form of the shallow lagoon (e.g., reef flats). In order to maintain healthy coral reefs, the growth rate (e.g., linear extension) of the reef (V_r) should be comparable to the rate of sea level rise (V_s) at a given position across the reef crest in the direction perpendicular to the coast line (Nakamura and Nakamori 2007). If V_r is considerably higher than V_s, corals will suffer from the effect of photo-damage and thermal stress, while in the case of smaller V_r than V_s, photosynthesis can be negatively affected, and coral will die, because the maximal depth limit of corals is 5–10% of surface irradiance (Cooper et al. 2007). From Nakamura and Nakamori (2007), the reef growth rate is strongly dependent upon the calcification rate of coral reefs, which in turn relies on gradients of total carbon dioxide and eddy diffusion rates. Thus, coral reefs in a dynamic environment, with an abundant supply of carbon dioxide and high eddy diffusion coefficients, will have better accommodations to the impact of sea level rise. This is consistent with the observations that growth rates of coral reefs are generally faster on the windward side than on the leeward side (Kan et al. 1997; Yamano et al. 2001).

5.6.3 Roles of Human Society from Land- and Marine-Based Activities

In addition to climate change, human activities will be intensified in many coastal zones in the future, particularly in the tropical and subtropical Western Pacific Region, where economies are booming (Chap. 2).

Riverine flux can be changed because of climate variability, such as tropical cyclones that impact watersheds and generate floods with a large amount of nutrients and terrestrial sediments. Coral reefs adjacent to a river mouth and/or affected by the along-shore circulation can be affected by increased loading of nutrients and sediments from land source. Fluxes from SGD can also be changed. Other impacts from the land sector include reclamation of tidal areas, which induces modification and even net loss of habitats for many marine species of economic value.

Coastal aquaculture is a very popular fishery activity in Southeast Asia and provides food, job opportunities, and incomes to millions of people and hence improves the economic situations of the country. However, release of solid wastes and discharge of wastewaters from aquaculture facilities can create problems of pollution and/or eutrophication in the adjacent marine environment and in extreme cases cause hypoxia and even anoxia, which can induce catastrophic consequences to the adjacent coral reefs.

Overfishing and illegal fishing activities may wipe top predators out of the food web. In Southeast Asia, fishing down the whole food web is a popular activity, including carnivores, herbivores, and omnivores. This may leave a niche for algae and benthic animals to compete with corals for habitats and for sources of nutrition (e.g., nutrients), and organic matter released by algae and animals can stimulate the microbial activity that can generate diseases fatal to corals.

5.6.4 Feedbacks to the Earth System

In the climate change science, feedbacks from coral reefs to other compartments of the Earth system need to be assessed because this is a missing part in current models. For example, the interactive relationship with the atmosphere can make coral reefs as a whole an important source of active and trace gas species.

The symbiotic algae of corals (e.g., zooxanthellae) contain a significant amount of dimethylsulfoniopropionate (DMSP), which is suggested to act as an osmolyte and/or a regulator of osmotic pressure, particularly in the situation of nitrogen limitation. In the nutrient enrichment experiments, it is found that DMSP shows a significant increase in coral colonies, particularly in those enriched with phosphorus (Koop et al. 2001). This suggests that coral reefs may be potentially important as an emission source of DMSP into the tropical atmosphere and hence contribute to the global sulfur cycle.

One of the remarkable characteristics of coral reefs is the diurnal variability of three cross-linked processes, that is, photosynthesis, respiration, and calcification, which collectively regulate the $p\mathrm{CO}_2$ of reef environments. Although photosynthesis can increase pH and reduce $p\mathrm{CO}_2$ in daytime, calcification and dominance of community respiration at night increase both the inventory of $p\mathrm{CO}_2$ and total alkalinity (e.g., HCO_3^-) in the water column. Thus, it is possible that some coral reefs and/or coral reefs in a certain time period (e.g., daily and seasonal scales) become a source of atmospheric CO_2, although the amount of CO_2 emitted from reef areas is difficult to quantify.

Iodine is considered as a basic nutrient element in marine ecosystems and can be enriched in some species of algae and seaweeds. Marine plant can remove iodate (IO_3^-) from seawater that is reduced to iodide (I^-) and then released. The redox reactions of iodine can generate molecular iodine (I_2) that is a volatile species and escape into atmosphere via air–sea exchange (Atkinson and Falter 2003).

It is not clear yet how the coral reef ecosystem services will change in the future. However, given the combined stresses of global warming, ocean acidification, and sea level rise, the sustainability of coral reefs is of great concern from a scientific research perspective to the issues of management at an ecosystem level.

In terms of system sustainability, the reported decline of coral reefs also has dramatic impacts on the human society. Given the fact that most of maritime developing countries are located in tropical and subtropical region and millions of people there have their livelihood relying on marine ecosystems, development of coral reefs under the influence of climate change is expected to have feedbacks for human society with notable consequences, such as:

- Decline of coral reefs has direct and negative impacts on the fish production, which affects people living in tropical coastal areas. Also reef systems provide with spawning and/or hatching habitats for many marine species of economically important value.
- Coral reefs are very attractive areas for tourism in tropical region, including diving, sightseeing, and other recreational activities. Therefore, degradation of reef ecosystems will have dramatic influences on the economic income for many developing countries.
- Shells of some species of coral reefs (e.g., giant clams and red corals) are traditionally considered as treasures in trade business of the Western Pacific Ocean. The unordered/illegal harvesting activities have exhausted the resources with negative consequences for biodiversity and ecosystem health, even extinction of rare species.
- Fringing corals have an important function of protecting the land mass from damage created at seashores (e.g., cyclonic storms). Mining activities for the purpose of house-building and lime production can destroy whole reef systems, inducing the erosion and even loss of the beach.

5.7 Modeling Approach to the Biogeochemistry of Coral Reefs

The symbiotic relationship between algae–zooxanthellae and coral host is crucial for the health of coral reefs. It has been identified that the interruption of this relationship will result in coral bleaching. Different theoretic models have been proposed for understanding the breakdown of zooxanthellae–coral symbiosis, with a basic framework of photo-physiology of the algal symbionts, mass and energy transfer between symbiotic algae and host animal, and breakdown of the symbiotic relationship caused by changing environment condition (e.g., light, temperature, and nutrients). Understanding the dynamics of the symbiosis is essential to predict how coral reefs respond to environmental stresses. Reconstruction of coral reef system biological and chemical processes in a dynamic environment by numerical simulations is becoming practical due to developments in computer simulation technology. Here, we reviewed the development of numerical models in exploring the coral–algae symbiosis and coral bleaching. We expect that the information introduced about numerical models will benefit the research of coral bleaching in a dynamic way.

5.7.1 Quantitative Description of the Coral Symbiosis

Identification of the underlying mechanisms which involved the trigger of coral bleaching could start from the mass/energy transfer in the symbiotic relationship of zooxanthellae and coral host. The symbiosis between the coral and zooxanthellae is a fragile relationship and sensitive to environment changes of irradiance, temperature, and nutrient concentration. Stability of coral symbiotic system requires balanced population growth of symbionts and energy translocation. How is the population density of zooxanthellae maintained and what happens to the symbiotic system if the translocation between coral and zooxanthellae is disturbed? To answer this kind of research questions would help us in understanding the mechanisms of the symbiotic system which is the fundamental learning part of bleaching.

Firstly, a steady-state solution of the mass and energy budgets in the coral–zooxanthellae system is necessary under non-bleaching condition. Many studies have been applied to quantify this symbiotic system photosynthesis, respiration, and calcification, as well as the various fluxes depicted in Fig. 5.8. The energy budget for *Stylophora pistillata* was examined by isotopic tracers along with in situ measurement; equations were developed to relate measurable values for relevant parameters, including photosynthesis, respiration, growth, and mucus and skeletal production (Falkowski et al. 1984, 1993; Muscatine et al. 1984). Photosynthesis rates, biomass of the zooxanthellae separate from the coral animal, and respiration rates were measured to estimate carbon and nitrogen translocation. Growth rates of the zooxanthellae and the coral animal, as well as the animal's mucus and skeletal production, were also included.

Early models have provided the fundamental framework of coral symbiosis and mathematically explored the functions and parameters used to describe the mixotrophic relationship of zooxanthellae and coral host. For the underlying mechanisms involved in disturbing and/or breakdown of this mixotrophic nutrition, especially how the variabilities of light, temperature, and nutrients could lead to perturbations of metabolic processes in the algae or their host cells and subsequent bleaching, more processes and/or pathways need to be identified in the physiological state, and coupling with environmental conditions needs to be considered as well.

One approach to look into the evolutionary success of the symbiotic association is to develop the cell-based basic features of the coral–algae symbiosis, which includes calculation of changes in the physiology of the autotrophic zooxanthellae and heterotrophic host cells. A cell-based phytoplankton growth model was used to describe

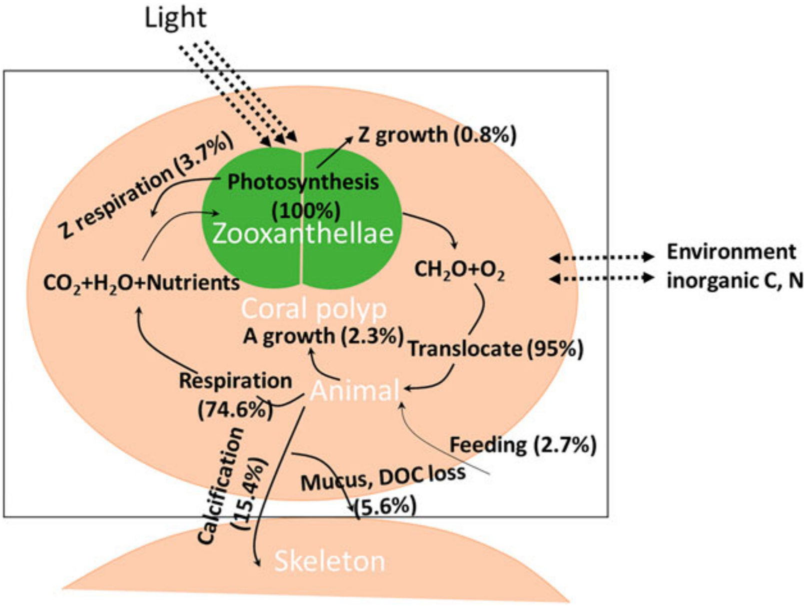


Fig. 5.8 The conceptual overview of coral–algae symbiosis. Using energy from the sunlight, zooxanthellae uptake nutrients, fix carbon dioxide, synthesize organic molecules, and translocate the photosynthetic products to coral host animals. Animals use this organic matter from zooxanthellae to satisfy the metabolic requirements and give back to algae inorganic nutrients and carbon dioxide that they need to survive. Host animal also absorbs calcium from seawater and uses dissolved inorganic carbon to deposit skeletal $CaCO_3$. The numbers in the parentheses denote carbon budgets denoted in Falkowski et al. 1984

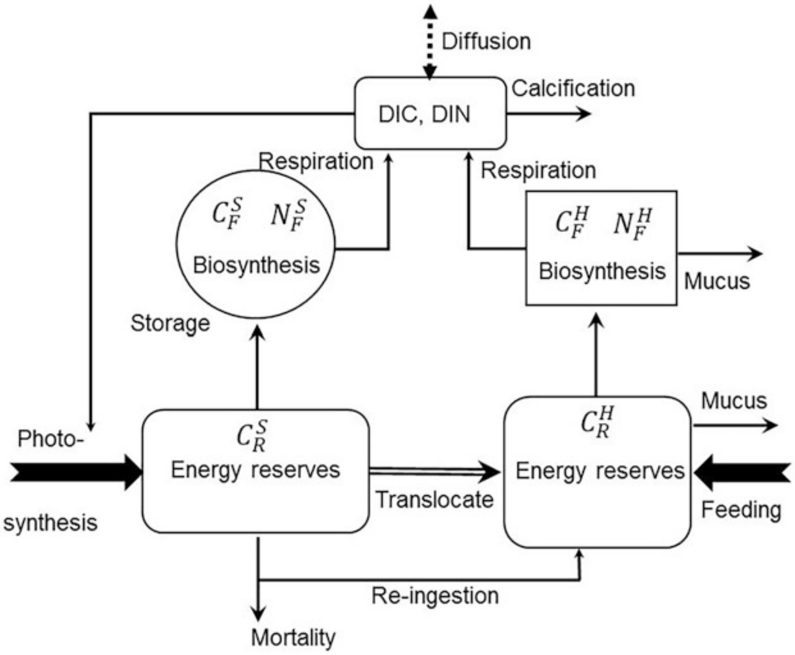


Fig. 5.9 Schematic illustrations of the coral symbiosis model developed by Gustafsson et al. (2013) with modifications. Eight state variables were considered in the model, including C_R^S–carbon in the symbiont reserve pool, C_F^S, N_F^S–carbon and nitrogen in the symbiont functional pool, C_R^H–carbon in the host reserve pool, C_F^H, N_F^H–carbon and nitrogen in the host functional pool, DIC–DIC in the host tissue, and DIN–DIN in the host tissue. The arrows in the figure indicate the fluxes and material/energy flow. Note that other nutrients, such DIP and DSi, as well as trace elements are not considered in the current model simulation

photosynthesis and photo-acclimation under nutrient-replete conditions (Ross and Geider 2009). The model differentiates between a functional pool which contains both carbon and nitrogen and an energy reserve pool which contains organic carbon storage reserve that contributes to the growth of algae. Through the explicit inclusion of different functions in a cell, the terms of chlorophyll synthesis are improved. Gustafsson et al. (2013) incorporated this basic energetic feature of model approach developed by Ross and Geider (2009) to zooxanthellae–coral host system. In this cell-based model, modeling the intracellular mechanism as well as the quantitative linkage of energy transfer between zooxanthellae and coral host has been approached (Gustafsson et al. 2013; herein after GBR13). In the model, major metabolic processes, i.e., nutrient cycling, respiration, cell division, mucus production, synthesis of tissues and chlorophyll, and calcification, are mathematically described (Fig. 5.9). In GBR13, total cellular carbon is divided into two cross-linked parts that are (1) a functional pool, which contains parts of the cell's biosynthetic apparatus and structural material (e.g., genome, cell membrane, and cell wall), and (2) an energy reserve pool, which contains organic carbon storage reserves. With regard to the relationship of zooxanthellae and coral host in the symbiotic system, there are state variables describing the carbon in the functional pool and the reserve pool. The change of zooxanthellae cells population is also described as when the symbiont structural biomass reached the maximum symbiont biomass, a cell starts to divide and the population of zooxanthellae cell increases. The updated version of GBR13 (Gustafsson et al. 2014) added photosystem model for zooxanthellae cell and other major associated processes such as antioxidant systems; nutritional cost of repairing the photosystem; producing antioxidants; synthesis of chlorophyll, diadinoxanthin, and diatoxanthin pigments; and the loss of symbionts due to damage caused by reactive oxygen substance (ROS) production (Fig. 5.10). The model is capable of capturing the diurnal change of the photosystem with light, as well as changes in the symbiont population and the coral host caused by different temperature, light, and feeding treatments.

5.7.2 Reef-Scale Model for Coral Ecosystems

Calcification models based on the coral polyp model (i.e., organismal level) have been developed to describe ion transport through epithelial cells via the transcellular pathway and intercellular transport through the paracellular pathway (Hohn and Merico 2012, 2015). These models have been used to scrutinize the day–night CO_2 system changes in the coral tissue, coelenteron, and calcifying fluid and have confirmed the importance of the different ion pathways under the scenario of ocean acidification.

A coral polyp model by Nakamura et al. (2013) was developed to study the response of coral photosynthesis, respiration, and calcification to combined environmental effects and reconstruct the combined responses to changes in light, flow field, ambient dissolved oxygen (DO), DIC, and TA, including under acidified water conditions. The coral polyp model separated the coral polyp into three compartments, including (1) ambient seawater, where diffusion of DO and DIC with outside water column take place;

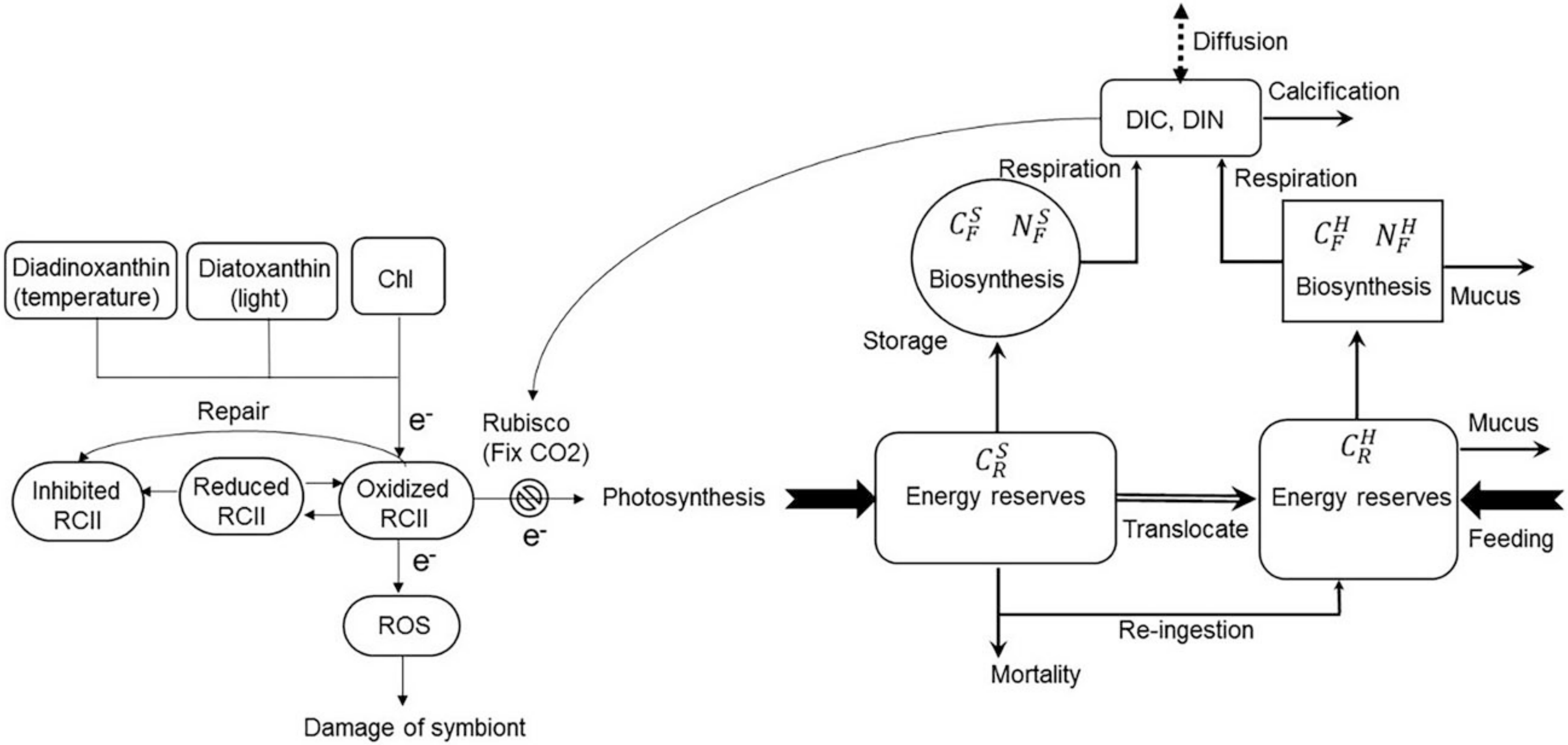
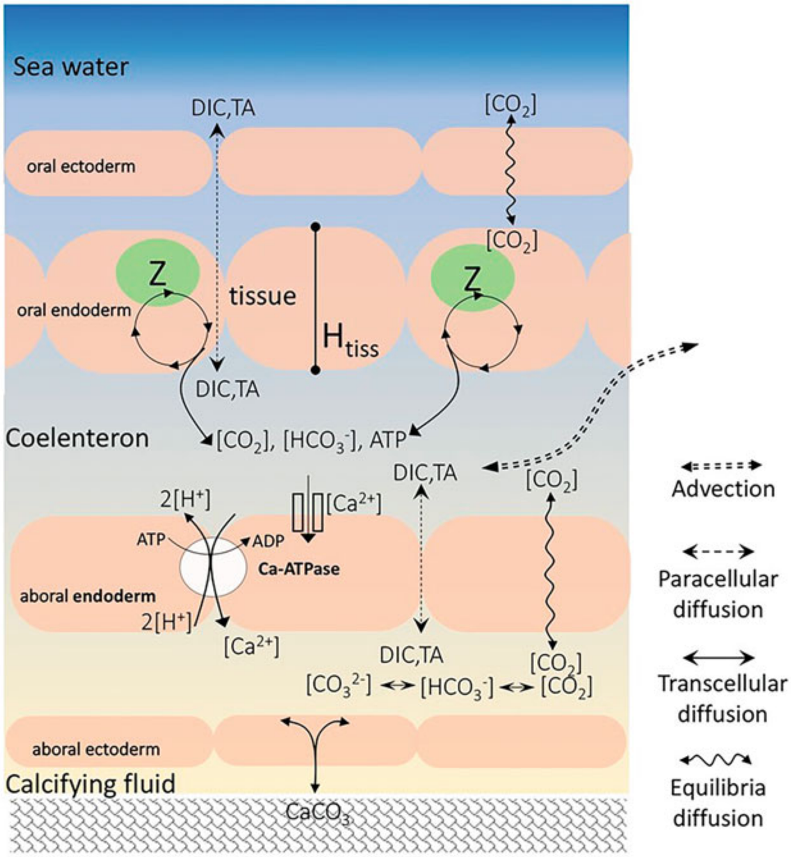


Fig. 5.10 Schematic diagram of the model developed by Gustafsson et al. (2014), with an updated module of photo-inhibition to study the interactions of temperature, light/radiation intensity, and rate of heterotrophic feedings on the coral bleaching

Fig. 5.11 Schematic illustrations of the coral polyp structure, including two main tissue layers with symbiotic algae in the coral's oral endoderm and underlying skeleton. The polyp model components include the host tissue, coelenteron, and calcifying fluid. The coelenteron is connected to the ambient seawater. Photosynthesis and respiration take place in the coral tissue, and calcification occurs in the calcifying fluid. Different types of fluxes are indicated with different arrow shapes



(2) the coelenteron, where photosynthesis and respiration occur; and (3) the calcifying fluid, where calcification exits. The "trans" calcification model (McConnaughey and Falk 1991; McConnaughey and Whelan 1997; Allemand et al. 2004) is mathematically described. There are diffusion fluxes between seawater and coelenteron and fluxes between coelenteron and calcifying fluid via the paracellular pathways (Fig. 5.11). This model was numerically solved by calculating the fluxes and mass balance equations of DIC, TA, DO, and CH_2O (organic matter) in the three components with forward difference scheme on time. This coral polyp model was also coupled with a three-dimensional hydrodynamic model and updated to a reef-scale model (Nakamura et al. 2013). The polyp model calculated DO, TA, and DIC were exchanged with these variables at the bottom grid of the hydrodynamic–biogeochemical model in the form of mass fluxes. Scenario analyses were applied to test the influence of sea level rise and increase of $p\mathrm{CO}_2$ on coral calcification rate. This model firstly built up the two-way coupling of coral polyp model with hydrodynamic–biogeochemical model and successfully presented the feedbacks between environment water chemistry (e.g., DO, DIC, and TA) and coral metabolism. The polyp model was built up on some simplified assumptions and with a few exclusions. For example, photosynthetic rate is related with light and HCO_3^- concentration, and the influence of temperature and other nutrients is not considered. The change of zooxanthellae population and heterotrophic feeding of organic carbon were not included in the polyp model. The model incorporates the metabolic process of coral as a whole system. More details of coral symbiosis, for example, the mass and energy transfer between zooxanthellae and host animal, were not included, which is an essential part to study the symbiotic associations. Therefore, to improve the reef-scale the model requires considering the zooxanthellae population dynamics under different temperature and nutrient conditions, as well as organic matter feeding, which will better describe the mixotrophic system and predict the response of corals to complex environmental stresses.

5.7.3 Examples of Numerical Simulations in Coral System

In this chapter, we give examples of mathematically described coral polyp photosynthesis, respiration, and calcification based on the frame shown in Fig. 5.8. These associated metabolism processes were mathematically described by equations and summarized in Table 5.6 with parameters specified in Table 5.7. For example, the symbiont

Table 5.6 Model equations for coral metabolism processes and biogeochemical dynamics in this study

Symbol	Description	Equation	Unit
A	Coral self-shading factor	$1.26 + 1.39\mathrm{e}^{\left(-6.48\frac{S}{S_{\max}}\right)}$	-
$f(\mathrm{I})$	Light function	AI	μmol m^{-2} s^{-1}
P_S	Photosynthesis	$P_S = \left(\frac{P_S^{\max}}{P_S^{\max}/f(I)\mathrm{I}+1}\right)\left(\frac{\left[\mathrm{HCO}_3^-\right]_{\mathrm{tiss}}}{K_{\mathrm{HCO}_3}+\left[\mathrm{HCO}_3^-\right]_{\mathrm{tiss}}}\right)$	μg C cell^{-1} day^{-1}
$P_S^{\max}$	Maximum C specific photosynthesis	$\mu_S^{\max} C_S^F$	μg C cell^{-1} day^{-1}
$V_{S,\max}^N$	Maximum N uptake rate by symbiont	$\begin{cases} \mu_S^{\max} C_S^F IR_{FS}, & \text{if} \quad I > 0 \\ \alpha\mu_S^{\max} C_S^F IR_{FS}, & \text{else} \end{cases}$	μg N cell^{-1} day^{-1}
V_S^C	The rate of C bind to the newly attained N	$\frac{V_{S,\max}^N}{IR_{FS}}\left(\frac{\mathrm{NH4}_{\mathrm{tiss}}}{K_{\mathrm{NH4\_tiss}}+\mathrm{NH4}_{\mathrm{tiss}}}\right)\left(\frac{C_S^R}{C_S^R+C_S^{\mathrm{thres}}}\right)\left(1-\frac{S}{S_{\max}}\right)$	μg C cell^{-1} day^{-1}
$M_{S,C}^R$	Mortality loss of carbon in the reserve pool	$m_C^S C_S^R$	μg C cell^{-1} day^{-1}
$M_{S,C}^F$	Mortality loss of carbon in the functional pool	$m_C^S C_S^F$	μg C cell^{-1} day^{-1}
M_{host}^S	C from dead symbiont cells re-ingested by host	$\left(M_{S,C}^R + M_{S,C}^F\right)\left(1-\frac{C_H^R}{C_{H,\max}^R}\right)$	μg C cell^{-1} day^{-1}
M_{out}^C	C from dead symbiont cells expelled	$\frac{C_H^R}{C_{H,\max}^R}\left(M_{S,C}^R + M_{S,C}^F\right)$	μg C cell^{-1} day^{-1}
T_C	Total translocated C from symbiont to host	$P_S\left(\frac{C_S^R}{C_S^R+C_S^{\mathrm{thres}}}\right)\left(1-\frac{C_H^R}{C_{H,\max}^R}\right)$	μg C cell^{-1} day^{-1}
T_{CF}	Translocated C from symbiont functional pool to host reserve pool	$\frac{IR_T T_C}{IR_{FS}}$	μg C cell^{-1} day^{-1}
$R_{S,\,C}$	Biosynthesis and respiration symbiont C	$V_S^C\delta_S + C_S^F\gamma_S$	μg C cell^{-1} day^{-1}
M_S^S	Symbiont population size change due to mortality	$m^S S$	cell cm^{-2} day^{-1}
μ_S	Symbiont growth rate	$\max\left(\frac{dC_S^F}{dt}/C_S^F, 0\right)$	day^{-1}
$F_{\mathrm{DIC\ \_\ tiss}}$	Host DIC uptake from the seawater	$V_{\mathrm{DIC\_tiss}} C_H^F\left(\frac{\mathrm{DIC}_{\mathrm{sea}}}{k_{\mathrm{DIC\_sea}}+\mathrm{DIC}_{\mathrm{sea}}}\right)$	μmol C cm^{-2} s^{-1}
$F_{\mathrm{NH4\ \_\ tiss}}$	Host DIN uptake from the seawater	$V_{\mathrm{NH4\_tiss}} C_H^F\left(\frac{\mathrm{NH4}_{\mathrm{sea}}}{k_{\mathrm{NH4\_sea}}+\mathrm{NH4}_{\mathrm{sea}}}\right)$	μmol N cm^{-2} s^{-1}
$R_{H,\,C}$	Host respiration	$V_H^C\delta_H + C_H^F\gamma_H$	μg C cm^{-2} day^{-1}
V_H^C	N-limited C translocation rate from the host reserve pool to the functional pool	$F_{\mathrm{DON}}/IR_{FH} + S\left[M_{S,C}^F\left(1-\frac{C_H^R}{C_{H,\max}^R}\right)IR_{FS} + IR_T T_C\right]/IR_{FH}$	μg C cm^{-2} day^{-1}
Mu_C	Total mucus C	$\mathrm{Mu}_C^R + \mathrm{Mu}_C^F$	μg C cm^{-2} day^{-1}
Mu_C^F	Mucus C from host functional pool	$\varepsilon_M C_H^F$	μg C cm^{-2} day^{-1}
Mu_C^R	Mucus C from host reserve pool	$\varepsilon_M C_H^R\left(\frac{C_H^R}{C_{H,\max}^R}\right)$	μg C cm^{-2} day^{-1}
$C_{H,\max}^R$	Max size of host reserve pool	$4C_H^F$	μg C cm^{-2}
F_{DOC}	Heterotrophic feeding of DOC	$12V_{\mathrm{DOC}}\frac{[\mathrm{DOC}]^2}{k_{\mathrm{DOC}}+[\mathrm{DOC}]^2}$	μg C cm^{-2} day^{-1}
F_{DON}	Heterotrophic feeding of DON	$0.176 * F_{\mathrm{DOC}}$	μg N cm^{-2} day^{-1}
$\frac{dC_H^R}{dt}$	Change of C in host reserve pool	$F_{\mathrm{DOC}} + \mathrm{ST}_C + \mathrm{SM}_{\mathrm{host}}^S - \mathrm{Mu}_C^R - V_H^C$	μg C cm^{-2} day^{-1}
$\frac{dC_H^F}{dt}$	Change of C in host functional pool	$V_H^C - \mathrm{Mu}_C^F - R_{H,C}$	μg C cm^{-2} day^{-1}
$F_{\mathrm{DIC\ \_\ coe}}$	DIC transport from host tissue to coelenteron	$V_{\mathrm{DIC\_coe}}\left(\frac{\mathrm{DIC}_{\mathrm{tiss}}}{k_{\mathrm{DIC}}+\mathrm{DIC}_{\mathrm{tiss}}}\right)E_I$	μmol C cm^{-2} s^{-1}
$F_{\mathrm{DIC\ \_\ cal}}$	DIC transport from host tissue to calcifying fluid	$V_{\mathrm{DIC\_cal}}\left(\frac{\mathrm{DIC}_{\mathrm{tiss}}}{k_{\mathrm{DIC}}+\mathrm{DIC}_{\mathrm{tiss}}}\right)E_I$	μmol C cm^{-2} s^{-1}
$F_{\mathrm{CO_2\_sea}}$	Diffusion of CO_2 from ambient seawater to host tissue	$d_{\mathrm{CO}_2}\left([\mathrm{CO}_2]_{\mathrm{sea}} - [\mathrm{CO}_2]_{\mathrm{tiss}}\right)$	μmol C cm^{-2} s^{-1}
$F_{\mathrm{CO_2\_coe}}$	Diffusion of CO_2 from coelenteron to host tissue	$d_{\mathrm{CO}_2}\left([\mathrm{CO}_2]_{\mathrm{coe}} - [\mathrm{CO}_2]_{\mathrm{tiss}}\right)$	μmol C cm^{-2} s^{-1}
$F_{\mathrm{CO_2\_cal}}$	Diffusion of CO_2 from calcifying fluid to host tissue	$d_{\mathrm{CO}_2}\left([\mathrm{CO}_2]_{\mathrm{cal}} - [\mathrm{CO}_2]_{\mathrm{tiss}}\right)$	μmol C cm^{-2} s^{-1}
$F_{\mathrm{TA\ \_\ p\ \_\ cal}}$	Paracellular diffusion of TA from coelenteron to the calcifying fluid	$K_P(\mathrm{TA}_{\mathrm{coe}} - \mathrm{TA}_{\mathrm{cal}})$	μmol cm^{-2} s^{-1}
$F_{\mathrm{DIC\ \_\ p\ \_\ cal}}$	Paracellular diffusion of DIC from coelenteron to the calcifying fluid	$K_P(\mathrm{DIC}_{\mathrm{coe}} - \mathrm{DIC}_{\mathrm{cal}})$	μmol cm^{-2} s^{-1}
$F_{\mathrm{TA\ \_\ p\ \_\ coe}}$	Paracellular diffusion of TA from ambient seawater to coelenteron	$K_P(\mathrm{TA}_{\mathrm{sea}} - \mathrm{TA}_{\mathrm{coe}})$	μmol cm^{-2} s^{-1}

(continued)

Table 5.6 (continued)

Symbol	Description	Equation	Unit
$F_{\mathrm{DIC\_p\_coe}}$	Paracellular diffusion of DIC from ambient seawater to coelenteron	$K_P(\mathrm{DIC_{sea}} - \mathrm{DIC_{coe}})$	μmol cm^{-2} s^{-1}
$F_{\mathrm{TA\_v}}$	Exchange of TA through the mouth of the polyp	$\omega(\mathrm{TA_{sea}} - \mathrm{TA_{coe}})$	μmol cm^{-2} s^{-1}
$F_{\mathrm{DIC\_v}}$	Exchange of DIC through the mouth of the polyp	$\omega(\mathrm{DIC_{sea}} - \mathrm{DIC_{coe}})$	μmol cm^{-2} s^{-1}
ω	Exchange rate through the mouth of the polyp	$(65.7\tau^{0.4} + 4.7) \times 10^{-4}$	cm s^{-1}
τ	Shear stress	$\frac{1}{2}\rho C_b U^2$	N m^{-2}
F_{R_H}	Carbon flux by host respiration	$R_{H,\,C}/12/86400$	μmol C cm^{-2} s^{-1}
F_{P_S}	Carbon flux by symbiont photosynthesis	$S * P_S/12/86400$	μmol C cm^{-2} s^{-1}
F_{R_S}	Carbon flux by symbiont respiration	$S * R_S/12/86400$	μmol C cm^{-2} s^{-1}
F_G	Carbon flux by calcification	$G/1000$	μmol C cm^{-2} s^{-1}
Q_{Ca}	Energy driven calcification	$R_{H,\,C}38(\Delta G)/6 - Q_{\mathrm{other}}$	μJ cm^{-2} s^{-1}
E_H	Nernst equation	$2.3R_gT(\Delta\mathrm{pH} + 0.5\Delta\mathrm{Ca}^{2+})$	J mol^{-1}
F_H	Proton flux by Ca-ATPase	$\eta Q_{Ca}/E_H$	μmol cm^{-2} s^{-1}
Ω_a	Aragonite saturation state in the calcifying fluid	$[\mathrm{Ca}^{2+}]_{\mathrm{cal}}[\mathrm{CO_3}^{2-}]_{\mathrm{cal}}/K_a$	–
G	Calcification rate	$\begin{cases} k_p(\Omega_a - 1)^{n_p}, & \text{if } \Omega_a > 1 \text{ (precipitation)} \\ -k_d(1-\Omega_a)^{n_d}, & \text{otherwise (dissolution)} \end{cases}$	nmol C cm^{-2} s^{-1}

produced fixed carbon through photosynthesis by using light and inorganic carbon. The HCO_3^- was considered in the model as the source of inorganic carbon for the symbiont photosynthesis (P_s).

$$P_S = \left(\frac{P_S^{\max}}{P_S^{\max}/f(I)I+1}\right)\left(\frac{[\mathrm{HCO}_3^-]_{\mathrm{tiss}}}{\mathrm{K}_{\mathrm{HCO}_3} + [\mathrm{HCO}_3^-]_{\mathrm{tiss}}}\right), \quad (5.4)$$

In Equation 5.4, $f(I)$ is the function of light. The symbiont photosynthesis energy will be stored in the cell functional pool (C_S^F) as the energy required for the algae to perform vital functions and structural maintenance, and the rest of energy will perform metabolic processes. So the symbiont respiration rate depends on the carbon size in the symbiont functional pool (C_S^F) and the basic energy needed for metabolic processes (V_S^C). In the model, V_S^C is a function of light. The symbiont respiration is defined as:

$$R_{S,C} = V_S^C\delta_S + C_S^F\gamma_S, \quad (5.5)$$

So the host respiration rate depends on the carbon size in the host functional pool (C_H^F) and the basic energy needed for metabolic processes (V_H^C). Here, V_H^C is a function of host feeding and other DOC sources, for example, from mucus release. The host respiration is defined as:

$$R_{H,C} = V_H^C\delta_H + C_H^F\gamma_H, \quad (5.6)$$

For coral calcification, it is an important process in the calcifying fluid and is regulated by the cellular supply of ions, such as Ca^{2+} and CO_3^{2-}. According to the "trans" calcification model (McConnaughey and Falk 1991), corals need energy to transport calcium, bicarbonate, and other ions to calcify their skeletons. Calcium ions are believed to be transported via a combination of calcium channels and an active calcium pump (Ca-ATPase) (Cohen and McConnaughey 2003), which transports 2 Ca^{2+} ions in exchange for 4 H^+ at the expense of 1 ATP across the cell membrane, where ATP is produced during cellular respiration. Therefore, when 1 mol of CH_2O (i.e., 1/6 mol of $C_6H_{12}O_6$) was consumed by respiration, 38(ΔG)/6 kJ of energy could be used for driving Ca-ATPase. The calcification can be mathematically described as:

$$G = \begin{cases} k_p(\Omega_a - 1)^{n_p}, & \text{if } \Omega_a > 1 \text{ (precipitation)} \\ -k_d(1-\Omega_a)^{n_d}, & \text{otherwise (dissolution)} \end{cases}, \quad (5.7)$$

where $\Omega_a = [\mathrm{Ca}^{2+}]_{\mathrm{cal}}[\mathrm{CO_3}^{2-}]_{\mathrm{cal}}/\mathrm{K_a}$ and a constant value of $[\mathrm{Ca}^{2+}] = 10.4$ mM was used. The CO_3^{2-} ions involved in the calcification process are sourced from the host DIC pool.

In this study, the amount of carbon translocated from the symbiont to host follows:

$$T_C = P_S\left(\frac{C_S^R}{C_S^R + C_S^{\mathrm{thres}}}\right)\left(1 - \frac{C_H^R}{C_{H,\max}^R}\right), \quad (5.8)$$

where $C_{H,\max}^R$ is the maximum carbon size in the host reserve pool. We use a threshold value C_S^{thres} to define that only the carbon in the reserve pool is bigger than it, there is energy left for biosynthesis in the functional pool.

Numerical simulations can successfully describe these processes with a cycle of 24 h (Fig. 5.12). Photosynthetic products made by zooxanthellae are stored as organic matter (CH_2O) and are inhibited by [HCO_3^-] and light intensity. The symbiont respiration rate increased with an increase in

Table 5.7 Model parameters of numerical simulation in this study

Symbol	Description	Unit	Value	Reference
α	Factor by which dark N update rate is reduced	–	0.55	Ross and Geider (2009)
H_{coe}	Length of coelenteron	cm	0.3	Gattuso et al. (1996)
H_{tiss}	Thickness of host tissue	cm	0.0003	Gattuso et al. (1996)
H_{cal}	Length of calcifying fluid	cm	0.0005	Gattuso et al. (1996)
E_k	Light related constant	μmol m^{-2} s^{-1}	275	Kühl et al. (1995)
δ_s	Symbiont C specific respiration and maintenance rate	gC gC^{-1} day^{-1}	0.06	Pupier et al. (2019)
γ_s	Symbiont C specific cost of biosynthesis	gC gC^{-1} day^{-1}	0.1	Pupier et al. (2019)
δ_H	Host C specific respiration and maintenance rate	gC gC^{-1} day^{-1}	0.06	Pupier et al. (2019)
γ_H	Host C specific cost of biosynthesis	gC gC^{-1} day^{-1}	0.1	Pupier et al. (2019)
$\mu_S^{\max}$	Maximum symbiont growth rate	day^{-1}	0.6	Falkowski et al. (1984)
$k_{\mathrm{DIC\_sea}}$	Half-saturation constant of host DIC uptake from the sea	μmol C L^{-1}	400	Al-Moghrabi et al. (1995)
k_{DIC}	Half-saturation constant of host DIC transport	μmol C L^{-1}	1.0	Hohn and Merico (2012)
$k_{\mathrm{NH4\_sea}}$	Half-saturation constant of NH4 uptake from the sea	μmol N L^{-1}	1.13	Domotor and D'Elia (1984)
$K_{\mathrm{NH4\_tiss}}$	Half-saturation constant of DIN uptake from the tissue by the symbiont	μmol N L^{-1}	1.4	Muscatine and D'elia (1978)
$K_{\mathrm{HCO_3}}$	Half-saturation constant for $[\mathrm{HCO_3^-}]$ uptake	μmol L^{-1}	408.0	Furla et al. (2000)
K_{DOC}	Half-saturation constant for DOC uptake	$(\mu mol\ cm^{-3})^2$	0.02	Mueller et al. (2014)
V_{DOC}	Constant of DOC uptake from the sea	μmol cm^{-2} day^{-1}	1	Levas et al. (2015)
IR_T	N:C ratio of translocated photosynthesis	gN gC^{-1}	0.0373	Falkowski et al. (1993)
IR_{FS}	N:C ratio in symbiont function pool	gN gC^{-1}	0.176	Gustafsson et al. (2013)
IR_{FH}	N:C ratio in the host functional pool	gN gC^{-1}	0.25	Ross and Geider (2009)
$IR_{H,\ \min}$	Minimum N:C ratio in host	gN gC^{-1}	0.05	Ross and Geider (2009)
m^S	Symbiont mortality rate	day^{-1}	0.04	Assumed
m_C^S	Symbiont C lose rate	day^{-1}	0.04	Assumed
ε_M	C specific mucus release rate	gC gC^{-1} day^{-1}	0.05	Assumed
$d_{\mathrm{CO_2}}$	Diffusion coefficient of CO_2 over eukaryotic cell membranes	cm s^{-1}	0.003	Süeltemeyer and Rinast (1996)
n_p	Reaction order for precipitation	–	1.63	Walter and Morse (1985)
n_d	Reaction order for dissolution	–	2.5	Walter and Morse (1985)
k_p	Precipitation rate law constant	nmol cm^{-2} s^{-1}	1.1 x 10^{-3}	Burton and Walter (1987)
k_d	Dissolution rate law constant	nmol cm^{-2} s^{-1}	2.7×10^{-2}	Burton and Walter (1987)
C_C	Colony coverage	%	70	Assumed
$S_{\max}$	Maximum packing of symbionts	cell cm^{-2}	2.55×10^6	Stimson, J. (1997)
$C_{S,\ \max}^F$	Maximum symbiont C biomass	pg C $cell^{-1}$	454	Muller-Parker et al. (1994)
$V_{\mathrm{DIC\_tiss}}$	Seawater DIC uptake rate by host	gC gC^{-1} day^{-1}	6	Muller et al. (2009)
$V_{\mathrm{NH4\_tiss}}$	Seawater NH_4 uptake rate by host	gN gC^{-1} day^{-1}	0.1	Hoegh-Guldberg (1999)
K_P	Conductivity coefficient for the paracellular diffusion	cm s^{-1}	3×10^{-4}	Hohn and Merico (2015)
$\Delta \mathrm{Ca}_{\mathrm{cons}}^{2+}$	Constant	–	0.02	Al-Horani et al. (2003)
ΔG	Free energy by ATP hydrolysis	kJ mol^{-1}	30.5	–
Q_{other}	Energy flux used for other metabolisms	μJ cm^{-2} s^{-1}	5	Nakamura et al. (2013)
$\mathrm{R_g}$	Gas constant	J mol^{-1} K^{-1}	8.314	–
η	Energy conversation efficiency	–	0.3	Assumed
μ_{POCmax}	Maximum POC to DOC transfer rate	day^{-1}	0.1	Hasumi and Nagata (2014)
f_{DOC}	Phytoplankton exudation to DOC rate	day^{-1}	0.066	Hasumi and Nagata (2014)
k_{ae}	Zooplankton carbon assimilation efficiency	–	0.75	Hasumi and Nagata (2014)
k_{Zexu}	Zooplankton exudation to labile DOC efficiency	–	0.75	Hasumi and Nagata (2014)
μ_{DOCmax}	Maximum DOC uptake by bacteria	day^{-1}	0.05	Hasumi and Nagata (2014)
C_b	Bottom drag coefficient	–	0.01	Reidenbach et al. (2006)
C_S^{thres}	Half-saturation constant for symbiont respiration and maintenances	μg C $cell^{-1}$	1×10^{-6}	Assumed

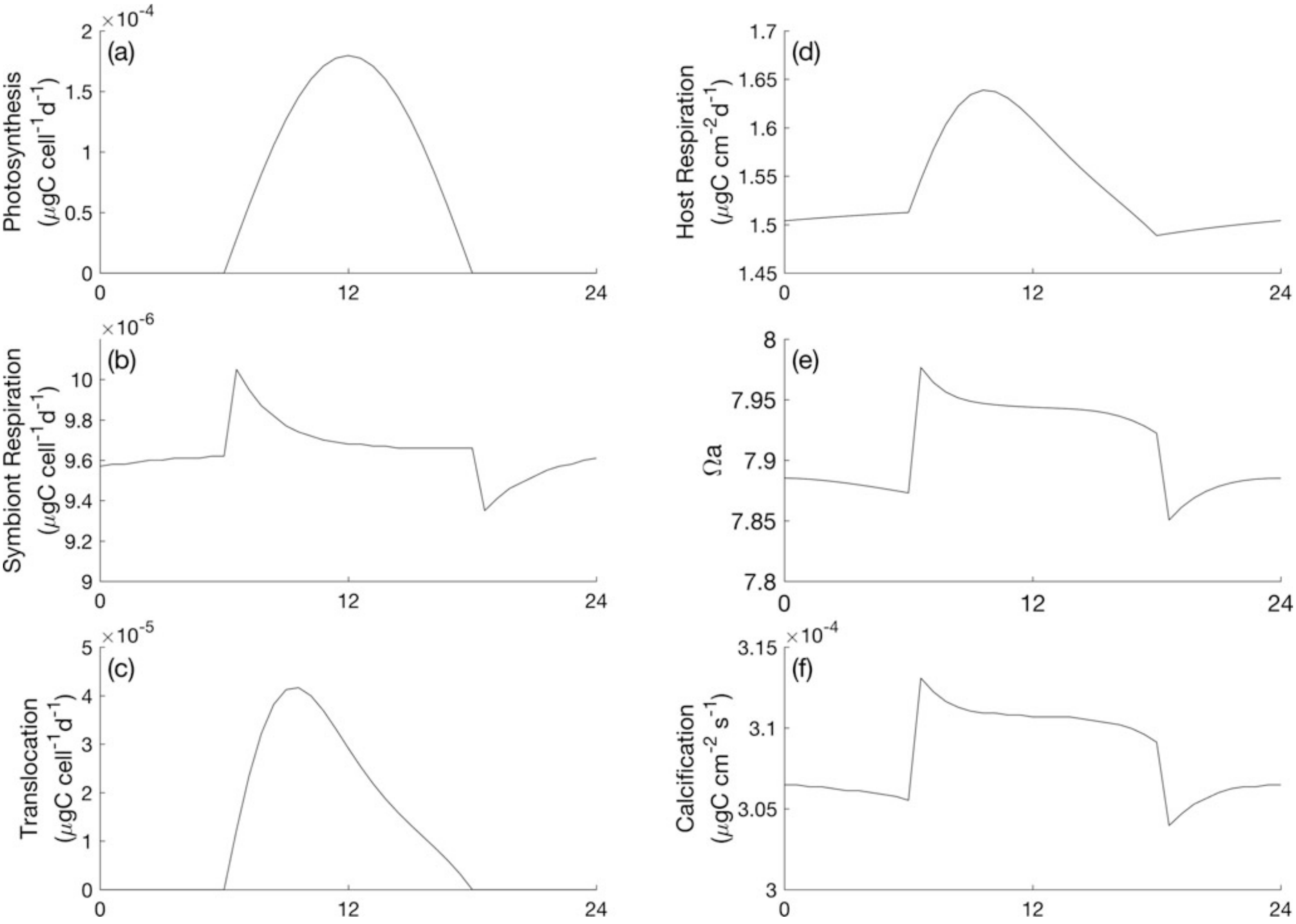


Fig. 5.12 Time series of the simulated coral metabolic processes in the 24-h cycle. Details of the model equations are described in Table 5.6. In the figure, we simulated the rate of photosynthesis (**a**), respiration of symbiont (**b**), translocation of organic carbon from symbiont to coral host (**c**), respiration of coral host (**d**), saturation index of aragonite (**e**), and calcification rate (**f**), respectively

carbon in the symbiont functional pool when photosynthesis enhanced in light. So the respiration rate under light condition is much greater than that under dark condition (Fig. 5.12b). The translocated carbon also increases with carbon accumulation during daytime in the symbiont (Fig. 5.12c). The translocated carbon from the symbiont is used for host respiration energy needs; thus, the host respiration rate increases with increased carbon translocation. The caudated calcification rate enhanced with increasing aragonite saturation (Fig. 5.12e, f).

For modeling purposes, the coral polyp can be simplified into four parts, that is ambient seawater, coral tissue, coelenteron, and calcifying fluid. Fluxes across these boundary layers connected the four parts with different chemical components, driving the dynamics of the polyp model (Table 5.6). For other carbon pathways, CO_2 was assumed to diffuse freely between the coral tissue and coelenteron through the oral endoderm and between the host tissue and calcifying fluid through the aboral endoderm ($F_{CO_2\_sea}$, $F_{CO_2\_coe}$, $F_{CO_2\_cal}$). The CO_2 diffusion works in both directions: if the flux diffuses into the calcifying fluid, DIC increases, and vice versa. The paracellular pathway driven by molecular diffusion through the lateral cell junctions also takes place ($F_{TA\_p\_cal}$, $F_{DIC\_p\_cal}$, $F_{TA\_p\_coe}$, $F_{DIC\_p\_coe}$). Free ions diffuse through the intercellular space and pass between the tight junctions of the endoderm, seawater and coelenteron, and coelenteron and calcifying fluid. As the polyp mouth connects the coelenteron with the ambient seawater, we considered the fluxes of advective exchange that influence state variables between the seawater and coelenteron (F_{H_v}, F_{TA_v}, F_{DIC_v}). The change of DIC and TA in each of the polyp components can be calculated as the state variables derived using differential equations, since their change with time is associated with fluxes.

5.7.4 Future Perspectives

The shallow coastal and shelf seas in the tropical and subtropical climate zone, where most of coral reefs habitat, are experiencing various physical, chemical, and biological changes. The symbiotic algae photosynthetically fix carbon compound; one proportion of the fixed energy is used for algae growth, while other parts are passed to the coral animals, respired, and then release back as dissolved organic carbon. This cycle can be finished in a cycle of 24-h period. There is also diffusion of dissolved inorganic carbon/nitrogen in the coral polyps with surrounding water; the diffusion rate is highly regulated by flow conditions that are related with bottom shear stress, wind-induced Ekman transport, waves, etc. These changes range in the scale from days to weeks, and there are seasonal and inter-annual variations. One part of net productions of this symbiotic system is calcium carbonate, with geologic records dating back to millions of years ago. The coral reef systems with biological and chemical temporal scales span over seconds to 100 years; spatial scale ranges from millimeters to tens of kilometers, influenced by the complexity of biology, chemistry, and physics of the ocean, of which the understanding needs to incorporate highly interdisciplinary sciences. Fully describing the coral ecosystem processes that cover a large range and considerable number of temporal scales requires a large number of biological and chemical equations and parameters that are not constant and interdependent among themselves. We believe that ongoing observations and experimental technology advances would override this limit/barrier. In very recent times, coral system model coupling into coastal ecosystem model can be an advantageous technique to study the mechanisms of bleaching and help predict the status of coral reefs in the future under climate change scenarios.

Oceanic physical data and models have advanced in terms of both quality and quantity. Currents and turbulence measurements from bottom can be made in conjunction with optical and acoustical measurements to get a better understanding for the underneath. The development of remote sensing method has been expanded to increase the numbers and types of biological data, including different types of benthic coverages (Paringit and Nadaoka 2011). Environmental factors (e.g., temperature, ultraviolet, and photosynthetically active radiation) have been investigated from satellite data to predict coral bleaching (Barnes et al. 2015). With these benefits, coastal ecosystem models have been developed to couple with physical, sedimentary, chemical, and biogeochemical processes with significant improvements in understanding biogeochemical processes, e.g., carbon chemistry (Hofmann et al. 2011), multiple seagrass, and macroalgae species (Baird et al. 2016). These 3-D coastal ecosystem models could provide the coral reef module with dynamically changed physical and chemical conditions and feed-backs to biogeochemical cycles in a changing tropical ocean, such as the currents field, the thermal stress, and nutrient competition. With regard to the coral bleaching, one of the important goals is to understand and ultimately predict how the health of coral system responds to natural and anthropogenic changes. This requires a combination of advanced observational strategy and innovation of numerical techniques in simulation for coral reefs.

5.8 Summary and Way Forward

Over the last century, the decline of coral reefs in the Western Pacific Region is considered to be a consequence of combined stressors from natural and anthropogenic processes. Biogeochemistry serves as a medium linking those multi-stressors and the functioning of coral reefs. Indeed, external forcings can drive the ecosystem through a shift and/or switch of biogeochemical pathways (e.g., element influx and species ratio). This affects the mass flow and energy partitioning between different function groups, formation of different organic molecules, and interaction between the main food chain and microbial loop, as well as the efficiency of material transfer from low to high trophic levels. The consequences of changing biogeochemistry on the coral reefs can be various. This includes, for example, the ratio between autotrophic and heterotrophic food availability for the symbiosis of corals and zooxanthellae, rate of calcification at coral species level, biodiversity for the whole reef systems, as well as the connectivity between different reef systems (e.g., larval dispersal). The decline of corals and degradation of reef systems have been observed almost everywhere across different areas of the Western Pacific Region at low latitudes, which is similar to other tropical and subtropical waters of the world ocean.

The offshore coral reefs are affected by oligotrophic waters from open and oceanic waters, with primary production limited by nutrients and/or trace elements. In the nearshore coast, fringing reefs can be in the eutrophic environment because of an increase in land-sourced influxes. While external nutrients can be a driving force to affect coral reefs (e.g., photosynthesis of symbiotic zooxanthellae), the impacts are often mixed with other stressors and sometimes are hard to distinguish. For example, influence of nutrients from terrestrial sources is combined with the change in salinity and turbidity, if the coral reefs are under the influence of riverine plumes. In offshore areas, high nutrients from upwelling waters often occur together with relatively low temperature and low dissolved oxygen. Changes in the calcification rate of coral reefs do not illustrate a simple relationship of water alkalinity, Ca^{2+}, and pH, shown in the simplified chemical equations. Coral calcification rates are affected by the dark and light reactions of photosynthesis and hence have diurnal variability, as well as by the changing ratio of autotrophic to heterotrophic energy pathways and hence the trophic situation.

In this study, we used a model simulation to understand the response of coral and zooxanthellae symbiosis toward the change in external nutrient sources and hydrographic properties. The model considers the light-driven photosynthesis, respiration, and calcification in the coral–zooxanthellae system. The model has also been used to undertake scenario simulations in order to understand the influence of temperature and nutrient conditions on carbon transfer between zooxanthellae and coral host, as well as the coral feeding rate, using parameterization techniques of simplified relationship between reactants and products. In numerical simulation, most of the results are in the form of rate calculation. For example, the carbon transfer between zooxanthellae and coral host is simplified by temperature-dependent growth efficiency rate, the ion exchanges among different components of coral are parameterized by different diffusion and advection rates. By coupling this coral–zooxanthellae symbiotic system module into a 3-D hydro-biogeochemical model, there is a potential of shedding insight on coral ecosystem response to environmental changes, such as the ocean warming, acidification, and coastal eutrophication.

Based on the synthesis of this study, it appears that the following aspects need to be considered in the multidisciplinary and biogeochemical studies of coral reefs in the near future:

- Co-limitations of nutrients and trace elements in coral reefs. While it can be expected that the primary production of fringing reefs can be affected by phosphorus limitation and offshore reefs by nitrogen limitation, there is a lack of trace element data in coral reef's environment, where supply and availability of certain trace elements can be of critical importance in affecting autotrophic processes (e.g., dissolved iron on nitrogen fixation) of reef systems.
- Effect of water exchange and flushing processes on the relative importance of new vs recycled nutrients. Data of field measurement and mesocosm experiments indicate that the zooxanthellae and coral symbiosis respond to the nutrient amendments in a complex way, which suggests that hydrodynamic processes (e.g., water residence time) play an important role in regulating nutrient uptake rates. In the system of rapid water exchange, there is a possibility that nutrients are flushed away before being taken up by the photosynthetic organisms.
- Biogeochemical links to the nature of coral reefs. External sources and status of metabolism for organisms can induce an effect of "bottom–up" to the function of coral reefs. The variability of biogeochemical cycles responds to the natural and anthropogenic stressors through changes in nutrient concentration and species ratio, as well as the flux at different compartments (e.g., function groups) and between different trophic levels of reef systems. The outreach can be the shift between main food chain and microbial loops with consequences for ecosystem sustainability, diversity, and food production (e.g., fishery).
- Coral calcification is not a simple function of water pH, $p\mathrm{CO}_2$, and temperature, but complicated results of metabolism of coral systems. It is known that calcification rates of corals can be affected by the energy partitioning depending upon the relations between the photosynthesis of symbiotic species and heterotrophic processes of the host. Apparently, corals with the ability to adapt to both autotrophic and heterotrophic food availabilities have an advantage in facing the predicted ocean acidification at the century scale and avoid the damages of episodic events such as bleaching at an inter-annual scale.

On this planet, corals have been living in the ocean for more than ca. 500 million years and survived the changes in climate in their history. The land-based human activities have induced the deterioration of coral reefs over the last several decades, including emission of greenhouse gases, coastal engineering, and pollutant drainages. Nevertheless, the effort of reducing anthropogenic perturbations in the marine environment will help maintain the coral reefs in a rather safe situation and alive for the future. Recent studies provide evidences of biodiversity richness for reef-building corals at species abundance in the Western Pacific Ocean (Dietzel et al. 2021; Pennisi 2021). This calls for reconsideration of evaluation for the coral extinction risk along the diversity gradient in basin-wide scales. However, the maintenance of biodiversity richness requires sustainable supply of energy and materials (e.g., nutrients and trace elements), which affects the life history and population size through biogeochemical cycles. Therefore, the population size and extinction risk of reef-building corals need to be coupled with system biogeochemistry, which allow the coral reefs to be resilient against external forcings at various biogeographic scales in the global ocean.

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Environmental and Climate Proxies Embedded in Coral Skeletons

6

Gi Hoon Hong, Suk Hyun Kim, and Mark Baskaran

Abstract

Scleractinian (hard layered) corals live for several centuries or longer in the tropical surface waters that comprise about half of the total surface area of the world's oceans. Coral reefs in the tropical surface waters are the largest biologically produced natural features over the Earth's surface. About 20% of modern carbonate accumulation takes place in coral reefs. The relatively thick annual growth bands of coral skeleton (usually around 10 mm a year) have provided a wealth of information on the climate and environmental changes that occurred in the past. These environmental archives are becoming essential to forecast the future climate and environmental changes in their local habitats in the tropical regions including the Indo-Pacific Warm Pool region that plays a significant role in the world ocean and atmospheric circulation, hence in the entire globe. Deep-sea scleractinian corals often living more than a millennium have been found in most oceans, and these slow-growing corals (a few micron meters a year) have also been found to faithfully record climate and environmental changes that occurred in the ocean. This chapter introduces the status of the scientific investigation on a coral skeleton climate and environmental proxies to the audience who are interested in coral reef with respect to climate and environmental change. It will briefly cover the biomineralization process, methods of sampling coral cores and subsequent cleaning for further chemical analysis, skeleton age determinations, and the utilities of selected chemical elements and selected isotope proxies (Li, B, C, N, O, F, Na, Ca, V, Cr, Mn, Fe, Ni, Cu, Zn, Y, Mo, Cd, I, Ba, REEs, Nd, Pb, U, Pu). This chapter is largely dealt with surface-dwelling tropical corals, but it also includes some proxy studies on deep corals.

Keywords

Coral skeleton · Chemical element and isotope compositions · Climate and environmental proxies/tracers · Dating

6.1 Introduction

6.1.1 Anatomy of Coral Skeleton

The skeletons of stony corals are made of orthorhombic aragonitic calcium carbonate crystals embedded with various chemical elements and organic matter in trace quantities. They are secreted by the lower portion of the polyp producing the calyx (cup). The walls surrounding the cup are called theca. Within the theca, septa (radiating plates within corallite) and dissepiment (horizontal strengthening structure) exist (AIMS 2018). Individual skeletal structures calcify at different times. The seasonal δ^{18}O profile from the endothecal skeleton was reported to be significantly lower and irregular than those from the exothecal skeleton (cited in Watanabe et al. 2002). Coral skeletal growth usually is described with two variables, linear extension and calcification. The annual extension rates of corals can be inferred from the annual density-band pattern and cyclicity of paleoclimatic tracers. Thickening of septal and columellar structures results in high-density bands (Helmle et al. 2000). Coral extension rates reflect several environmental variables such as temperature, nutrient or food availability, water transparency, and sediment input. The calcification rate is the product of the linear extension rate and the average density at which the skeleton is deposited in making that extension. Interestingly, the annual calcification rate was

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more strongly correlated with sea surface temperature (SST) variations compared to the annual extension rate. The density variations may be measured by gamma densitometry (Felis and Pätzold 2004).

6.1.2 Basic Chemical Reactions Leading to Aragonite Formation in Coral

Basic chemical reactions on the precipitation of $CaCO_3$ are briefly given here from Kleypas and Langdon (2006). Calcium carbonate saturation state (*Ω*) is a measure of the ion activity product (IAP) of Ca^{2+} and $CO_3{}^{2-}$ relative to the apparent solubility product (K_{sp}') for a particular calcium carbonate mineral, aragonite (Eq. 6.1).

$$\Omega = \left[Ca^{2+}\right]\left[CO_3{}^{2-}\right]/K_{sp}{}' = IAP/K_{sp}{}' \qquad (6.1)$$

Gaseous $CO_2(g)$ dissolves in seawater to form aqueous CO_2 (aq) (Eqs. 6.2–6.4).

$$CO_2(aq) + H_2O \leftrightarrow H_2CO_3(\text{carbonic acid}) \qquad (6.2)$$

$$H_2CO_3 \leftrightarrow H^+ + HCO_3{}^-(\text{bicarbonate ion}) \qquad (6.3)$$

$$HCO_3{}^- \leftrightarrow H^+ + CO_3{}^{2-}(\text{carbonate ion}) \qquad (6.4)$$

Carbonate ion does not react spontaneously with calcium ion to form calcium carbonate mineral as one might intuitively imagine, $Ca^{2+} + CO_3{}^{2-} \leftrightarrow CaCO_3$, because carbonic acid is a weak acid, and all of the various carbon species exist simultaneously (note that all of the above reactions are reversible). The relative proportion of each species, particularly the proportion of $HCO_3{}^-$ to $CO_3{}^{2-}$, is governed by the pH and the need to maintain the ionic charge balance in seawater. This is related to the concept of total alkalinity (TA). TA equals the charge difference between cations and anions in seawater. This difference is compensated by the changing proportion of monovalent bicarbonate and divalent carbonate ions. If positively charged ions, such as Ca^{2+}, are removed from seawater, then TA decreases through the conversion of some of the carbonate to bicarbonate. Thus, the formation of calcium carbonate where the degree of saturation of aragonite (*Ω*) is much higher than 1 produces CO_2. The apparent solubility product, K'_{sp}, with solid $CaCO_3$ depends on mineralogy (calcite < aragonite < Mg-calcite) as well as temperature (T) and pressure (P). When $\Omega > 1$, solution is supersaturated and when $\Omega < 1$, solution is undersaturated. When photosynthesis occurs (Eq. 6.5)

$$CO_2 + H_2O = \text{“}CH_2O\text{”} + O_2 \qquad (6.5)$$

Then $\Delta\Sigma CO2 = -1$ and $\Delta Alk = 0$. So $\Delta[CO_3{}^{2-}] = \Delta Alk - \Delta\Sigma CO2 = 0 - (-1) = +1$, and $[CO_3{}^{2-}]$ increases, while *Ω* increases (that leads to precipitation of calcium carbonate, calcification). When respiration occurs, organic matter decomposes into carbon dioxide and water (Eq. 6.6),

$$(CH_2O) + O_2 \rightarrow CO_2 + H_2O \qquad (6.6)$$

Then $\Delta\Sigma CO2 = +1$ and $\Delta Alk = 0$. So $\Delta[CO_3{}^{2-}] = \Delta Alk - \Delta\Sigma CO2 = 0 - 1 = -1$, and $[CO_3{}^{2-}]$ decreases, while *Ω* decreases (that leads to dissolution). The overall reaction involved in the precipitation of carbonate is described as Eq. (6.7).

$$Ca^{2+} + 2HCO_3{}^- = CaCO_3 + CO_2 + H_2O \qquad (6.7)$$

The formation of $CaCO_3$ precipitate absorbs heat (endothermic); therefore, solubility decreases with rising temperature (Eq. 6.8, Mucci 1983).

$$K'_{sp(\text{aragonite})} = -171.945 - 0.077993 \times T + 2903.293/T + 71.595 \times \log_{10}(T) \quad (T \text{ in } ^\circ\text{Kelvin}). \qquad (6.8)$$

6.1.3 Solubility of $CaCO_3$ and Water Temperature

The solubility of $CaCO_3$ increases with decreasing temperature and with increasing pressure. Most surface coral reefs occur in tropical latitudes between 22 °S and 22 °N where water temperature varies seasonally within narrow range (4–5 °C) with average maximum temperatures of ~30 °C. However, coral reefs also flourish in higher temperature around ~34–36 °C such as the Persian/Arabian Gulf (Schoepf et al. 2015) and lower temperatures of ~21.7 °C (Guan et al. 2015), although they appear to be withstood as low as 12 °C for a short period of <12 h (Hoegh-Guldberg et al. 2005).

6.1.4 Biomineralization Process for Aragonite Precipitation in Coral

Coral skeletons exhibit annual growth and elemental and isotopic variations within their skeletons. These annual growth bands of coral skeleton (aragonite) and incorporation of various chemical elements and materials into the coral skeletons are the two pillars of archives for the paleoenvironment at the time of coral growth. Precipitation of aragonite crystals is partly governed by thermodynamic principles (e.g., temperature, activity concentration of participating ions); however, aragonite crystals are made by animal corals; therefore, precipitation of skeleton is also governed by biological process of coral themselves. For example, early mineralization zones (centers of calcification or centers of rapid accretion) have distinct compositions compared with the surrounding fibrous skeleton, as observed for $\delta^{11}B$, $\delta^{13}C$, $\delta^{18}O$, B/Ca, Mg/Ca, Sr/Ca, Ba/Ca, U/Ca, and organically bound sulfur (Rollion-Bard et al. 2009). Therefore, it is necessary to assess potential intra-skeletal variations in chemical proxies of concern prior to taking subsamples for analysis. The incorporation mechanism of metals and substances other than calcium and carbonate into intra- or inter-aragonite crystals of coral skeletons have not been well understood despite recent significant discoveries. This incomplete knowledge results in considerable uncertainties in delineating proxy concentrations in the skeleton into environmental variables. However, for the sake of this chapter, it may be useful to summarize the current understanding of the biomineralization process occurring in reef-building corals at the beginning of this chapter.

The precipitation of aragonite at the calcifying fluid lined by the ectodermal calicoblastic cells appears to be initiated and controlled by and organized on an extracellular organic matrix containing a suite of proteins (acid-rich proteins, collagens, galaxins, and carbonic anhydrase-related proteins), lipids, and polysaccharides. Four major components of inorganic carbon, calcium ions, and proteins are involved in calcification processes. Proteins catalyze the nucleation reaction and organize crystals to form macroscopic structures. Proteins in the skeletal organic matrix constitute an extracellular matrix that adheres to newly formed skeleton and attach calicoblastic cells to this skeleton-blanketing matrix (Fig. 6.1). Calcium and carbonate sources are different. Calcium (or other metals) is mainly transported from the ambient seawater into the calcifying fluid via a calcium channel paracellularly with minimal contribution from calcium-ATPase which also removes protons from the site of calcification. Dissolved inorganic carbon comes mainly from metabolic CO_2 from the coral itself via a bicarbonate transporter (e.g., Goldberg 2001; Clode and Marshall 2003; Cuif et al. 2003; Bhattacharya et al. 2016; Mass et al. 2012, 2014; Drake et al. 2013; Gothmann et al. 2016).

According to Mass et al. (2017a, b), aragonite formation in coral skeleton takes place in five steps:

(i) Seawater (rich in Ca^{2+}, Mg^{2+}, Sr^{2+}, bicarbonate, carbonate ions) is captured by endocytosis, that is, a process in which the calicoblastic cell membrane invaginates, such that the external seawater is incorporated into an intracellular vesicle (~400 nm in diameter).

(ii) Amorphous calcium carbonate (ACC) particles are gradually formed in the vesicle. The vesicle may be the site where the calcifying fluid (CF) and ACC are produced through proteins in the skeletal organic matrix.

(iii) The carbonate ions are injected into the vesicle at a time by an active multicomponent biological pathway. The vesicle, initially containing only seawater, gradually and actively is injected with carbonate ions. After enough Ca^{2+} ions are paired with carbonate ions, an amorphous hydrated form of calcium carbonate aggregates.

(iv) The vesicle containing amorphous precursors is transported toward the cell membrane near the biomineral, and its ACC content is ejected by exocytosis. Thus, aragonite crystal growth is extracellularly made by being attached to the ejected ACC.

(v) After a day or so, most or all the ACC-H_2O transformed into ACC and then into crystalline calcium carbonate (CCC). Nanoparticles are initially amorphous, then they attach and fill space, and hours later, they crystallize. The attachment growth is about 100 times faster than inorganic ion precipitation growth.

6.1.5 Organic Matter in Coral Skeleton

Organic matter in the intracrystalline coral skeletons is well preserved over century timescales. Its concentration is less than 0.5 total organic carbon wt.% (Table 6.1). It is derived from organic matrix synthesized by coral to control aragonite precipitation in the subcalicoblastic space where it occludes new skeleton while being attached to the calicoblastic cells (Ramos-Silva et al. 2014). Organic matter is also originated from endolithic algae, bacteria, and fungi as well as material adsorbed from ambient seawater. This skeletal organic matrix (SOM) SOM is largely made of soluble proteins rich in amino acids and insoluble proteins rich in glycine. Lipids, including *n*-alkanes, fatty acids, and cholest-5-en-3β-ol (cholesterol), are also present in coral skeleton about 0.2–2.2 % (Samori et al. 2017). Pigmented bands are also commonly found in coral skeletons. They originate from endolithic algae, usually *Ostreobium quekettii*, that bore through the skeleton and grow just beneath the coral tissue. The organic matter from these algae, including extremely labile compounds such as chlorophyll-a, can still be present in skeletal material of hundreds of years old (Ingalls et al. 2003).

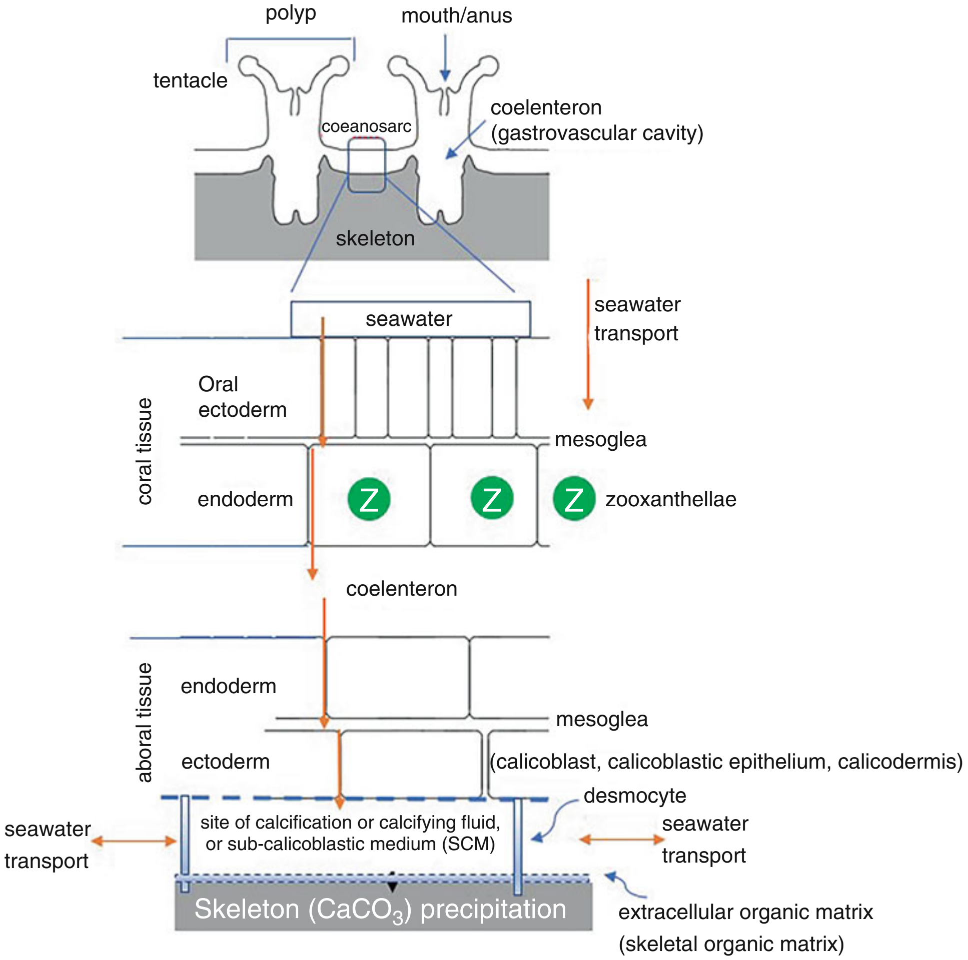

Fig. 6.1 Sketch of key coral anatomy that plays a role in calcification (modified from Gothmann et al. 2016 and Comeau et al. 2017b). Coenosarc is a thin horizontal sheet of tissue that connects polyps laterally. Polyps and coenosarc constitute a thin layer of living tissue over the block of limestone they have secreted. Mesoglea is a noncellular gelatinous matrix separating an ectoderm and an endoderm. In symbiotic corals, the endoderm hosts unicellular algae of the genus *Symbiodinium*, zooxanthellae. Calicoblast is the primary cell of the calicoblast epithelium (calicodermis). Coral tissues are mechanically anchored to the skeleton by desmocytes (Mass et al. 2012). Organic fibrils of a diameter of about 26 nm are located between calicoblastic ectodermal cells and the underlying $CaCO_3$ skeleton (Clode and Marshall 2003). The calicoblast secretes the organic matrix leading to the calcification and formation of the calcareous skeleton of scleractinian corals (Falini et al. 2015). Most corals in the past 240 million years or longer have produced aragonite skeletons except one species formed calcite one in the Cretaceous (ca. 70 to 65 Ma). A modern deep-sea coral, *Paraconotrochus antarcticus*, living in the Southern Ocean, was recently found to form a two-component carbonate skeleton, with an inner layer made of high-Mg calcite and an outer one composed of aragonite (Stolarki et al. 2021).

Table 6.1 Organic matter in coral skeletons (data from Ingalls et al. 2003)

	Montastraea annularis	*Porites lutea*
Total organic carbon (TOC)	39–85 μmol C/g coral 0.04–0.11 wt %	26–60 μmol C/g coral (0.02–0.04 wt %)
Intracrystalline OC/TOC	~0.35	~44
Total hydrolysable amino acid (THAA)	10–30 μmol THAA/g coral	13–25 μmol THAA/g coral
Intracrystalline THAA/total THAA	~0.40	~0.33
Total lipids (total fatty acids)	1.8 μmol C/g coral	0.36 μmol C/g coral
Intracrystalline lipid/total lipids	~0.30	~0.47
Chl-*a* or Chl-*b*	0~0.035 mmol/g coral	

6.2 Coral Core Sampling and Handling for Further Chemical and Isotopic Measurements

6.2.1 Retrieval of Coral Core and Slab Cutting

The coral core is usually taken using a handheld submersible underwater hydraulic or pneumatic drill fitted with a 7-cm-diameter, 60-cm-long diamond-bit core barrel along the maximum axis of upward growth. Colony selection should be made ideally on the following conditions: (i) it should be alive, (ii) there should be no visible signs of partial or mass mortality at the top of the colony, and (iii) there should be no apparent cut or bioerosion at the base of the colony. Upon retrieving coral specimen, they need to be closely examined and carved out any evidence of endolithic activity possible reprecipitation of $CaCO_3$ by boring worms of sponges on the surface. Each core segment is longitudinally usually slabbed a 4–7-mm-thick slice using a rock saw equipped with a diamond-tipped blade. Due to the intra-skeletal variabilities of chemical elements to calcium ratio across the various distinct skeletal micro-structures (e.g., Robinson et al. 2014), sampling and time assignment can have a large impact on coral proxy calibration and reconstruction of the past climate and environmental changes. DeLong et al. (2018) have suggested that slabs taken from a coral core must transect the extending corallite walls so the user can extract samples along a continuous growth-time skeletal feature. Computer-aided micro-mills (e.g., computer-controlled micro-milling used in medical industry) are preferred for sampling to control the sample location and penetration depth into the coral skeleton, which is needed to avoid nontarget skeletal elements. This method allows for sampling increments smaller than the diameter of the bit since the movement is lateral, whereas the up-down drilling sets increment size to drill bit diameter. For complex coral skeletons, laser ablation (LA) can be used to extract weekly samples from coral skeletons but require the coral to be cut into 1–2 cm pieces; however, advances in LA large chamber technology will help resolve this issue. They also strongly recommend checking the reproducibility of geochemical analysis of the same coral core for ensuring sampling quality control.

6.2.2 Slab Cleaning

Slices are rinsed usually with freshwater and ultrasonicated three times in ultrapure 17 Ω water for 10-min periods, removing all surficial particles, also cleaned with compressed filtered air between ultrasonicating to remove all remaining loose particles, and dried at 40 °C ~80 °C in a laboratory oven or for 24 h in a laminar flow hood. For the entire slice, residual organic matter associated with the coral tissue layer and/or endolithic algae should be removed using oxidative cleaning for 24 h with sodium hypochlorite (NaOCl, 10–13% reactive chloride). The presence of organic matter may be checked by scanning it for spectral luminescence (Grove et al. 2010).

6.2.3 Micro-Sampling

Advances in micro-analytical sampling techniques, including but not limited to micro-milling, ion microprobes, laser ablation, and highly focused radiation measurements, have made micron-meter or submicron-meter sampling or observation become possible. For example, samples of 150–350 μm thick were precisely shaved along a continuous strip of 2 mm by 2 mm in cross-sectional area (Gagan et al. 1998). Secondary ion mass spectrometry (SIMS) and laser ablation ICP-MS are also able to provide major and trace element abundances as well as isotope ratios at spatial scales as small as 1 μm (NanoSIMS). This micro-sampling procedure provided a minimum of 50 samples per annual growth increment (e.g., Uhlmann et al. 2014). Micron-meter scale sampling has revealed intra-skeleton variations that have resulted in deepening our understanding on non-calcium metal incorporation mechanisms in coral skeletons (Gabitov et al. 2013). This micro-sampling allows us to see the intra-skeletal variability of trace elements and stable isotopes in theca walls and dissepiments, such as $\delta^{11}B$, $\delta^{13}C$, $\delta^{18}O$, B/Ca, Mg/Ca, Sr/Ca, Ba/Ca, U/Ca, and organically bound sulfur (Rollion-Bard et al. 2009).

6.2.4 Subsample Cleaning for Chemical and Isotope Analysis

Cleaning subsamples needs to be optimized for the specific target chemicals and isotopes embedded in coral skeleton. For example, to determine radiocarbon, trace elements, and uranium decay series radionuclide bounded to the aragonite lattice, samples are usually rinsed with deionized water and scrubbed with a brush to remove sediment from coral skeleton between septa (e.g., Adkins et al. 2002a). Samples are immersed sequentially in an oxidant (alkaline solution of 50/50 mixture of 30% H_2O_2 and 1N NaOH), reductant (ammonia hydrazine and citric acid), and strong acid (HNO_3), with ultrasonication for 15 min. These oxidizing and reducing steps are repeated several times. Occasionally, samples are again scrubbed with a brush to remove black crusts in small sheets. Oxidizing steps are repeated until there is little black crust or polyp organic matter left on the sample, after oxidizing treatment subsamples are rinsed thoroughly with clean distilled water (e.g., Lee et al. 2014; Adkins et al. 2002a). To isolate intracrystalline organic matter, bleaching agent (e.g., 5% NaClO) is used for a fine (<40 μm) coral skeleton powder (Ingalls et al. 2003).

6.3 Intra- and Inter-skeletal and Colony Variability in the Chemical and Isotope Compositions

The architecture of coral skeleton is extraordinarily complex to include various skeleton structural constituents of calyx, theca wall, dissepiment, septum, band, center of calcification, etc., and different parts appear not to develop at the same time and vary with differing extension rates. Thus, sampling resolution could be significantly biased to certain structural formations as discussed in Sect. 6.2.2. This inhomogeneity in different structural constituents of coral skeleton is another contributor to the uncertainties in the interpretation of climate and environment based on the coral proxy observations. Inter-skeletal and inter-colony variability were also observed across different coral species and different localities.

6.3.1 Intra-skeletal Variations

Coral skeletal fasciculi are composed of bundles of aragonite crystals which are constructed from the repeated superimposition of growth layers of a few micron meters thick. Therefore, intra-skeletal variations are expected. For example, centers of calcification (CoCs ~ 10 μm) are overgrown by a composite fibrous aragonite crystals and organic macro-molecules organized into growth layers (Meibom et al. 2004). Sulfur concentrations in the CoCs and fibers for zooxanthellate corals of *Monstatrea curta* and *Favia stelligera* and azooxanthellate coral (deep-sea coral) *Lophelia pertusa* species were 3570 and 1700 ppm, 2510 and 1700 ppm, and 1720 and 1260 ppm, respectively (Cuif et al. 2003). Mg are also shown to be concentrated as much as ten times more ($Mg > 8 \times 10^3$ ppm) at the boundaries between these growth layers and in the CoCs than other parts ($Mg < 2 \times 10^3$ ppm) of skeleton of *Pavona clavus* based on a Nano Secondary Ion Mass Spectrometry (SIMS) ion microprobe (Meibom et al. 2004) and X-ray Absorption Fine Structure (XAFS) observations (Finch and Allison 2008). δ^{18}O and δ^{13}C from the theca wall and a mixture of endothecal and exothecal materials were found to be different as much as 1‰ and 3‰, respectively, in the skeleton of *Montastraea faveolata* (Watanabe et al. 2002). Many similar intra-skeletal variations were also observed for metals. For example, the intra-skeleton variation in metal to Ca ratios in deep-sea coral *Lophelia pertusa* Sr/Ca varied from 9.98 to 10.25 mmol/mol, Li/Ca varied from 9.023 to 15.222 μmol/mol, Mg/Ca varied from 2.938 mmol/mol, and Mg/Li varied from 0.326 to 0.265 mmol/μmol from theca wall to the CoC. The Sr/Ca values showed no systematic variation within the microstructure, but showed a variability of 0.53 mmol/mol, which is significant when compared to its annual variation. But Li/Ca and Mg/Ca ratios vary systematically across skeleton between theca and COC (Raddatz et al. 2013). The intra-skeleton U/Ca ratios of coral, *Lophelia pertusa* (azooxanthellate deep-sea coral), vary from 1.14 at the center of calcification (COC) and 2.07 μmol/mol, and this would result in the predicted pH values between 7.8 (theca wall) and 8.3 (COC) (Raddatz et al. 2014). Raddatz et al. (2014) took samples from thecal wall only for their subsequent analysis for a climate reconstruction.

6.3.2 Inter-colony and Gender Variability

Inter-colony variation of chemical proxies incorporated in coral skeletons is also widely reported. For example, the oxygen isotope ratios displayed a large inter-colony variability (~1‰) due to the kinetic isotopic effects that related to variations in the skeletal growth rate rather than species-specific variability or genetic differences within species. δ^{18}O was also found to decrease with increasing photosynthesis of a coral's symbiotic algae, and the δ^{18}O-temperature relationship differs significantly among conspecific corals even at the same site. δ^{18}O was found to vary with a growth rate of a coral skeleton under identical conditions in a single coral (Saenger et al. 2012). The inverse correlation of carbon isotope ratios with linear growth rates was also attributed to a kinetic isotope control at low growth rates based on the micro-profiling technique applied along the major growth axis on the cultured *Porites* corals (Suzuki et al. 2005). Inter-colony variation was also estimated to be about 10–30% in P/Ca ratios of the *Porites gigantean* and *Porites lobata* in the Gulf of Panama (LaVigne et al. 2010). The gender of coral shows a variation in chemical element concentration in its skeleton. For example, Carricart-Ganivet et al. (2013) reported for *Siderastrea siderea* that maximum skeletal density in the female coincided with low winter SSTs, whereas in the male, it coincided with high summer SSTs. Furthermore, maximum skeletal densities in the female coincide with peak Sr/Ca values, whereas, in the male, they coincide with low Sr/Ca values. Similarly, tissue thickness, density, and calcification rate were observed to be significantly lower in the females than in males, though there was no difference in extension rate between sexes for *Montastraea cavernosa* (Mozqueda-Torres et al. 2018).

6.3.3 Calcite Formation Within the Aragonite Lattice

Geochemical proxies archived in the coral skeleton are assumed to be bounded to the aragonite lattice. However, over the years some coral skeletons are subject to the diagenetic alterations to include calcite in their lattice through the dissolution of primary coral aragonite (orthorhombic $CaCO_3$) and subsequently to fill skeletal pore spaces with secondary cement or to recrystallize to stable calcite (rhombohedral $CaCO_3$). In Vanuatu waters, the amount of intra-skeletal lattice calcite was found to vary from less than 3% to 13–32% in *Porites* sp. (Lazareth et al. 2016). Lazareth et al. found that, for coral skeleton containing more than 10% of calcite, the relationship between geochemical proxies with environmental variables is significantly impacted as much as 0.26 °C and 0.011 pH unit based on Sr/ca ratio, Li/Mg ratio, and boron isotope. Therefore, the percentage of calcite should be determined prior to interpreting paleo-proxies. The luminescence emission of Mn^{2+} occurs at higher energy in the longer metal-to-oxygen distance. Therefore, the emission spectrum of calcite is discernable from that of aragonite. Using the difference of emission spectrum between aragonite and calcite and greater Mn partition coefficient in calcite than aragonite, diagenetic alteration in coral skeleton was detected using thermoluminescence technique (Takada et al. 2017).

6.4 Age Model

Climate is defined as "weather of some locality averaged over some time period plus extremes in weather behavior observed during the same period or during the entire record" (Moran 2006). Therefore, understanding mechanisms of climate variability requires absolute age control of the proxy records accumulated in coral skeletal columns. Current approaches to dating coral skeletons collected from living colonies are to counting annual growth markers such as high- and low-density growth bands or luminescence bands discernable under UV light. These growth bands are usually complemented with chemical or isotopic ratio records showing seasonal cycles. However, some corals undergo extremely slow growth or no growth due to environmental stress for certain periods or experience very weak seasonality in temperature or rainfall or solar radiation; therefore, annual markings on their skeletons may not be easily discernable. In these cases, including fossil corals, skeletal markings cannot be used to assign dates to coral skeletons as in the case of fossil coral skeletons. Various radiometric dating techniques have been applied successfully so far. The notable dating methods are using disequilibrium of radionuclides of their uranium-238, thorium-232, and uranium-235 decay series, radiocarbon, anthropogenic radionuclides, and amino acid racemization archived in coral skeletons. A short summary is given here.

6.4.1 Annual Growth Band

Light and dark density couplets of coral skeleton constitute annual banding in certain types of hermatypic corals and have been utilized as time markers at the times of their formation. It is significant to note that circadian cycles dominate the physiology and behavior of almost every biological organism on the earth, and animals with habitats in the intertidal zone also often display biological rhythms in relation to the tidal cycle. A complete cycle of seasonal variability determines a year. Therefore, if there is no change for the entire 12 months with respect to available solar radiation, wind, precipitation, and/or suspended sediment load, then we may not be able to designate the beginning and end of the year. And we will not see the annual growth band in coral. Thanks to the fact that the geographical equator does not correspond to the thermal equator (Intertropical Convergence Zone, ITCZ), seasonality is rather strong for the entire tropical waters where corals grow.

The ITCZ is the region that circles the Earth near the equator where the trade winds of the Northern and Southern Hemispheres come together. The ITCZ is a tropical belt of deep convective clouds and a zone of maximum precipitation. Seasonally, it migrates towards a hemisphere that warms relative to the other. Over the central Atlantic and Pacific Oceans, the ITCZ migrates between 9 °N in boreal summer and 2 °N in boreal winter. Over the Indian Ocean and adjacent land surfaces, the ITCZ swings more dramatically between average latitudes of 20 °N in boreal summer and 8 °S in boreal winter, prompting the big seasonal rainfall variations called the South Asian monsoon (Schneider et al. 2014). The seasonal north-south migration of the ITCZ defines the position of the tropical rain belt (TRB) which is a region of enormous terrestrial and marine biodiversity and home to 40% of people on Earth. Therefore, coral living in the tropics including at the equator experiences seasonal changes in their habitat to leave an annual mark on top of the circadian and tidal ones in their skeleton. However, the impact of the annual cycle on coral biology is much less obvious than circadian cycles that dominate coral physiology as well as the photosynthesis of zooxanthellae.

Assigning Coral Year for Growth Band

The preliminary age model of a living coral chronology is usually based on counting the annual density-band pairs of high-density (HD) and low-density (LD) bands, which are revealed by X-radiography, often aided by X-ray computed tomography assuming that one HD band and one LD band are equivalent to a year's growth (e.g., Wang et al. 2018).

Given that sea surface temperature (SST) is an important positive driver of calcification (McNeil et al. 2004), HD bands are usually associated with summer and LD bands with winter. Therefore, coral-year starts in midsummer (the month with the highest SST in the sampling site) and ends at the next midsummer.

Nevertheless, annual density banding is dependent on the corals' growth history and skeletal architecture. In corals that have their own walls and solid skeletons, such as *Montastraea* and *Diploria*, density banding results from different amounts of thickening deposit over skeletal structures laid down at different times of the year. However, in corals with porous skeletons, such as *Porites*, the coral tissue layer penetrates the previously formed skeleton, and the density banding arises from the thickening of the skeleton throughout this layer. Consequently, there is a difference between the actual and apparent timing of HD-band formation, which depends on the thickness of the tissue layer and extension rate. In colonies of *Porites*, a difference in the apparent timing of HD-band formation was found to be with an average 3 months (Brown et al. 1986). Multiple high-density bends were found also within a single annual band pair of *Porites lobata* off Guam (Asami et al. 2004). The annual extension rate has been reported to be proportional to sea surface temperature (Brachert et al. 2006). Thermal stress on massive corals (*Porites* colonies) was observed to yield an anomalously high-density bend (Barkley and Cohen 2016).

To assign the approximate calendar date, we need to know when the low density (or high density) bend forms in situ. Benninger and Dodge (1986) assigned the coral year based on the information that high-density skeleton in *Montastraea annularis* at St. Croix, US Virgin Island, deposited during the months of highest water temperature; therefore, they assign a coral year (the length of an annual growth) from a low-density region through the next outermost high-density region corresponding autumn to the next autumn. They assigned the coral year 1975 to begin 1 October 1974 and to have its midpoint on 1 April 1975. In most studies, the preliminary age model based on banding needs to be refined using the seasonal cyclicity of geochemical signals such as isotopic or elemental profiles (e.g., δ^{18}O or Sr/Ca and Ba/Ca ratios or δ^{13}C) in coral skeletons that reflects the seasonal cycle of temperature, light, rainfall, etc. (Asami et al. 2004). Sharp and narrow peaks of Sr/Ca and Mg/Ca in winter were also utilized to dating purpose. Chen et al. (2010) investigated Sr/Ca and Mg/Ca values in *Porites* coral skeletons with the ambient sea surface temperature (SST) and found them to be synchronized with SST seasonal variations. Using this relationship, they confirmed growth chronologies of the annual growth bands using sharp and narrow winter peaks observed corresponding to low SST values in *Porites* species growing in the southern China Sea. Deng et al. (2014) also assigned Sr/Ca maximum to the beginning (January) of each year at the Leizhou Peninsular, northern South China Sea. Fallon and Guilderson (2008) constructed an initial age model using the seasonal variability in δ^{13}C values in a coral skeleton (*Porites lutea*) collected from Makassar Straits. They pinned the minimum δ^{13}C to February of each year, and linearly interpolated the data between marker points, then, used the seasonal cycle of δ^{18}O to to fine-tune the dates as much as ±2 months.

Luminescence Bands

Luminescence is a phenomenon which involves the absorption of energy and subsequent emission of light. The process of emission is a release of energy in the form of photon. Activator within the host lattice (aragonite) is directly excited by incoming energy to be raised to an excited state, and subsequently, the excited state returns to the ground state by emitting radiation in a form of photon either fluorescence or phosphorescence. Fluorescence and phosphorescence refer to the fast (ns timescale) and slow (longer timescale, up to hours or days) emission, respectively (Shinde et al. 2012). In the latter case, falling of electrons from the excited state proceeds through intermediate levels, thus taking more time, so the energy of the emitted light is less. Various excitation energy sources are used, such as electron (cathode rays), photon (electromagnetic radiation, such as UV rays, etc.), electric voltage, a chemical reaction, ionizing radiation (X-rays or gamma rays), heat, or ultrasonic waves, and their light emissions and their resulting luminescence are termed as cathodoluminescence, photoluminescence, electroluminescence, chemiluminescence, radioluminescence, thermoluminescence, and sonoluminescence, respectively. Bioluminescence refers to the chemiluminescence occurring in a biological organism, frequently encountered in the deep sea. Mechanical energy such as scratching or rubbing can also induce the emission of luminescence (triboluminescence). Activators of luminescence in carbonate minerals were identified to be electron defects of the crystal lattice, inorganic ions (Mn^{2+}, Fe^{3+}, Tb^{3+}, Er^{3+}, Dy^{3+}, Eu^{3+}, Eu^{2+}, Sm^{3+}, and Ce^{3+}), ions substituting structural ions in the crystal lattice (e.g., Pb^{2+} and Mn^{2+}), molecules, ions, or radicals adsorbed inside of the lattice (e.g., UO_2^{2+}, organic molecule, fulvic and humic acids, organic esters) (Shopov 2004; MacRae and Wilson 2008). The abovementioned activators are present in some coral skeleton; therefore, luminescence measurements may be helpful to screen the sample prior to further analysis for assessing the integrity of the coral skeleton. By irradiating a coral slab with UV light, luminescent lines are clearly visible, and those lines have been used to complement to identify annual growth bands, provided circumstantial environmental variables (e.g., rainfall) are known (Staines-Urías 2017). Photoluminescence under UV light has been utilized to link to river flood plume presence in the inshore coral habitat to pay attention to green (humic acid signal) relative to blue portions (skeletal density signal) in the emission spectra (Grove et al. 2010, 2012; Maina et al. 2012).

6.4.2 ^{14}C Dating ($t_{1/2} = 5730$ Years) (Valid for $< 5 \times t_{1/2}$ Years Old Coral)

Dating using various radionuclides incorporated into the coral skeleton requires the assumption that both the specific activities of radionuclides concerned in surface seawater incorporated by the corals at the time of deposition of each layer (annual band) remain constant or known in time, and chemical fractionation in biomineralization process by corals remains constant or known, and the skeletal $CaCO_3$ becomes a chemically closed system with respect to those radionuclides of concern, such as ^{14}C, ^{90}Sr, Th, and Pb (Dodge and Thomson 1974). The aragonite skeleton is made of $CaCO_3$; therefore, ^{14}C incorporated in $CaCO_3$ as C component has been utilized to determining date of the time of skeleton formation. In accelerator mass spectrometry (AMS), the filamentous carbon or "graphite" derived from a sample is compressed into a small cavity in some aluminum "target" which acts as a cathode in the ion source. The surface of the graphite is sputtered with heated ionized cesium, and the ions produced are extracted and accelerated in the AMS system. After acceleration and removal of electrons, the emerging positive ions are magnetically separated by mass and the ^{12}C and ^{13}C ions are measured in Faraday cups where a ratio of their currents is recorded. Simultaneously ^{13}C ions are recorded in a gas ionization or solid-state detector, so that ratios of ^{14}C to ^{13}C and ^{14}C to ^{12}C may be recorded. These are the raw signals that are ultimately converted to a radiocarbon age. The following are largely taken from National Ocean Sciences Accelerator Mass Spectrometry (2018).

Therefore, to calculate ^{14}C ages, ^{14}C/^{13}C ratios in the samples and standards were compared to determine the fraction of modern carbon (F) values, defined as Eq. (6.9).

$$F \equiv \left({}^{14}\mathrm{C}/{}^{13}\mathrm{C}\right)_{\mathrm{sample}} / \left({}^{14}\mathrm{C}/{}^{13}\mathrm{C}\right)_{\mathrm{STD}}, \tag{6.9}$$

where $({}^{14}\mathrm{C}/{}^{13}\mathrm{C})_{\mathrm{sample}}$ is the measured ratio in the sample, normalized to $\delta^{13}\mathrm{C} = -25‰$, and $({}^{14}\mathrm{C}/{}^{13}\mathrm{C})_{\mathrm{STD}}$ is calculated modern standard ratio (1950 AD) determined from measurements of NBS oxalic acid standards, also normalized to $-25‰$. The age of the sample is computed with the Eq. (6.10).

$$^{14}\mathrm{C}_{\mathrm{age}} = -\tau \ \ln F, \tag{6.10}$$

where τ is the Libby mean life of ^{14}C (8033 years). In order to compare ^{14}C dates with atmospheric ^{14}C values, the ^{14}C ages were reservoir-corrected using Eq. (6.11).

$$^{14}\mathrm{C}_{\mathrm{ageRC}} = {}^{14}\mathrm{C}_{\mathrm{age}} - \mathrm{RC}, \tag{6.11}$$

where $^{14}\mathrm{C}_{\mathrm{ageRC}}$ is the reservoir-corrected age and RC is the reservoir correction in years. The following is directly quoted from Burr et al. (1998). To calculate the reservoir-corrected fraction of modern values (F_{RC}), we define the relationship (Eq. 6.12).

$$^{14}\mathrm{C}_{\mathrm{ageRC}} = -\tau \ \ln F_{\mathrm{RC}}. \tag{6.12}$$

Combining Eqs. (6.10, 6.11, and 6.12) yields Eq. (6.13).

$$F_{\mathrm{RC}} = F \ e^{(\mathrm{RC}/\tau)}. \tag{6.13}$$

The uncertainty in F_{RC} depends on the uncertainty in F and on the uncertainty in RC. Propagating these two sources of errors yields Eq. (6.14), where the σ's represents the uncertainties in FRC, F, and RC.

$$\sigma_{F_{\mathrm{RC}}} = \left\{ \left(e^{\mathrm{RC}/\tau}\right)^2 (\sigma_F)^2 + \left[\left(\frac{F}{\tau}\right)\left(e^{\mathrm{RC}/\tau}\right)\right]^2 (\sigma_{\mathrm{RC}})^2 \right\}^{½}. \tag{6.14}$$

Δ C values were computed from Positive values indicate an excess relative to 1950 and negative values indicate a relative C deficit. Δ^{14}C values are computed with the following expression (Eq. 6.15), where λ is the decay constant for the 5730-year half-life and t is the calendar age of the sample in years BP (before 1950), determined with the ^{230}Th techniques.

$$\Delta^{14}\mathrm{C} = \left(F_{\mathrm{RC}} e^{\lambda t} - 1\right) \times 1000‰. \tag{6.15}$$

The total uncertainty of Δ^{14}C includes uncertainties in FRC and ^{230}Th ages. Propagating these yields the following expression (Eq. 6.16), where σ_Δ is the total uncertainty in Δ^{14}C, t is the calendar age in years BP, σ_t is the standard deviation reflecting the uncertainty in the age (uncertainty in the ^{230}Th data), and σF_{RC} is the uncertainty in F_{RC}.

$$\sigma_{\Delta} = 1000e^{\lambda t}\left[\left(F_{\mathrm{RC}}\lambda\, {\sigma_t}^2 + \sigma {F_{\mathrm{RC}}}^2\right)^{1/2}\right. \qquad (6.16)$$

One of the examples is that deep-sea corals, Antipatharia, that have been growing continuously for over 2000 years at 304–317 m depth were dated using the ^{14}C method utilizing the known surface ocean ^{14}C reservoir age of the Gulf of Mexico (Prouty et al. 2014). Visual growth ring counts based on scanning electron microscopy, 8–2 μm year^{-1}, were in good agreement with ^{14}C-derived ages.

6.4.3 ^{230}Th Dating (Valid < 123,000 Years Old Coral)

Dating of coral skeletons can be also made using the disequilibrium of ^{234}U ($t_{1/2} = 244.5 \times 10^3$ year) and its daughter ^{230}Th ($t_{1/2} = 75.4 \times 10^3$ year). The following summary is largely taken directly from Burr et al. (1998). Both isotopes accumulate in the coral skeleton as relatively long-lived intermediate daughter products from ^{238}U decay. While dissolved U is usually incorporated into aragonite precipitates produced by a coral animal, ^{230}Th is not incorporated due to its extremely low solubility. Typical uranium concentrations for the coral samples are about 3 ppm.

Assuming a closed system and zero initial ^{230}Th, the ^{230}Th age of the coral can be calculated using Eq. (6.17), where the value [^{230}Th/^{238}U] is the ^{230}Th/^{238}U activity ratio, λ_{230} and λ_{234} are the decay constants for ^{230}Th and ^{234}U, and T is the sample age in years.

$$\left[{}^{230}\mathrm{Th}/{}^{238}\mathrm{U}\right] - 1 = -e^{(-\lambda_{230}\times T)} + \left(\delta^{234}\mathrm{U_m}/1000\right) \times \left[\lambda_{230}/(\lambda_{230}-\lambda_{234}) \times \left(1 - e^{(\lambda_{230}-\lambda_{234})\times T}\right)\right. \qquad (6.17)$$

And δ^{234}U$_m$ is the measured δ^{234}U value, defined as Eq. (6.18), where (^{234}U/^{238}U)$_{se}$ is the ratio at secular equilibrium.

$$\delta^{234}\mathrm{U_m} = \left\{\left[\left({}^{234}\mathrm{U}/{}^{238}\mathrm{U}\right)_{\mathrm{measured}}/\left({}^{234}\mathrm{U}/{}^{238}\mathrm{U}\right)_{\mathrm{se}}\right] - 1\right\} \times 1000. \qquad (6.18)$$

The initial ^{234}U/^{238}U ratio of the corals reflects that of seawater, which is present in excess of the secular equilibrium activity concentration value by ca. 1.16. This value has not varied by more than 2‰ over the last 13,000 years. Coral ^{230}Th ages were usually measured using thermal ionization mass spectrometry (TIMS) on 250 mg of coral samples (Burr et al. 1998).

6.4.4 ^{210}Pb Dating (Valid <100 Years Old Coral)

^{210}Pb ($t_{1/2} = 21.5$ years) exhibits very constant uptake as evidenced by its uniform exponential disappearance over time in coral skeletons that means a closed system with respect to the ^{210}Pb as well as ^{228}Ra/^{226}Ra pair (Moore et al. 1973). Therefore, it can be used for coral dating purposes. Recently Baskaran (2011) gave a comprehensive review on ^{210}Pb dating methodology and closed system of the coral lattice. In this model, lattice-bound Pb should be used; therefore, a rigorous sequence of oxidative, reductive, and dilute acid treatment needs to be applied to the annually banded corals to eliminate the pre-existing surface contamination (detrital and organic phases of Pb) and contamination introduced in sample recovery and preparation, which are often higher than that in the lattice-bound phase. A typical lattice-bound Pb mole ratio relative to Ca is about ~100 × 10^{-9} (Shen and Boyle 1987).

The ground coral samples are acidified to obtain an acid solution. ^{210}Po is plated onto silver foil from the acid solution and used to determine ^{210}Pb activities (assuming secular equilibrium between the two isotopes). ^{226}Ra is measured using the ^{222}Rn emanation method or gamma spectrometry. The ^{226}Ra activity is subtracted from the total ^{210}Pb activity to calculate the unsupported or excess ^{210}Pb (^{210}Pb$_{ex}$). ^{210}Pb$_{ex}$ values are plotted against mean distance from the outer edge. The growth rate (A in mm year^{-1}) of the coral is determined from the best fit to the exponential curve through the values using the following Eq. (6.19), where (^{210}Pb$_{ex}$)$_0$ is the activity of excess ^{210}Pb at time zero, λ is the radioactive decay constant of ^{210}Pb (=0.0311 year^{-1}), and D is the distance from the edge (Druffel et al. 1990; Tracey et al. 2007).

$${}^{210}\mathrm{Pb_{ex}} = \left({}^{210}\mathrm{Pb_{ex}}\right)_0 \times e^{(-\lambda/A)\times D}. \qquad (6.19)$$

For the deep-sea corals, the exponential decrease of initially incorporated ^{210}Pb and the increase in ^{210}Pb from the decay of ^{226}Ra were both utilized to determine coral growth chronology (Sabatier et al. 2012). Radial distribution of excess ^{210}Pb in the cross section of black coral, *Cirrhipathes* spp., in the South China Sea yielded an exponential decrease with distance from the edge of the black coral to its center and thus was used for its growth estimates (17.8–28.5 μm year^{-1}) (Zhang et al. 2015).

6.4.5 ^{228}Th Dating (Valid <30 Years Old Coral)

The determination of the rate of growth of coral *Montastraea annularis* was to be done by α spectrometric analysis for in situ ^{228}Th ($t_{1/2} = 1.9$ years) growing from ^{228}Ra ($t_{1/2} = 5.75$ years) which had been precipitated from seawater with the aragonite coral skeleton. The in situ ^{228}Th method depends on the assumption that the coral incorporates ^{228}Ra into its skeleton at a fixed ratio to Ca from the surrounding seawater and that this initial ratio has been constant throughout the life of the coral. Analysis for ^{228}Th at time intervals defined by the growth bands should then conform to an ingrowth curve of ^{228}Th towards transient equilibrium with the initial ^{228}Ra specific activity (Dodge et al. 1974).

6.4.6 ^{90}Sr Dating (Valid Since the 1950s)

^{90}Sr ($t_{1/2} = 28.79$ years) has been introduced in the early 1950s from the close-in and stratospheric testing of nuclear weapons largely over the Pacific and the Russian Arctic, respectively. The activity concentration of ^{90}Sr in the surface water depends on the source term as well as the mixing of different water masses. So, the time of its initial appearance in a coral can be used as a time marker, e.g., 1955 in Jamaica and North Carolina, in the Caribbean, and in the North Atlantic (Moore et al. 1973). Because the stable Sr/Ca ratio of seawater is constant to ±2 % and its discrimination factor of corals for strontium is very close to 1.0, the Sr/Ca ratio of corals is almost constant. Since most of the ^{90}Sr introduced into the ocean is in soluble form, the corals should incorporate ^{90}Sr in proportion of ^{90}Sr/Ca ratio in the water. Unfortunately, ^{90}Sr time series in the tropical ocean has not been extensively measured to exploit ^{90}Sr chronology in coral skeletons.

6.4.7 Amino Acid Racemization (Valid Up to 40,000 Years Old Coral)

Proteins are incorporated in the coral aragonite crystal's interstitial sites to precipitate aragonite (Rademaker and Launspach 2011; see Sect. 6.1.4). Amino acids are the building blocks of proteins. All amino acids, with exception of glycine, have an asymmetric carbon at their center that results in each amino acid having two enantiomeric isomers (L or D). Living organisms keep all their amino acids in the "L" configuration, and when an organism dies, its control over the configuration of the amino acid ceases, and the ratio of D to L moves reversibly from a value near 0 towards an equilibrium value near 1, a process called racemization (Eqs. 6.20 and 6.21).

$$\text{L-amino acid} \xrightarrow{k_1} \text{D-amino acid} \tag{6.20}$$

$$\text{L-amino acid}^{k_2} \leftarrow \text{D-amino acid} \tag{6.21}$$

Therefore, the rate equations above can be expressed as Eq. (6.22), where [L] and [D] are the concentrations of the L and D amino acids.

$$-d[\mathrm{L}]/dt = k_1[\mathrm{L}] - k_2[\mathrm{D}]. \tag{6.22}$$

Solving the differential equation of Eq. (6.22) will yield Eq. (6.23), where $K' = 1/K = k_2/k_1$ and t = time (s) and "constant" accounts for racemization induced by sample preparation.

$$\begin{aligned} &\ln\{(1+\mathrm{D/L})/(1-K'(\mathrm{D/L}))\} - \text{constant} \\ &\quad = (1+K') \times k_1 t. \end{aligned} \tag{6.23}$$

For most amino acids, the forward and reverse rate constants, k_1 and k_2, are the same (= k), therefore the above equation can be simplified to Eq. (6.24).

$$\ln\{(1+\mathrm{D/L})/(1-(\mathrm{D/L}))\} - \text{constant} = 2kt \tag{6.24}$$

And the reaction constant k is a function of temperature (Eq. 6.25), where k is rate constant (s^{-1}), A = frequency factor (s^{-1}), EA = activation energy (KJ mol^{-1}), R = molar gas coefficient (KJ mol^{-1}K^{-1}), and T = temperature (K, Kelvin).

$$k = \mathrm{A_{exp}}(-\mathrm{EA/RT}). \tag{6.25}$$

The abovementioned amino acid racemization (AAR) chronology assumes that it occurs in a closed system. Therefore, intracrystalline amino acids (proteins) need to be isolated from the inter-crystalline, and any exogenous proteins incorporated into the coral skeleton have to be removed. Oxidative pre-treatment with NaOCl (sodium hypochlorite) has been shown effective to isolate intracrystalline proteins (Hendy et al. 2012). Amino acid racemization (AAR) dating assumes that the initial D/L values of the target amino acid(s) are zero, all racemization occurs in the post-mortem period, and D/L values increase with age, and the amino acids are within a closed system. Racemization reaction constant varies widely depending on the specific amino acid and temperature (Crisp 2013). At 100 °C the various amino acids would be totally racemized on a timescale ranging from a few days to years, and at lower temperatures the rates are lower. Aspartic acid racemizes rapidly and is suitable for a date shorter than 150 years, while glutamic acid and alanine are more suitable for over 500 years. In fossils, the racemization half-lives are on the order of 10^4–10^5 years (Bada 1985). Free amino acid (FAA) D/L for dating can be as accurate as ± 10 years within a core from a single colony (Hendy et al. 2012).

6.5 Principles of Application of Proxies/Tracers to the Past Climate and Environment

Any climate or environmental phenomenon on the surface of the Earth has resulted from the interplay among the physics of ocean-atmospheric circulation and biogeochemistry of the carbon cycle including life processes. These systems are complex with multiple feedbacks. Paleoclimatology is the study of past climates. Since it is not possible to go back in time to see what climates were like, scientists use climate proxies imprinted in long-lived coral skeletons along with other repositories, such as glacial ice, tree rings, lake, and ocean bottom sediments (e.g., Henderson 2002). A proxy here stands for something in the coral skeleton that represents something else in the coral habitat environment including seawater adjacent to coral lived at the time of its growth. Something and something else have a common trait for both, but the two also have other traits that may not be shared. Therefore, a proxy is usually narrowly defined in the context of given circumstances as something else is equal to something. "Given circumstances" here are equivalent to scientific assumptions that constrain the something else is equal to something. We need to ensure that something else faithfully represents something through scientific testing. Therefore, all proxies are useful as far as in the well-defined situation where those assumptions hold. The validity of the assumptions should be met with empirical evidence.

Each chemical element or chemical compound proxy is different due to their chemical behavior in the ocean including their involvement in calcification reaction in coral. Therefore, a few exemplary climate proxies are given here for illustrative purpose to demonstrate scientific principles pertaining to the selected application of proxies/tracers embedded in the coral skeleton to the past climate and environment. The reader who wishes for fuller empirical and theoretical developments in various climate proxies should consult the relevant original literature.

Stable Oxygen Isotope Ratio in the Coral Skeleton

Among water molecules with different oxygen isotopes, a lighter oxygen isotope-laden water molecule, $H_2{}^{16}O_2$, is preferentially evaporated from the sea relative to its heavier oxygen isotope-laden water molecule $H_2{}^{18}O_{2.}$ Therefore, when the wind blows faster, the water evaporates greatly from the sea and moves higher altitude and eventually poleward due to the prevailing planetary wind system and precipitates along its path. Thus, the remaining water in the sea becomes isotopically heavier than before. This isotopic fractionation during evaporation/precipitation does depend on temperature as any other chemical reactions. If water is locked as a glacier on the continent, the sea level becomes lower than before. When the glacier melts due to the elevation of temperature, the isotopically light oxygen-laden water from the glacial melt is introduced into the sea and it lightens seawater isotopically than before, and sea level also rises to the higher stand than before. A reef-building coral animal living in the sea precipitates its skeleton with calcium and carbon and oxygen from seawater to form calcium carbonate aragonite mineral and keeps it intact afterward. Therefore, we may infer water temperature at the time of coral skeleton formation from the oxygen isotope compositions in the skeleton. Similarly, we may also infer the position of sea level and continental glacial volume, hence salinity (Adkins et al. 2002b). Sharp (2017) summarized the development of carbonate oxygen isotope paleothermometry in the early 1950s that opened a new era of paleoceanography. The basic idea for the carbonate oxygen isotope paleothermometer came originally with the assumption that the fractionation between biologically produced carbonates and water is a function of temperature. Using biologically produced calcite minerals and seawater in their habitats from modern oceans, Epstein et al. (1953, referenced in Sharp 2017) obtained the numerical relationship on the temperature dependence of the isotopic fractionation between biogenic calcite carbonate and water as described in Eq. (6.26).

$$T(^\circ\mathrm{C}) = 16.5 - 4.3\left(\delta^{18}\mathrm{O}_{\mathrm{carbonate}} - \delta^{18}\mathrm{O}_{\mathrm{seawater}}\right) + 0.14\left(\delta^{18}\mathrm{O}_{\mathrm{carbonate}} - \delta^{18}\mathrm{O}_{\mathrm{seawater}}\right)^2. \qquad (6.26)$$

The following relationship (Eq. 6.27) is shown here as an example obtained in aragonite secreted by corals, *Montastraea annularis* (Watanabe et al. 2002).

$$T(^\circ\mathrm{C}) = 5.33 - 4.519\left(\delta^{18}\mathrm{O}_{\mathrm{carbonate}} - \delta^{18}\mathrm{O}_{\mathrm{seawater}}\right). \quad (6.27)$$

In these equations, $\delta^{18}O_{carbonate}$ is the $\delta^{18}O$ value of CO_2 liberated from the reaction between the carbonate and phosphoric acid at 25 °C, and $^{18}O_{seawater}$ is the $\delta^{18}O$ value of CO_2 equilibrated with water at 25 °C. There is no theoretical basis for both equations; it is simply the best fit of the data to a second and first polynomial, respectively, although theoretical studies were followed in later (e.g., Mucci 1983; Kim et al. 2007; Wang et al. 2013a). These equations have two independent variables, $\delta^{18}O_{carbonate}$ and $\delta^{18}O_{seawater}$. Because

$\delta^{18}\mathrm{O}_{\mathrm{carbonate}}$ is the measured value, the validity of the dependent variable, T, depends on $\delta^{18}\mathrm{O}_{\mathrm{seawater}}$ that cannot be measured directly as the seawater no longer exists. In a short timescale in the modern ocean, $\delta^{18}\mathrm{O}_{\mathrm{seawater}}$ increases due to evaporation and decreases due to the influx of freshwaters via precipitation and river discharge. In the longer time of the recent 2.6 million years (Quaternary period), $\delta^{18}\mathrm{O}_{\mathrm{seawater}}$ varies with the ice volumes on the continents. Therefore, the accuracy of $T(^{\circ}\mathrm{C})$ derived from these equations depends on the validity of the assumptions estimating $\delta^{18}\mathrm{O}_{\mathrm{seawater}}$ at the time of carbonate shell formation.

Chemical Element to Calcium Ratio in Coral Skeleton

Scientists found that the ratios between chemical elements and calcium (Ca) in coral skeletons correlated with climate variables (such as water temperature, salinity, or chemical composition of the ambient seawater) at selected sites. They further elaborated those observed correlations with thermodynamic considerations by culturing live corals in aquariums. They have applied those correlations to the coral core samples in which no direct environmental observations are not available (Eq. 6.28).

$$\frac{\left(\frac{\mathrm{CE}}{\mathrm{Ca}}\right)_{\mathrm{coral}}}{\left(\frac{\mathrm{CE}}{\mathrm{Ca}}\right)_{\mathrm{seawater}}} = D_{\mathrm{CE}}^{\mathrm{coral}} = f\left(T, S, X_j\right), \tag{6.28}$$

where f stands for function and T, S, X_j are the seawater temperature, salinity, and seawater component j, respectively, of the ambient seawater at the time of calcium carbonate precipitation generated by corals. $D_{\mathrm{CE}}^{\mathrm{coral}}$ is the Nernst partition coefficient that is dependent on temperature (Eq. 6.29).

$$\Delta G^{\circ} = -RT \ln D_{\mathrm{CE}}^{\mathrm{coral}}, \tag{6.29}$$

where D can be easily determined at two different temperatures, and it is possible to obtain the variations in standard enthalpy ΔH^0 and entropy ΔS^0 (Eqs. 6.30 and 6.31).

$$\Delta G^0 = \Delta H^0 - T\,\Delta S^0. \tag{6.30}$$

$$\frac{d\ \ln\ D_{\mathrm{CE}}^{\mathrm{coral}}}{dT} = \frac{\Delta H}{RT^2}. \tag{6.31}$$

The observed Nernst distribution coefficient of Sr/Ca in Eq. (6.32) was reported by Gaetani et al. (2011).

$$D_{\mathrm{Sr}}^{\mathrm{coral-seawater}} = -7.1 \times T(^{\circ}\mathrm{C}) + 2199.7. \tag{6.32}$$

In the calcifying fluid located beneath the coral tissue and above the coral skeleton, aragonite mineral forms as a fashion of Rayleigh fractionation. The average Sr/Ca ratio of coral aragonite precipitated from an isolated reservoir of calcifying fluid is given by an analytic solution to the Rayleigh fractionation equation (Eq. 6.33) as given by Gaetani et al. (2011):

$$\frac{\overline{C}_{\mathrm{Sr}}}{\overline{C}_{\mathrm{Ca}}} = \frac{C_{\mathrm{Sr}}^0}{C_{\mathrm{C_a}}^0} \times \frac{1 - \mathrm{FL}^{D_{\mathrm{Sr}}^{\mathrm{coral-seawater}}}}{1 - \mathrm{FL}^{D_{\mathrm{Ca}}^{\mathrm{coral-Seawater}}}}, \tag{6.33}$$

where $\overline{C}_{\mathrm{Sr}}$ and $\overline{C}_{\mathrm{Ca}}$ are the average concentration of Sr and Ca in aragonite precipitated from a single "batch" of fluid and C_{Sr}^0 and $C_{\mathrm{C_a}}^0$ are the concentrations of Sr and Ca in the calcifying fluid at the time when precipitation begins. FL is the mass fraction of the initial fluid that remains when aragonite precipitation ends, and $L^{D_{\mathrm{Ca}}^{\mathrm{coral-Seawater}}}$ and $L^{D_{\mathrm{Sr}}^{\mathrm{coral-seawater}}}$ are the Nernst aragonite-seawater partition coefficients of calcium ad strontium, respectively.

Stable Nitrogen Isotope Ratio in the Coral Skeleton

Surface reef-building corals are well-known to have a nutritional symbiosis between corals and photosynthetic dinoflagellates from the genus *Symbiodinium* (zooxanthellae). This symbiosis augments the carbon supply to the coral, while the symbionts benefit from nutrients provided by the host coral. Corals also obtain carbon and nutrient through heterotrophic feeding on a variety of sources, zooplankton, bacteria, pico- and nano-plankton, and particulate and dissolved organic matter using their tentacles (Hoogenboom et al. 2010). Nitrogen-laden organic material has been found in coral skeletons for some time. This skeleton-bound organic nitrogen is reasoned to be originated from the symbiont planktons within the coral body or from feeding nitrogen-laden organic matter in the overlying waters. When heterotrophs utilize nitrogen-laden food source, their body nitrogen isotope ratios between $^{15}\mathrm{N}$ and $^{14}\mathrm{N}$, $\delta^{15}\mathrm{N}$ value, usually increase 3–4‰ per a tropic level; therefore, this enrichment through food chains compromises the utility of nitrogen isotope ratio as a proxy of the sources of nitrogen. However, recently, Wang et al. (2015) observed that symbiotic coral skeleton $\delta^{15}\mathrm{N}$ faithfully reflects the isotopic composition of its N sources. Based on their study of *Diploria labyrinthiformis* of Bermuda reefs, they hypothesized that a coral's metabolic nitrogenous waste, as well as any dissolved inorganic nitrogen taken up from ambient water, is assimilated by the symbionts; a fraction of the assimilated nitrogen is transferred back to the coral host. In this way, the coral symbiotic system is able to sequester and efficiently recycle the nitrogen with little loss to the environment. Lacking this release of low $\delta^{15}\mathrm{N}$ ammonium, coral skeleton $\delta^{15}\mathrm{N}$ would be similar to the $\delta^{15}\mathrm{N}$ of its N sources in the ambient seawater. Wang et al. (2015) further developed a noble high-precision analytical method using a small sample (~5 mg), and they were able to track the N cycle of the coral's external environment. They also pointed out that abrupt coral skeleton δ^{15}N peaks may mark times of coral bleaching events when coral lost its host/symbiont N cycling.

In general, proxies become useful under the following conditions. These usually include (i) understanding the processes or the factors governing proxy behavior in the skeleton formation at the time of precipitation of coral skeleton and (ii) concurrent development in analytical capacity to handle sufficiently small size samples to resolve temporal variability stored in coral skeleton. As more multiple feedbacks occurring in the coral biomineralization process are still unraveling, the established proxies will be also continued to be refined and new proxies will emerge in the coming years.

6.6 Chemical Elements and Isotopes Proxies

6.6.1 Lithium (Li) and Lithium Isotopes

Li^+ is a conservative cation in seawater, and its concentration is about 26 μM kg^{-1} in oceans (Misra and Froelich 2012). The ionic radius of Li^+ (92 pm) and Mg^{2+} (89 pm) is much smaller than Sr^{2+} (126 pm) or Ba^{2+} (142 pm) compared to Ca^{2+} (112 pm) (Shannon 1976); therefore, the ionic substitution of Li^+ and/or Mg^{2+} does not occur in aragonite as the ionic radius of an element differs by more than 5% from that of calcium (Montagna et al. 2014). However, Penniston-Dorland et al. (2017) suggested that Li does not substitute Ca in aragonite, but it enters interstitial sites in calcite crystal. Montagna et al. and Marchitto et al. (2018) have modeled that corals actively modify seawater within a calcifying fluid by raising its [Ca^{2+}], using a pump that discriminates against both Li^+ and Mg^{2+}. Rayleigh fractionation during calcification effectively reverses this process by removing Ca^{2+} while leaving most Li^+ and Mg^{2+} behind in the calcifying fluid. The net effect of these two processes is that Li/Mg in the calcifying fluid remains close to the ambient (outside of coral) seawater value.

Li/Ca mole ratios in coral skeletons are about 5–22 μmol/mol and exhibit systematic enrichment in rapid accretion deposits (RADs) compared to that in surrounding fibers (Raddatz et al. 2013; Rollion-Bard and Blamart 2015). It is also known that Li/Ca mole ratios decrease with temperature, but Mg/Ca ratios increase with temperature, in general. In contrast to relatively poor correlations observed in Li/Ca and Mg/Ca with temperature, Li/Mg molar ratio is strongly anticorrelated with temperature in a wide range of scleractinian coral skeletons such as several zooxanthellate coral species such as *Acropora* sp. at 22–28 °C, *Porites* sp. at 24–27 °C, and *Cladocora caespitosa* at 15–23 °C and azooxanthellate coral species such as *Lophelia pertusa* at 5.9–13.8 °C that live in 100–950 m depth, *Madrepora oculata* at 11.2 °C in 775–880 m depth, and *Flabellum impensum* at 0.8 °C in 760 m depth with a precision of ±0.9 °C (Eq. 6.34, Montagna et al. 2014).

$$\mathrm{Li/Mg\ \ (mmol/mole)} = 5.41 \times \exp^{-(0.049\times \mathrm{T})}\left(r^2 = 0.98\right). \tag{6.34}$$

Similar temperature sensitivity of Li/Mg was also found in benthic aragonitic foraminifera *Hoeglundina elegans* (Marchitto et al. 2018). Li/Mg molar ratio was found to be relatively high (3.80) in the center of calcification and low (2.84) in theca walls in deep-sea coral, *Lophelia pertusa,* living at the temperature range from 5.9 °C to 13.8 °C, in the European waters (Raddatz et al. 2013). The intra-skeleton variability in Li/Mg molar ratio should be taken into account for designing a sampling strategy for further analysis.

Lithium Isotopes

Lithium has two stable isotopes of ^{6}Li (7.52%) and ^{7}Li (92.48%) with percentage abundance in parenthesis (Meija et al. 2016a). The sources of Li into the oceans are river (8 × 10^9 mol Li/year, δ^7Li = 23‰) and hydrothermal fluxes (3–8 × 10^9 mol Li/year, δ^7Li = 9‰). The isotopic composition is typically expressed as Eq. (6.35), where the NIST SRM 8545 (LSVEC) lithium carbonate is the certified isotope reference material originally prepared by Harry John Svec of Iowa University (Brand et al. 2014), but this material is no longer available and the standard IRMM-016 is used as a replacement standard (Penniston-Dorland et al. 2017).

$$\delta^7\mathrm{Li\ \ (‰)} = \left({}^7\mathrm{Li}/{}^6\mathrm{Li}_{\mathrm{sample}}/{}^7\mathrm{Li}/{}^6\mathrm{Li}_{\mathrm{standard}} - 1\right) \times 10^3. \tag{6.35}$$

The Li isotopic composition of the present-day ocean is uniform at a value of +31.2 ± 0.5‰. δ^7Li of skeletons of surface and deep-sea corals were reported to be around +19.0 ± 1.2‰ and significantly lower than that of seawater (Rollion-Bard et al. 2009). Rollion-Bard et al. further showed that lithium isotope ratios δ^7Li are nearly homogeneous, though slightly lower in fibers relative to centers of rapid accretion (CRA) (Gabitov et al. 2011). Li isotopic ratio can be used, therefore, to trace changes in Li isotope ratios in seawater and the rate of continental weathering (Burton and Vigier 2011), because of the large relative mass difference in two stable isotopes (^{6}Li and ^{7}Li), and low-temperature Li isotope fractionation exhibits a large range (more than 31‰) in δ^7Li values (Misra and Froelich 2012).

6.6.2 Boron (B) and Boron Isotopes

In seawater, the relative abundance of the two aqueous boron species of boric acid ($B(OH)_3$) and borate ($B(OH)_4{}^-$) is pH-dependent with a constant fractionation factor between the two species (Eq. 6.36).

$$B(OH)_3 + H_2O = B(OH)_4{}^- + H^+ \qquad (6.36)$$

In modern seawater (pH = 8.2) borate ion comprises ~28.5% of boron species (assuming the dissociation constant of boric acid pK_B is about 8.6 at 25 °C), representing ca. 6% of seawater alkalinity. And borate ion is incorporated into aragonite crystal in the coral skeleton (Holcomb et al. 2016) as Eq. (6.37).

$$0.5\ CaCO_3 + B(OH)4- = Ca_{0.5}B(OH)_4 + 0.5\ CO_3{}^{2-} \qquad (6.37)$$

B/Ca ratio was found to depend primarily on the relative concentrations of borate and carbonate ions in the calcifying fluid in synthesizing aragonite in the laboratory (Holcomb et al. 2016). Therefore, the B/Ca ratio can be also utilized as a proxy of $[CO_3{}^{2-}]$ in seawater of the past.

Boron Isotopes

There are two stable boron isotopes of ^{10}B (19.8%) and ^{11}B (80.1%) in nature (Meija et al. 2016a). Boron isotope ($^{11}B/^{10}B$) ratios of the samples are normalized to the SRM 951 boric acid and are expressed in per mil notation relative to the standard in Eq. (6.38).

$$\delta^{11}B = \left(^{11}B/^{10}B_{sample}/^{11}B/^{10}B_{standard} - 1\right) \times 10^3 \qquad (6.38)$$

Differences in molecular coordination and vibrational frequencies between species in solution control the magnitude of isotope fractionation ($\alpha = 1/^{11-10}K_B$). The isotope exchange of ^{10}B and ^{11}B between the two species is described by the reaction in Eq. (6.39).

$$^{10}B(OH)_3 + ^{11}B(OH)_4{}^- = ^{11}B(OH)_3 + ^{10}B(OH)_4{}^- \qquad (6.39)$$

with an isotopic equilibrium constant defined by Eq. (6.40).

$$^{11-10}K_B = \left\{\left[^{11}B(OH)_3\right] \times \left[^{10}B(OH)_4{}^-\right]\right\}/\left\{\left[^{10}B(OH)_3\right] \times \left[^{11}B(OH)_4{}^-\right]\right\} \qquad (6.40)$$

The time for attaining the isotopic equilibrium between boric acid and borate ion is estimated to be about 95 μs ~ 125 μs at 25 °C in seawater of salinity with 35 (Zeebe et al. 2001). Corals modify seawater to concentrate carbonate ions and maintain saturation at the site of calcification (extracellular calcifying fluid, ECF). Saturation is achieved by seawater vacuolization within the cytoplasm which elevates both pH and alkalinity. Endergonic enzymatic reactions that exchange protons for Ca^{2+} result in higher pH at ECF. pH in the symbiotic coral *Galaxea* rises from 8.2 to 8.5 at the polyp surface and further 9.3 in ECF (Eq. 6.41, Trotter et al. 2011).

$$pH_{ECF} = pK_B{}^* - \log\left[-\left(\delta^{11}B_{sw} - \delta^{11}B_{coral}\right)/\left(\delta^{11}B_{sw} - \alpha_B\delta^{11}B_{coral} - (\alpha_B - 1) \times 10^3\right)\right]. \qquad (6.41)$$

The ambient seawater pH can be constructed from the internal coral $\delta^{11}B_{sw}$–pH relationship by applying the pH-$\delta^{11}B$ equation and substituting a constant (β_B) that best fits the species-specific relationship, for α_B (Eq. 6.42, Krief et al. 2010):

$$pH_{ambient\ sw} = pK_B{}^* - \log\left[-\left(\delta^{11}B_{sw} - \delta^{11}B_{coral}\right)/\left(\delta^{11}B_{sw} - \beta_B\delta^{11}B_{coral} - (\beta_B - 1) \times 10^3\right)\right]. \qquad (6.42)$$

The best fit β_B is 1.0186 for *Porites*. Wu et al. (2018) collected a modern slow-growing massive scleractinian coral, *Diploastrea heliopora*, from the open-ocean island of New Caledonia in the South Pacific Ocean that yielded more than 300 years of annually resolved $\delta^{11}B$ based on Eq. (6.43).

$$pH_{ambient\ \ sw} = (pH_{ECF} - 5.954)/0.32. \qquad (6.43)$$

Wu et al. clearly showed a gradual reduction in seawater pH due to the increases in atmospheric CO_2 since the late nineteenth century as much as 0.2 pH unit. Such a sudden drop of 0.2 pH units also occurred earlier in the last glacial period based on the boron isotope ratio in coral skeleton retrieved from the equatorial Pacific (Douville et al. 2010).

6.6.3 Carbon (C) Isotopes

$^{13}C/^{12}C$ Isotope Ratios

Carbon has two stable isotopes of ^{12}C (98.84%) and ^{13}C (0.96%) in nature (Meija et al. 2016a). Carbon isotope values of the samples are represented in the common δ notation, $\delta^{13}C$, as the per mil (‰) deviation from a standard (usually PDB) in Eq. (6.44).

$$\delta^{13}C(‰) = \left[\left(^{13}C/^{12}C\right)_{sample}/\left(^{13}C/^{12}C\right)_{standard} - 1\right] \times 10^3 \qquad (6.44)$$

$\delta^{13}C_{\text{coral skeleton}}$, for example, of *Porites lobata* off Guam varied from −4.2‰ to −0.81‰ with clear seasonal variation (Asami et al. 2004). Fallon and Guilderson (2008) also used the seasonal variability in coral skeleton $\delta^{13}C$ to construct their tropical coral *Porites lutea* age model assuming higher (lower) light levels are associated with more positive (negative) $\delta^{13}C$ and that $\delta^{13}C$ inflection points are interpreted as markings of seasonal change in Indonesian waters. Over 4 years of *Porites australiensis* culture experiment, Hayashi et al. (2013) found that the seasonal variation in $\delta^{13}C_{\text{coral skeleton}}$ was related to coral photosynthetic efficiency but not to solar radiation intensity variation nor $\delta^{13}C$ of dissolved inorganic carbon in seawater. $\delta^{13}C$ of dissolved inorganic carbon in seawater is in the range of −1‰ to +4‰ during the Phanerozoic ocean (Veizer et al. 1999). More recently, using photoemission electron spectromicroscopy (PEEM) and X-ray absorption near-edge structure spectroscopy with the 20-nm resolution, Mass et al. (2017b) showed that metal and carbonate ions incorporated into aragonite crystal are originated from the completely different origin. Metal ions (Ca^{2+}, Mg^{2+}, and Sr^{2+}) are from seawater, and C and O are both parts of the carbonate ion (CO_3^{2-}) that is formed in the tissue by organism coral, not from the atmospheric CO_2 or dissolved HCO_3^- or CO_3^{2-} in seawater. Because photosynthesis and heterotrophy have been shown to strongly affect $\delta^{13}C$ values in coral (Ferrier-Pagès et al. 2011), C and O isotopes in coral skeleton are not faithfully reflecting the thermodynamic nature of seawater.

Bomb-Produced ^{14}C

C-14 is one of the three naturally occurring carbon isotopes and is radioactive ($t_{1/2} = 5730$ years) and decays by emitting a β particle with an energy of about 156 keV. On the surface of the earth, the abundance of natural ^{14}C is about $1.2 \times 10^{-10}\%$ (Key 2001). Natural radiocarbon is produced in the atmosphere by the collision of cosmic rays-produced neutrons with nitrogen. The atmospheric production rate varies by changes in the solar wind and in the earth's geomagnetic field intensity with a mean of 1.57 atom $cm^{-2}\ s^{-1}$. Prior to 16 July 1945, all radiocarbon on the surface of the earth was produced naturally. The concentration of the ^{14}C on the surface of the Pacific Ocean was around −50 per mil of $\Delta^{14}C$. Approximately five hundred atmospheric nuclear tests between 1946 and 1963 by the USA, USSR, France, and the UK with additional tests between 1964 and 1980 by China significantly added ^{14}C in the atmosphere and surface ocean. And $\Delta^{14}C$ values reached around 160‰ in the middle of the 1970s and decreased afterward to about 60‰ in the tropical Southeast Pacific in 2013 (Broecker and Peng 1982; Jenkins et al. 2018).

Radiocarbon (^{14}C) concentration is generally reported as $\Delta^{14}C$, the activity ratio relative to a standard (NBS oxalic acid, 13.56 dpm per gram of carbon) with a correction applied for dilution of the radiocarbon by anthropogenic CO_2 with age corrections of the standard material to 1950 CE as Eqs. (6.45–6.46) where "2 × ($\delta^{13}C$ + 25)" corrects for fractionation effects.

$$\Delta^{14}C\,(‰) = \delta^{14}C - 2 \times \left(\delta^{13}C + 25\right) \times \left(1 + \delta^{14}C/1000\right) \tag{6.45}$$

$$\text{where } \delta^{14}C = \left({}^{14}C/{}^{12}C_{\text{sample}}/{}^{14}C/{}^{12}C_{\text{standard}} - 1\right) \times 10^3. \tag{6.46}$$

The details of ^{14}C calculations may be referred to in the relevant literature (e.g., references in Lee et al. 2017). As the coral skeleton is made of $CaCO_3$, the radiocarbon of its aragonite mineral has been exploited to observe its concentration on the surface of the ocean. For example, a coral collected from Langkai in the Indonesian Throughflow area showed that pre-bomb (1870–1955) concentration was ~−56.5‰ and it began to slowly increase in February 1955 and jumped to −7.2‰ in July 1955. Subsequently, $\Delta^{14}C$ values decreased until October 1957 after which time they slowly rose to reach their maximum of 163.3‰ in January 1974. The strong $\Delta^{14}C$ seasonal cycle (15–65‰) was attributed to variations in the ^{14}C of surface waters passing the coral in Makassar Strait due to the seesaw effect of the regional monsoon (Fallon and Guilderson 2008). Fallon and Guilderson were able to resolve a complicated North Pacific water intrusion during the summer NW Monsoon using time series distribution of radiocarbon recorded in the coral. Glynn et al. (2013) were able to estimate the traveling time of water mass from the Bikini Atoll to Palau via NEC and NECC over 5000 km for about 90 days using $\Delta^{14}C$ concentration recorded about 3 months after the Bikini Atoll thermonuclear detonation in 1954 in a coral collected from Palau Island where trade winds prevail. In much further south in the Solomon Sea, the post-bomb maximum occurs much later in 1985 with a value of much reduced 117‰ (Guilderson et al. 2004). High-resolution radiocarbon analyses on a coral skeleton from Guam also allowed us to identify three high-yield thermonuclear testings in the Pacific Proving Grounds at Bikini and Enewetak atolls in 1954, 1956, and 1958 (Andrews et al. 2016). A 600-year-old coral colony *Enallopsammia rostrata* living at 1410 m depth off Bermuda was also utilized to estimate the mixing timescale (~25 years) between the surface water and 1400 m deep water by analyzing the bomb-produced ^{14}C recorded in their skeletons (Lee et al. 2017).

6.6.4 Nitrogen (N) Isotopes

Nitrogen has two stable isotopes of ^{14}N (99.6%) and ^{15}N (0.4%) in nature (Meija et al. 2016a). The isotope composition is usually expressed as in Eq. (6.47).

$$\delta^{15}\mathrm{N} = \left({}^{15}\mathrm{N}/{}^{14}\mathrm{N}_{\mathrm{sample}}/{}^{15}\mathrm{N}/{}^{14}\mathrm{N}_{\mathrm{standard}} - 1\right) \times 10^{3}. \quad (6.47)$$

The standard material is usually taken as the atmospheric N_2 as it is isotopically homogeneous within current analytical uncertainty (Brand et al. 2014). The nitrogen fixed by coral algae is rapidly incorporated into coral (animal) tissue as well as an organic matrix (SOM) in the coral skeleton. Stable nitrogen isotope ratios in coral skeletal organic matrix, $\delta^{15}N_{\mathrm{coral}}$, for modern symbiotic corals taken from the Pacific, Atlantic oceans, and Red Sea, are 2.6 ∼ 6.6‰, 3.0‰ ∼ 7.6‰, 2.2‰ ∼ 6.6‰ in zooxanthella, animal tissue, and SOM, respectively (Table 6.2). In non-symbiotic species, $\delta^{15}N_{\mathrm{coral}}$ were found to be 7.0–10.1‰ and 9.9–15.5‰, respectively (Muscatine et al. 2005). In a symbiotic coral, there is no indication of trophic enrichment in $\delta^{15}N_{\mathrm{coral.}}$

Therefore, the nitrogen isotope of this SOM ($\delta^{15}N_{\mathrm{coral}}$) has the potential to record the origin of nitrogenous nutrients with their own nitrogen isotope compositions. $\delta^{15}N_{\mathrm{coral}}$ varies with that of nitrogenous sources. Reef-corals take up both inorganic N through zooxanthellae, organic nitrogen in the form of a particle and dissolved organic nitrogen produced by zooplankton, or other animals in the ambient water, and nitrogen fixed by symbiotic cyanobacteria within the coral. In general, the $\delta^{15}N_{\mathrm{coral\ skeleton}}$ in symbiotic corals is similar to those in algae and animal tissue. In the river-influenced coral reef, $\delta^{15}N_{\mathrm{coral\ skeleton}}$ decreased from +8.6‰ to +3.0‰ that are close to the variation of seawater nitrate that decreased from + 8.3‰ to + 2.9‰ (Yamazaki et al. 2011). Wang et al. (2015) also found that δ^{15}N in the coral skeletal organic matrix is dictated by its zooxanthellae. Yamazaki et al. also found that $\delta^{15}N_{\mathrm{coral\ skeleton}}$ of the corals in the tropical (Okinotori Is., 20 °N, 137 °E), subtropical (Ishigaki Is., 24 °N, 124 °E), and temperate regions (Koshiki Is., 31 °N, 129 °E) was about + 2.5‰, +3.4‰, and +8.3‰, respectively. These differences in $\delta^{15}N_{\mathrm{coral\ skeleton}}$ were attributed to the fact that corals take nitrogen from N_2 fixation (δ^{15}N −2–0‰) in the nitrate-depleted tropical ocean surface, but surface ocean nitrate becomes enriched where it is away from the subtropics to the temperate waters in the Northwest Pacific Ocean.

Sub-surface water nitrate δ^{15}N is also recorded in the corals growing at the surface ocean, and this feature was utilized to estimate the upwelling events, monsoonal events, and mixed layer depth variation with time and long-term ocean variation, such as the North Atlantic Oscillation (Wang et al. 2016, 2018). In the South China Sea, the decrease in δ^{15}N values of sea surface nitrate due to the input of the ^{15}N depleted anthropogenic atmospheric nitrogen ($\delta^{15}N = \sim-2.7‰$) was estimated based on the reduction of $\delta^{15}N_{\mathrm{coral\ skeleton}}$ as much as + 1.3 ‰ from + 7.6 ± 0.4 ‰ in the period of 1968–1977 to + 6.3 ± 0.5 ‰ in the period of 2003–2012 (Ren et al. 2017). Ren et al. were able to estimate that atmospheric N input accounted for 20 ± 5 % of the total input to the surface of the northern South China Sea as well as the seasonal variation of atmospheric N input to the northern South China Sea during the last 40 years. Waste discharge from the adjacent land was also reflected in skeletons of corals living downstream (Sherwood et al. 2010; Abaya et al. 2018). In the case of the heterotrophic lifestyle coral such as deep-sea coral that does not take food from the symbiotic algae, about 3‰ enrichment between the δ^{15}N food (4–5‰) and animal tissue (7–8‰) was observed. For example, *Cladocora caespitosa* in the Mediterranean Sea showed a similar enrichment factor in $\delta^{15}N_{\mathrm{coral\ skeleton}}$ between the two consecutive trophic levels in other marine ecosystems (Ferrier-Pagès et al. 2011). Therefore, if heterotrophy exceeds autotrophy in coral due to unfavorable environmental conditions for symbiotic algae, e.g., adverse light, turbidity, or temperature, greater deviation from δ^{15}N values of seawater nitrogen sources is expected (Wang et al. 2016). As deep-sea corals (non-symbiotic heterotrophic coral) feed on the organic nitrogen falling from the surface layer of the ocean, δ^{15}N of coral skeleton organic matrix has been used to reconstruct N export fluxes over time, and to trace variation of δ^{15}N value of shallow subsurface nitrate that fueled new production at the sea surface mixed layer (Wang et al. 2014). Additionally, the large difference in $\delta^{15}N_{\mathrm{coral\ skeleton}}$ values between symbiotic corals and non-symbiotic corals allows us to use it as a proxy for distinguishing the existence of photosymbiosis for unknown fossil corals (Muscatine et al. 2005).

6.6.5 Oxygen (O) Isotopes and Carbonate Clumped Isotopes

Oxygen has three stable isotopes, ^{16}O, ^{17}O, and ^{18}O, with isotopic abundances of 99.76%, 0.04%, and 0.20% in nature. The ^{18}O/^{16}O ratio is commonly used for its isotopic composition and described in Eq. (6.48).

$$\delta^{18}\mathrm{O} = \left({}^{18}\mathrm{O}/{}^{16}\mathrm{O}_{\mathrm{sample}}/{}^{18}\mathrm{O}/{}^{16}\mathrm{O}_{\mathrm{standard}} - 1\right) \times 10^{3}. \quad (6.48)$$

The standard material is usually taken as VSMOW, VPDB, and air O_2 for water, carbonates, and gas (Brand et al. 2014). Because δ^{18}O of carbonate is usually reported relative to VPDB (Vienna Pee Dee Belemnite), $\delta^{18}O_{\mathrm{aragonite}}$ values can be converted from VPDB to VSMOW values as following (Eq. 6.49).

Table 6.2 Stable carbon and nitrogen isotopes in symbiotic and non-symbiotic corals (taken from Muscatine et al. 2005)

Isotopes	Coral	Symbiotic coral	Non-symbiotic coral
$\delta^{13}C$	Algae	−13.84 ± 2.02‰	–
	Animal tissue	−16.53 ± 2.22‰	−20.30 ± 0.83‰
	Skeletal organic matrix	−24.31 ± 5.60‰	−26.08 ± 5.52‰
$\delta^{15}N$	Algae	4.35 ± 1.23‰	–
	Animal	4.56 ± 1.40‰	8.08 ± 1.23‰
	Skeletal organic matrix	4.09 ± 1.51‰	12.08 ± 1.81‰

$$\delta^{18}\mathrm{O}_{\mathrm{VSMOW}} = 1.03091 \times \delta^{18}\mathrm{O}_{\mathrm{VPDB}} + 30.91. \qquad (6.49)$$

Oxygen Isotope Ratio ($\delta^{18}O$)

The development of the oxygen isotope paleothermometer by McCera, Epstein, Urey, and other pioneers in the late 1940s is one of the most important achievements in Earth sciences by providing a new and powerful tool to study the complex climate history of the Earth as shown in Sect. 6.5. The oxygen isotope temperature scale has been constantly refined over time, and until these days it remains a key proxy in paleoclimatology (Schmid and Bernasconi 2010). The basic idea is that the fractionation of oxygen isotopes, $\delta^{18}O$, between coral aragonite and seawater is a function of temperature and this difference in the $\delta^{18}O$ values of aragonite and seawater can be used for determining the temperatures of the ambient seawater at the time the coral accredited its skeleton. The utility of the oxygen isotope as a proxy for temperature depends on the temperature sensitivity of the isotope exchange reactions (Eq. 6.50).

$$\mathrm{H_2{}^{18}O + CaC^{16}O^{16}O^{16}O = H_2{}^{16}O + CaC^{18}O^{16}O^{16}O} \qquad (6.50)$$

The equilibrium constant for this reaction decreases with increasing temperature. Therefore, the temperature of the carbonate formation can be determined if (i) an equilibrium isotopic signature is acquired during crystallization and subsequently retained, (ii) $^{18}O/^{16}O$ ratios of carbonate minerals can be measured with sufficiently accurate and high precision, (iii) the equilibrium isotopic fractionation between carbonate and water as a function of temperature is known, and (iv) the $^{18}O/^{16}O$ ratio of the parent water that the carbonate precipitated from is known. This last condition is often not met (Schauble et al. 2006). Seawater $\delta^{18}O$ value has been increased from −8‰ in the Cambrian to a present value of about 0‰ with short-term variations in cold and glaciation periods (Veizer et al. 1999). Modern surface ocean $\delta^{18}O$ value is subject to evaporation and precipitation and mixing with ocean waters of differing $\delta^{18}O$ values. Wang et al. (2013a) suggested strong depletion of ^{18}O to occur in coral skeleton at the time of calcification. Therefore, oxygen isotope fractionation between aragonite and seawater should be regarded also as a function of pH, salinity, and temperature of the calcifying fluid. The oxygen fractionation factor (αaragonite-water) between aragonite and water was experimentally assessed to be dependent on the temperature (Kelvin, T) at the time of precipitation of aragonite, and their relation is given by Kim et al. (2007) in Eq. (6.51).

$$1000\ \ln\left(\alpha_{\text{aragonite-water}}\right) = 17.88 \pm \left(10^3/T\right) - 31.14 \pm 0.46, \qquad (6.51)$$

$$\alpha_{\text{aragonite-water}} = \left(1000 + \delta^{18}\mathrm{O}_{\text{aragonite}}\right)/\left(1000 + \delta^{18}\mathrm{O}_{\text{water}}\right),$$

where $\delta^{18}O_{\text{aragonite}}$ (‰) is the $\delta^{18}O$ of the aragonite (relative to VSMOW-Vienna Standard Mean Ocean Water) and $\delta^{18}O_{\text{water}}$ (‰) is the $\delta^{18}O$ of the seawater (relative to VSMOW). $\delta^{18}O_{\text{coral skeleton}}$-based coral paleothermometry has been exploited several decades at tropical sites; however, a close examination of $\delta^{18}O_{\text{coral}}$ revealed that it is also influenced by coral biology (vital effect) in some cases. For example, coral health-related growth retardation was found to enrich more than ^{18}O in coral skeleton (Hayashi et al. 2013). $\delta^{18}O_{\text{coral}} - T$ (°C) relationship is reported to be −0.196‰ per °C for *Diploria strigosa* (Felis et al. 2015) and −0.08 to −0.22‰ per °C for *Porites australiensis* (Hayashi et al. 2013) and −0.179‰ per °C for *Porites lutea* (Gagan et al. 1998). A few site-specific examples are given here for exemplary cases.

$\delta^{18}O_{\text{coral}} = -(0.18 - 0.23) \times T + (0.35 - 1.13)$ (Okinawa, Hayashi et al. 2013)

$\delta^{18}O_{\text{coral}} = -(0.1514 \pm 0.01176) \times T + (9.801 \pm 0.2773)$ (Red Sea, Felis et al. 2004)

$\delta^{18}O_{\text{coral}} = -0.179 \times T + 0.146$ (Great Barrier Reef, Indian Ocean, Gagan et al. 1998)

Salinity of seawater has been also retrieved from the $\delta^{18}O$ of the coral skeleton as $\delta^{18}O$ of the coral skeleton also depends on the $\delta^{18}O_{\text{seawater}}$. As water evaporates from a parcel of water at sea to the air, water vapor takes preferentially lighter isotopes ^{16}O relative to heavier isotope ^{18}O, and the remaining solution becomes saltier and becomes enriched with heavier isotope. For a given parcel of water isolated from the sea, evaporation and precipitation will change salinity and its $\delta^{18}O_{\text{sw}}$ (Conroy et al. 2014). The variability of

$\delta^{18}O$ of precipitation may derive variability of the $\delta^{18}O_{seawater}$-salinity relationship. However, the seas and oceans have connected each other; changes in salinity and its $\delta^{18}O_{sw}$ are controlled by a combination of surface forcing (evaporation and precipitation), advection, and vertical mixing of offshore waters or groundwater discharge. The relative importance of each of these terms in shaping the spatiotemporal variability of $\delta^{18}O_{sw}$ should be site-specific. For example, the equation $\delta^{18}O_{seawater} = 0.31 \times \text{Salinity} - 10.38$ was derived from the surface mixed layer (0–75 m) of the central tropical Pacific (Conroy et al. 2014) and $\delta^{18}O_{seawater} = 0.24 \times \text{Salinity} - 8.03$ in the coastal waters of Okinawa (Hayashi et al. 2013). Gagan et al. (1998) attempted to reproduce the parent sweater $\delta^{18}O_{seawater}$ by utilizing Sr/Ca ratio that more faithfully follows thermodynamics in aragonite mineral formation. The difference in $\delta^{18}O_{coral}$ between the water temperatures derived from Sr/Ca and $\delta^{18}O_{coral}$ thermometers, residual signal, is given in Eq. (6.52).

$$\Delta\delta^{18}O = \partial\delta^{18}O/\partial T \times \left[T_{\delta^{18}O} - T_{Sr/Ca}\right], \tag{6.52}$$

where $\partial\delta^{18}O/\partial T$ is the empirically derived temperature-dependent oxygen isotope fractionation ($-0.18‰/°C$) for the *Porites* and the residual $\Delta\delta^{18}O$ value is the isotopic composition of seawater. Gagan et al. attributed the enrichment of $\delta^{18}O$ of 0.5 per mil to the enhanced ocean evaporation in the southwestern Pacific in response to the higher SST at the end of deglaciation (~ 5350 years ago). $\delta^{18}O$ and Sr/Ca thermometers were also applied to the case where depletion of ^{18}O of the coral skeleton occurs due to the heavy monsoonal rainfall in order to determine the variation in the timing of the rainy seasons (August–December, January–April, December–March, and August–December at around AD 487, 541 BC, 3011 BC, and 4789 BC, respectively) in the northern South China Sea during the middle to late Holocene (Deng et al. 2014). Where temperature change over a year is very little but precipitation varies greatly, then $\delta^{18}O_{coral}$ may be useful to retrieve the rainfall events (Morimoto et al. 2002). Morimoto et al. (2002) measured seawater $\delta^{18}O_{seawater}$ biweekly over 2 years as well as $\delta^{18}O_{coral}$ and temperature, and they obtained the Eqs. (6.53) and (6.54).

$$\delta^{18}O_{seawater}(‰\text{SMOW}) = 0.42 \times S - 14.3. \tag{6.53}$$

$$\delta^{18}O_{coral} = \delta^{18}O_{seawater}(‰\text{SMOW}) - 0.189 \times T(°C) - 0.12. \tag{6.54}$$

They estimated that coral $\delta^{18}O_{sewater}$ has more effect on $\delta^{18}O_{coral}$ than does temperature due to the formation of the stratified surface freshwater pool by the heavy rainfall near Palau. They also noted that local $\delta^{18}O_{seawater}$-salinity calibration was necessary to estimate paleo-salinity based on $\delta^{18}O_{coral}$. Although $\delta^{18}O_{coral}$ is a function of both water temperature and the net effect of precipitation and evaporation that influence seawater salinity, it primarily reflects water temperature where interannual variations in the net effect of precipitation and evaporation are small.

Triple Oxygen Isotopes

The ^{17}O anomaly ($\delta^{17}O$) of natural waters has been shown to be also sensitive to evaporation in a way analogous to deuterium excess, with evaporated bodies of water (e.g., leaf waters, lake waters, animal body waters) tending to have lower $\delta^{17}O$ than primary meteoric waters. Carbonates have the potential to record the triple oxygen isotope compositions of parent waters, allowing reconstruction of past water compositions, but such investigations had awaited high-precision measurement of $\delta^{17}O$ of carbonate. The overall analytical procedure to measure oxygen isotopes is (i) extraction of CO_2 from carbonate (coral) using acid, (ii) the reduction of CO_2 with hydrogen to yield water, and (iii) production of molecular oxygen via fluorination, and (iv) analyzing mass ratios of 34/32, and 33/32 of O_2 in a mass spectrometer, and (v) then normalization to standards applied (Passey et al. 2014). Passey et al. provided the application of three oxygen isotopes as a proxy to carbonate deposits. The following materials are largely taken from them. The triple oxygen isotope deviation from an expected trend λ_{ref} (commonly referred to as triple oxygen isotope “anomaly”) may be defined as Eq. (6.55).

$$\Delta^{17}O \equiv \delta'^{17}O - \lambda_{ref}\delta'^{18}O, \tag{6.55}$$

where $\delta \equiv (R_{sample}/R_{standard} - 1) \times 10^3$, where R stands for the ratio between water containing heavy isotopes ($H_2{}^{17}O$, $H_2{}^{18}O$, or HDO) and $H_2{}^{16}O$. In dealing with high-precision ratios in multiple isotope systems, a modified δ, delta prime δ’, is defined as Eq. (6.56).

$$\delta' \equiv \ln(\delta + 1) = \ln\left(R_{sample}/R_{standard}\right) \tag{6.56}$$

Passey et al. chose λ_{ref} as 0.528, the trend of the global meteoric water line. This definition of $\Delta^{17}O$ is equivalent to the “^{17}O-excess” used by students working triple oxygen isotopes in meteoric waters. “Delta prime” values are defined as Eq. (6.57).

$$\delta'^{x}O \equiv \ln\left(R_{sample}/R_{standard}\right), \tag{6.57}$$

where R_{sample} and $R_{standard}$ refer to $^{x}O/^{16}O$ ratios of samples and standards, respectively, and x is 18 or 17. And the parameter in relating two samples *a* and *b* may be defined as Eq. (6.58).

$$\lambda \equiv \ln\left({}^{17/16}R_a/{}^{17/16}R_b\right)/\ln\left({}^{18/16}R_a/{}^{18/16}R_b\right). \tag{6.58}$$

The three-isotope fractionation exponent has been defined as Eq. (6.59).

$$\theta_{a-b} \equiv \ln\left({}^{17/16}\alpha_{a-b}\right)/\ln\left({}^{18/16}\alpha_{a-b}\right), \tag{6.59}$$

where α_{a-b} is the fractionation factor ($= R_a/R_b$) between the two phases that exchange isotopes with each other. Although θ and λ are mathematically equivalent, that θ is generally reserved for simple processes including fractionation between two phases. Δ, *δ'*, and *δ* values are expressed in per mil (‰) multiplied by 10^3. The triple oxygen isotope composition of carbonate minerals should primarily reflect the triple oxygen isotope compositions of their parent waters. The $\delta^{17}O$ and $\delta^{18}O$ values of modern-day global ocean water (the Atlantic and Pacific oceans and the Mediterranean and Red seas) vary from −0.225 to 1.276‰ and from −0.236 to 2.426‰, respectively (Luz and Barkan, 2010).

Carbonate Clumped Isotope Thermometry (Δ_{47})

An internal isotopic ordering (clumping) reaction to form ${}^{13}C^{18}O^{16}O_2{}^{2-}$ in carbonate minerals was utilized to get the temperature of the formation (Eiler 2011; Fernandez et al. 2017). The following are taken from Schauble et al. (2006). Aragonite mineral is a molecular crystal containing separate $CO_3{}^{2-}$ groups with strong internal C–O bonds bound to the crystal lattice by weaker cation-oxygen (Ca^{2+}–O) bonds. The isotopic “clumping” reactions involve the exchange of ^{13}C, ^{18}O, and ^{17}O between carbonate molecules in the crystal lattice (Eqs. 6.60 and 6.61) and result in a distribution of singly and multiply substituted species (isotopologues).

$$\begin{aligned}&{}^{12}C^{18}O^{16}O_2{}^{2-} + {}^{13}C^{16}O_3{}^{2-}\\ &\quad = {}^{13}C^{18}O^{16}O_2{}^{2-} + {}^{12}C^{16}O_3{}^{2-}\end{aligned} \tag{6.60}$$

$$\begin{aligned}&{}^{12}C^{17}O^{16}O_2{}^{2-} + {}^{12}C^{18}O^{16}O_2{}^{2-}\\ &\quad = {}^{12}C^{18}O^{17}O^{16}O + {}^{12}C^{16}O_3{}^{2-}\end{aligned} \tag{6.61}$$

The above two reactions differ from the water-carbon dioxide oxygen isotope exchange reaction as all the exchange components are present in one mineral phase. That makes the equilibrium constant an internal property that is not affected by the isotopic compositions of other phases in the system. The multiply substituted isotopologues ${}^{13}C^{18}O^{16}O_2{}^{2-}$ and ${}^{12}C^{18}O^{17}O^{16}O$ contribute ~96% and 3% of the mass-47 signal in CO_2 generated by phosphoric acid digestion, respectively. Because the total zero-point energy of the right-hand side is lower than that of the left-hand side at equilibrium, multiply heavy isotopes substituted isotopologues of ${}^{13}C^{18}O^{16}O_2{}^{2}$ and ${}^{12}C^{18}O^{17}O^{16}O$ exist in excess about ~0.4‰ and ~0.1‰, respectively, at room temperature. The equilibrium constants decrease with increasing temperature. The predicted temperature sensitivity of $K_{eq}[3866]$ is ~0.003‰/°C at 25 °C (Schauble et al. 2006). [3866] is a shorthand notation indicating the doubly substituted species, ${}^{13}C^{18}O^{16}O_2{}^{2-}$. The abundance of the doubly substituted CO_2 isotopologue ${}^{13}C^{18}O^{16}O$ in CO_2 produced by phosphoric acid digestion of biogenic aragonite is proportional to the concentration of ${}^{13}C$–${}^{18}O$ bonds in it, and the concentration of these bonds is a function of the temperature of carbonate growth. Evolved CO_2 is analyzed in a dual inlet mass spectrometer with the simultaneous collection of ion beams corresponding to masses 44–49. The mass 47 beams are composed of ${}^{13}C^{17}O^{17}O$, ${}^{12}C^{17}O^{18}O$, and predominantly ${}^{13}C^{18}O^{16}O$. R^{47} is defined as the abundance of mass 47 isotopologues divided by the mass 44 isotopologue (Huntington et al. 2009; Thiagarajan et al. 2011) in Eq. (6.62).

$$R^{47} = \left[{}^{13}C^{17}O^{17}O + {}^{12}C^{17}O^{18}O + {}^{13}C^{18}O^{16}O\right]/\left[{}^{12}C^{16}O^{16}O\right]) \tag{6.62}$$

$$\begin{aligned}\Delta_{47} = \Big[&\left(R^{47}{}_{\text{measured}}/R^{47}{}_{\text{Stochastic}} - 1\right)\\ &-\left(R^{46}{}_{\text{measured}}/R^{46}{}_{\text{Stochastic}} - 1\right)\\ &-\left(R^{45}{}_{\text{measured}}/R^{45}{}_{\text{Stochastic}} - 1\right)\Big] \times 1000.\end{aligned} \tag{6.63}$$

Δ_{47} is the difference per mil between the measured 47/44 ratio of the sample and the 47/44 ratio expected for that sample if its stable carbon and oxygen isotopes were randomly distributed among all isotopologues. Kelson et al. (2017) provided the relationship between clumped isotopes of carbonate and temperature in Eq. (6.64).

$$\begin{aligned}\Delta_{47}(‰) = {}&(0.0417 \pm 0.0013) \times 10^6 \times T(°\text{K})^{-2}\\ &+ (0.139 \pm 0.014)\end{aligned} \tag{6.64}$$

This thermometer has an ideal precision of ±2 °C (Ghosh et al. 2006) but can be improved as much as ± 1 °C (Thiagarajan et al. 2011). Saenger et al. (2012) confirmed strong temperature dependence on the carbonate clumped isotopes with temperature in *Porites* coral living in the Red Sea.

6.6.6 Fluorine (F)

Fluorine contents in coral (*Porites*, *Acropora*, and *Pocillopora* species) skeletons were reported to be 650–1300 μg/g, and F/Ca ratios were 3.4–7.0 (mmol/mol). Fluorine is incorporated into aragonite mineral through the following ion-exchange reaction (Eq. 6.65, Tanaka and Ohde 2010).

$$\mathrm{CaCO_3(s) + 2\,F^-(aq) = CaF_2(s) + CO_3{}^{2-}} \qquad (6.65)$$

And its equilibrium constants depend on the temperature and concentration of fluoride ion in seawater as well as the carbonate ion concentration.

6.6.7 Sodium (Na)

Sodium exists as both $NaSO_4{}^-$ and Na^+ in aragonite minerals. Na/Ca molar ratio in coral is about 15–24 mmol/mol and much higher than Sr/Ca (8–10 mmol/mol), S/Ca (4–10 mmol/mol), P/Ca (3–7 mmol/mol), and Mg/Ca (2.5–6.5 mmol/mol) ratios (Mitsuguchi et al. 2010). The correlation between the Na/Ca ratios and the water temperature was relatively poor ($R^2 = 0.34$) than that of the Sr/Ca and Mg/Ca ratios (Bell et al. 2017). The majority (~90%) of Na is present in the aragonite skeleton and the rest being in the organic matrix, and Na/Ca in coral is not related to that of the concentration in seawater (Rollion-Bard and Blamart 2015). Na is enriched in the rapid aragonite accretion zone in the skeleton, and therefore it exhibits a large intra-skeletal variation (Rollion-Bard and Blamart 2015). Mitsuguchi et al. suggested that the primary mechanism for the incorporation of Na, S, and Mg into coral skeleton is the ion incorporation into lattice defects and distortions and/or ion adsorption.

6.6.8 Magnesium (Mg) and Magnesium Isotopes

Thermodynamic calculations and inorganic precipitation experiments indicate a strong relationship between aragonite Mg/Ca and water temperature. And the empirical evidence of the increasing trend of the mole ratio of Mg/Ca in the coral skeleton with ambient water temperature has been applied to fossil coral specimens to reconstruct past ocean temperature. For example, Reynaud et al. (2007) found the following relation between water temperature and Mg/Ca in the coral skeleton by cultivating *Acropora* sp. in water tanks (Eq. 6.66).

$$\mathrm{Mg/Ca(mmol/mol)} = 0.138 \times T(^\circ\mathrm{C}) + 0.898\left(R^2 = 0.98\right). \qquad (6.66)$$

However, Reynaud et al. also found that Mg/Ca ratio in coral *Acropora* sp. skeleton increased with temperature from about 3.8 at 21 °C to about 4.9 at 29 °C and increased with light intensity from below 4.5 at a light intensity of 100–200 μmol photons m^{-2} s^{-1} to about 4.9 at 400 μmol photons m^{-2} s^{-1}. As the calcification rate increases with both temperature and light intensity, the Mg/Ca ratio remained in the coral skeleton which reflects both the water temperature and solar radiation at the time of coral skeletal formation. Wei et al. (2000) found that Mg/Ca ratio did also highly correlate ($r = 0.97$) with the water temperature in corals living in the coastal waters, *Porites lutea*, subject to extreme high runoff, in Sanya Bay of Hainan Island in the South China Sea.

The underlying assumption of Mg paleothermometry is that Mg^{2+} exchanges for Ca^{2+} within the carbonate lattice and that its substitution is temperature-dependent in a manner that can be modeled consistently by inorganic partitioning between aqueous fluids and solids. However, Mg was found to be not in aragonite mineral but hosted by a disordered Mg-bearing material or hosted in organic materials or as a highly disordered inorganic phase, e.g., a nanoparticulate form of Mg carbonate or hydroxide (Finch and Allison 2008). In contrast to aragonite biomineral, Mg in the calcite biomineral, e.g., foraminifera calcite, was found to be uniformly substituted for Ca within the calcite mineral lattice (Branson et al. 2013). It is also noted that intra-skeleton variability of Mg/Ca mole ratio between theca wall (2.938 mmol/mol) and center of calcification (3.884 mmol/mol) was observed in deep-sea coral *Lophelia pertusa* from Little Galway Mound at the water depth of 881 m (Raddatz et al. 2013). NanoSIMS analyses revealed a significant (50~100%) variation in Mg/Ca elemental ratios in the coral skeleton across the micron meter scale layered fibrous ultrastructure (Reynaud et al. 2007). It is also noted that the temperature dependencies of elemental ratios in the coral skeleton are highly variable among individual corals (Gaetani et al. 2011).

Mg Isotopes

Magnesium has three isotopes of ^{24}Mg (78.881 %), ^{25}Mg (9.988%), and ^{26}Mg (10.960%) in the natural environment (Meija et al. 2016a). The magnesium isotope composition is usually given as δ^{25}Mg and δ^{26}Mg (Eqs. 6.67 and 6.68).

$$\delta^{26}\mathrm{Mg} = \left(\left({}^{26}\mathrm{Mg}/{}^{24}\mathrm{Mg}_{\mathrm{sample}} / {}^{26}\mathrm{Mg}/{}^{24}\mathrm{Mg}_{\mathrm{standard}} \right) - 1 \right) \times 10^3 \quad (6.67)$$

$$\delta^{25}\mathrm{Mg} = \left(\left({}^{25}\mathrm{Mg}/{}^{24}\mathrm{Mg}_{\mathrm{sample}} / {}^{25}\mathrm{Mg}/{}^{24}\mathrm{Mg}_{\mathrm{standard}} \right) - 1 \right) \times 10^3 \quad (6.68)$$

For standard material, DSM3, a standard of 10 g of pure Mg metal from the Dead Sea Metal Company, dissolved in one liter of 0.3 N HNO_3 is widely used, and modern seawater or SRM3131a from NIST has been also used. $\delta^{25}\mathrm{Mg}_{\mathrm{DSM}}$ and $\delta^{26}\mathrm{Mg}_{\mathrm{DSM}}$ of modern seawater (Woods Hole seawater) are -0.43 ± 0.01‰ and -0.82 ± 0.01 ‰, respectively (Foster et al. 2010). Coral skeletal standard material is made of aragonite coral (*Porites* sp.); JCp-1, exhibits $\delta^{26}\mathrm{Mg}_{\mathrm{DSM}}$ of -1.03 ± 0.02‰ (Hippler et al. 2009). Isotope fractionation theory predicts equilibrium isotope fractionation factors should have a linear relationship with $1/T$(°K) at low temperatures and are independent of experimental conditions other than temperature. Fractionations among the three stable isotopes of Mg are expected to arise from physical, chemical, and biological processes partly due to their relatively large mass differences. The fractionation factor of Mg isotopes between carbonate mineral and solution ($\alpha_{\mathrm{carb\text{-}sol}}$) is defined using the standard notation in Eq. (6.69) where x is 25 or 26.

$$\begin{aligned}(\alpha_{\mathrm{carb\text{-}sol}}) &= \left({}^{x}\mathrm{Mg}/{}^{24}\mathrm{Mg}\right)_{\mathrm{carb}} / \left[{}^{x}\mathrm{Mg}/{}^{24}\mathrm{Mg}\right]_{\mathrm{sol}} \\ &= (1000 + \delta^{x}\mathrm{Mg}_{\mathrm{carb}})/(1000 + \delta^{x}\mathrm{Mg}_{\mathrm{sol}}). \quad (6.69)\end{aligned}$$

Because $\alpha_{\mathrm{carb\text{-}sol}}$ is close to unity, there is precedence for expressing Mg isotope fractionation $\Delta^{x}\mathrm{Mg}$ between carbonate and solution (Saenger and Wang 2014) in Eq. (6.70).

$$\Delta^{26}\mathrm{Mg}_{\mathrm{carb\text{-}sol}} = \delta^{26}\mathrm{Mg}_{\mathrm{carbonate}} - \delta^{26}\mathrm{Mg}_{\mathrm{solution}}. \quad (6.70)$$

The Mg isotope fractionation (^{26}Mg and ^{24}Mg) factors were observed to be well correlated with a temperature between aragonite and seawater (Wang et al. 2013b) in Eq. (6.71).

$$\begin{aligned}\Delta^{26}\mathrm{Mg}_{\mathrm{carb\text{-}sol}} &= 1.67(\pm 0.36) \\ &\quad - 0.82((\pm 0.11) \times 1000/T(^\circ\mathrm{K}) \quad (6.71)\end{aligned}$$

Values of $\delta^{26}\mathrm{Mg}_{\mathrm{carbonate}}$ of *Porites lutea* were found to observe this equation, and considering the current analytical uncertainty of ~0.02‰, $\Delta^{26}\mathrm{Mg}_{\mathrm{carb\text{-}sol}}$ and temperature relationship could resolve SST variability within ±3–4 °C. Therefore, it was utilized to monitor annual SST cycles in tropical and subtropical oceans (Wang et al. 2013b). Also, knowledge of seawater δ^{26}Mg variability over long timescales or in specific environments could be important for constraining variables affecting Mg cyclings such as continental weathering, dolomitization, and hydrothermal activity (Saenger and Wang 2014).

6.6.9 Phosphorus (P)

Skeletal P/Ca ratios in the tropical surface zooxanthellate corals are about 6–65 μmol/mol. Corals incorporate P from seawater in their skeletons as both anionic substitution of biphosphate ($HPO_4{}^{2-}$) for carbonate ion ($CO_3{}^{2-}$) and organic phases. The majority of P occurs as phosphate defects and occurs in crystalline hydroxyapatite inclusions that were revealed by solid-state NMR spectroscopy (Mason et al. 2011). P was also found to be largely present as organic phase (>60%) in *Pavona gigantea* (LaVigne et al. 2008). Particulate matter in seawater was also suggested to be adsorbed or trapped in the surface of microporous structures in skeletons (Chen and Yu 2011). The distribution coefficient, $(\mathrm{P/Ca})_{\mathrm{sample}}/(\mathrm{P/Ca})_{\mathrm{seawater}}$, is reported to be about 1.5 for Bermuda *Montastraea annularis* coral (Dodge et al. 1974). LaVigne et al. (2010) compared skeletal P/Ca in colonies from geographically distinct oceanic nutrient regimes with respect to their seawater phosphate ($\mathrm{PO}_{4\ \mathrm{SW}}$) concentration, and they found a species-specific strong linear correlation as shown in Eqs. (6.72) and (6.73).

$$\begin{aligned}P/\mathrm{Ca}_{\mathrm{Porites\ lutea}}&(\mu\mathrm{mol/mol}) \\ &= 31.9 \times [\mathrm{PO}_{4\mathrm{sw}}](\mu\mathrm{mol/kg}) + 5.12\left(r^2 = 0.93\right) \quad (6.72)\end{aligned}$$

$$\begin{aligned}P/\mathrm{Ca}_{\mathrm{Montastrea\ sp}}&(\mu\mathrm{mol/mol}) \\ &= 84.8 \times [\mathrm{PO}_{4\mathrm{sw}}](\mu\mathrm{mol/kg}) + 11.6\left(r^2 = 0.91\right) \quad (6.73)\end{aligned}$$

Chen and Yu (2011) reported that coral P/Ca was more related to the total P concentration than the reactive phosphate ion concentration in seawater in the coastal ocean. P/Ca ratio has been used to reconstruct the time variation of the ambient seawater PO_4 concentration and made it possible to infer sea surface temperature variation, upwelling (e.g., LaVigne et al. 2008), wave and wind at the sea surface, or input from the application of fertilizer in coastal land (Mallela et al. 2013).

6.6.10 Sulfur (S) and Sulfur Isotopes

Sulfur contents in the coral skeleton were reported to be about 0.7% for *Porites* (Tanaka and Ohde 2007). Sulfur appears to be substituted carbonate to form $CaSO_4$ based on the following reaction (Eq. 6.74).

$$CaCO_3(s) + SO_4{}^{2-}(aq) = CaSO_4(s) + CO_3{}^{2-}(aq) \quad (6.74)$$

In this reaction, the equilibrium constant is a function of both temperature and sulfate concentration. Sulfur identified via X-ray absorption near edge structure spectroscopy (XANES) in the skeletal organic matrix was in the form of three major amino acids (H–S–C bonds in cysteine; C–S–C bonds in methionine; one disulfide bond C–S–S–C bonds in cysteine) and a sulfated sugar (C–SO_4 bonds in chondroitin sulfate) (Cuif et al. 2003). Calcite coral (deep-sea coral, *Corallium rubrum*) skeleton contained about 0.3% S. It also exhibited Mg-rich band and S-rich band formed in spring to summer and in autumn to winter, respectively (Vielzeuf et al. 2013).

Sulfur Isotopes

Sulfur has four stable isotopes, ^{32}S, ^{33}S, ^{34}S, ^{36}S, whose percentage abundances are approximately 95.0%, 0.75%, 4.20%, 0.015%, respectively, in nature (Meija et al. 2016a). Isotope abundance variations are generally considered in terms of the abundance ratio of $^{34}S/^{32}S$ of the two principal isotopes (Eq. 6.75).

$$\delta^{34}S(‰) = \left(^{34}S/^{32}S_{sample}/^{34}S/^{32}S_{stanardard}\right) - 1) \times 10^3. \quad (6.75)$$

The generally used standard is troilite from the Canyon Diablo meteorite (Brand et al. 2014). The sulfur isotopic composition of coral skeleton was measured as a proxy for the composition of seawater sulfate and the redox balance of seawater as sulfate reduction to sulfide and subsequent formation of pyrite precipitation is linked via microbial metabolism to the global carbon and oxygen cycles. The relative size of the pyrite sink determines largely the isotopic composition of sulfur in seawater. Coral skeleton preserved in limestone formed at around 445 million years ago was found to have 4923 ppm of S and + 22.38‰ of $\delta^{34}S$ that is similar to the $\delta^{34}S$ value of seawater at that time (about +25‰) more depleted relative to the modern seawater value of 21.15‰ (Present et al. 2015).

6.6.11 Calcium (Ca) Isotopes

Calcium has six stable isotopes of ^{40}Ca (96.941%), ^{42}Ca (0.647%), ^{43}Ca (0.135%), ^{44}Ca (2.086%), ^{46}Ca (0.004%), and ^{48}Ca (0.187%) in nature (Meija et al. 2016a). Due to easy measurement based on the abundance, $^{44}Ca/^{40}Ca$ are mostly determined and presented as Eq. (6.76), where the standard is usually modern seawater or NIST SRM 915a.

$$\delta^{44/40}Ca = \left(^{44}Ca/^{40}Ca_{sample}/^{44}Ca/^{40}Ca_{standard}\right) - 1) \times 1000 \quad (6.76)$$

Lighter Ca isotopes are preferentially incorporated into coral organs. They move more rapidly to the site of calcification', rapidly accredited zone (kinetic isotope effects), or non-biogenic precipitation zone than heavier isotopes. Consequently, the remaining seawater becomes enriched with heavier isotope ^{44}Ca. The $^{44}Ca/^{40}Ca$ ratios of cultured (*Acropora* sp.) and wild coral (*Pavona clavus* and *Porites* sp.) are positively correlated with growth temperature as shown in Eq. (6.77) (Böhm et al. 2006).

$$\delta^{44/40}Ca(‰, SRM915a) = (0.3 \pm 0.4) + (0.020 \pm 0.015) \times T(^\circ C)(R = 0.62) \quad (6.77)$$

However, Böhm et al. observed that the temperature dependence of Ca isotope fractionation in fast calcifying coral was significantly weaker than the slow precipitated inorganic aragonite. $\delta^{44/40}Ca$ values in modern and fossil (~161 million years old) coral skeletons are −1.24‰ to −1.01‰ relative to modern seawater and exhibit a systematic decrease in ^{44}Ca with increasing geological age. For example, coral skeletons formed in the Jurassic Period exhibit $\delta^{44/40}Ca$ of −2.16‰ which is about 1‰ lighter than that of modern corals, due to probably a vital effect of calcification (Gothmann et al. 2016).

6.6.12 Vanadium (V), Chromium (Cr), Manganese (Mn), Iron (Fe), Nickel (Ni), Copper (Cu), and Zinc (Zn)

Vanadium

Skeletal vanadium is presumably incorporated as oxyanion vanadate ($HVO_4{}^{2-}$) and has a distribution coefficient (V/Ca) of ~0.03 (Shen and Boyle 1987). Vanadium in coral skeleton was utilized to track oil pollution in the Caribbean as V is abundant (~300 ppm) in crude oil (Guzman and Jarvis 1996).

Chromium Isotopes

Naturally, four different isotopes of chromium of ^{50}Cr (4.35%), ^{52}Cr (83.79%), ^{53}Cr (9.50%), and ^{54}Cr (2.36%) exist in nature (Meija et al. 2016a). Chromium isotopic composition is usually reported relative to the certified SRM 979 (Brand et al. 2014) and expressed as Eq. (6.78).

$$\delta^{53/52}\mathrm{Cr}(‰) = \left[{}^{53}\mathrm{Cr}/{}^{52}\mathrm{Cr}_{\mathrm{sample}}/{}^{53}\mathrm{Cr}/{}^{52}\mathrm{Cr}_{\mathrm{SRM\ 979}} - 1\right] \times 10^3 \tag{6.78}$$

Crustal Cr (III)-bearing minerals release ^{53}Cr-enriched mobile Cr (VI) through oxidative weathering to the ocean as a form of chromate (CrO_4^-) oxyanion via rivers. Thus, modern seawater is more enriched with ^{53}Cr (+0.41‰ to +1.55‰) than the earth's crust (−0.12‰). Terrestrial Cr (III) oxidation occurs by reaction with manganese (Mn) oxides. Cr is incorporated into the lattice of carbonate minerals with no change in oxidation state. This redox-sensitive nature of chromium has been utilized to track the evolution of oxygen of the Earth (Gilleaudeau et al. 2016). Corals (*Siderastrea stellata*, *Porites* sp., and *Montastraea cavernosa*) contain about 0.04 to 0.07 ppm of Cr and exhibit about −0.06 to +1.9‰ of δ^{53}Cr values in the tropical South Atlantic (Pereira et al. 2015). Pereira et al. further suggested that Cr (VI) species in seawater is reduced to nontoxic Cr (III) in the endodermal layer containing zooxanthellae, and there, photoreduction of Cr (VI) is followed by efficient re-oxidation of isotopically light Cr (III) to Cr (VI) and preferential transport of isotopically lighter Cr (VI) species to the calcifying fluid where they are incorporated into the growing coral skeleton. Pereira et al. suggested also that this coral-specific feature could be used to reconstruct the Cr-isotope composition of the seawater in which these corals grow.

Manganese, Iron, Nickel, Copper, and Zinc

Mn/Ca molar ratios of the corals growing in the Gulf of California (*Pavona gigantean*, *Povona clivosa*, *Porites panamensis*) were about 10 ~ 42 nmol/mol and vary interannually (Carriquiry and Villasecusa 2010). They were higher during ENSO years than non-ENSO years because the relaxation of upwelling during ENSO increased the residence time of particulate-Mn in surface waters; thus, it allowed an increase in the photoreduction of particulate-Mn and the release of available Mn into the dissolved phase for incorporation into coral skeleton. An elevated level of Mn/Ca (0.0–16.21 μmol/mol) was observed in *Porites* sp. in Daya Bay, China (Chen et al. 2010). Chen et al. also reported that Fe/Ca and Zn/Ca ratios of skeletons of *Porites* sp. were 26–580 (μmol/mol) and 0.04–49.02 (μmol/mol), respectively. In Daya Bay, China, the Fe/Ca and Mn/Ca peaks corresponded to the terrestrial material inputs such as deforestation, blasting, flattening of the hilltops, and land leveling originated from a nuclear power plant construction at the coast. The increase in Zn concentration of coral skeleton over 1994–2007 was attributed to the chronic input of zinc from sewage discharge. In Sabah, Borneo, corals of *Hydnophora microconos*, *Favia speciosa*, and *Porites lobata* exhibited metal concentration of Mn (5–14 μg/g), Fe (11–64 μg/g), Ni (18–26 μg/g), Cu (6–11 μg/g), and Zn (2–6 μg/g) in their skeletons. The distribution coefficient was estimated to be for Mn (2.4–3.14), Fe (1.28–1.77), Ni (2.2–2.3), Cu (0.34–0.37), and Zn (4.6–5.2) (Mokhtar et al. 2012). The concentration of Zn in Daya Bay corals increased dramatically relative to the baseline value since 1994, and it corresponded well to the period of rapid local population increase and industrial development (Zn/Ca = 0.04 − 49.02 μmol/mol) (Chen et al. 2010).

6.6.13 Strontium (Sr) and Sr Isotopes

Sr/Ca Mole Ratio

Bivalent cations like Sr^{2+} substitute Ca^{2+} via an ion exchange reaction ($CaCO_3 + X^{2+} = XCO_3 + Ca^{2+}$) and are lattice bound within the aragonite. However, there is some controversy whether Sr^{2+} simply replaces Ca^{2+} in the aragonite lattice or resides in discrete strontianite ($SrCO_3$) domains. Sr^{2+} has a similar ionic radius to Ca^{2+} and may substitute for Ca^{2+} in Ca^{2+} transport mechanisms (Allison et al. 2010). Coral skeleton is believed to be precipitated extracellularly through the mediation of aboral tissue of calicoblastic epithelium. Extracellular precipitation necessarily invokes some calcifying fluid where precipitation occurs. By exposing live coral to the seawater medium inoculated with a stable isotope of Ca, Sr, and Ba and observing calcein fluorescence and ion images, Gagnon et al. (2012) suggested that cations are directly exchanged between the calcifying fluid and the ambient seawater. In deep-sea coral *Lophelia pertusa*, intra-skeleton variability of Sr/Ca was not observed between theca wall and center of calcification (Raddatz et al. 2013).

The partition coefficient of Sr/Ca was reported to be ~1.13 in aragonite. Strontium is the second most abundant co-precipitant next to Na in the coral skeleton (about 1 mol % of calcium). The incorporation of Sr into the lattice is regarded to be mainly temperature-dependent, but also controlled by the Sr/Ca composition of the ambient seawater. Additionally, biological and kinetic effects, as well as growth and calcification rates, affect the incorporation process. Besides Sr, other elements (e.g., Ba, Mn, Zn, Pb, Y) substituting Ca in the aragonite have the potential to provide sub-annual information on sediment flux and river runoff and pollution (Mertz-Kraus et al. 2009). The empirical evidence of the decreasing trend of the mole ratio of Sr/Ca in the coral skeleton with ambient water temperature has been applied to fossil coral specimens to reconstruct past ocean temperature (Eq. 6.79, Inoue et al. 2007).

$$\mathrm{Sr/Ca} = 10.31 - 0.057 \times \mathrm{T}(^{\circ}\mathrm{C}), r = -0.83; P < 0.01. \quad (6.79)$$

This Sr/Ca thermometer is employed under three assumptions: (i) temperature is the primary control on coral skeletal Sr/Ca uptake, and biological controls are negligible, (ii) the Sr/Ca content of seawater is constant on the time window of interest (e.g., glacial-interglacial timescales), and (iii) the Sr/Ca measurement should be accurate enough to resolve the targeted temperature difference (e.g., precision of <0.1% is equivalent to ~0.1 °C). The skeletal Sr/Ca appears to vary also with the rate of skeletal growth. Sr/Ca ratios of the coral colonly *Pavona clovus* in the Galapagos Islands were higher in slow extension rate coral (6 mm year^{-1}) than fast extension rate coral (14 mm year^{-1}) as much as 0.20 mmol/mol at the same temperature for the temperature range between 19 to 25 °C (de Villiers et al. 1995). On the other hand, Inoue et al. (2007) demonstrated, by culturing corals in thermostatic tanks (21 °C < T < 29 °C), there was no significant relationship between extension rate and Sr/Ca ratio in coral *Porites* spp. The temperature dependencies of Sr/Ca were reported to be 0.0283–0.0707 for various coral species in various marine areas (e.g., Armid et al. 2011; Bell et al. 2017). Reynaud et al. (2007) also proposed the second-order relationship (Sr/Ca (mmol/mol) $= 0.007 \times T^2 - 0.393 \times T + 14.807$, $r^2 = 0.97$ for *Acropora* sp.) than usual first-order relationship. About 130 ka old fossil corals recovered from the Caribbean island have been precisely dated using ^{230}Th/U method yielded to monthly resolution of variation of Sr/Ca derived temperature (Brocas et al. 2016). It should be also noted that the Sr/Ca ratio in the surface water of the ocean on latitudinal transects has been shown to vary by ~2% between 10 °S and 30 °N, which represents an uncertainty of 2–3 °C in the Sr/Ca thermometer (de Villiers et al. 1995). Sr/Ca analyses along synchronous growth transects produced three significantly different trends in Sr/Ca values and thus Sr/Ca-SST calibrations. The difference within the same reef was as much as 2 °C to 3 °C, even 20 m apart. Also, although the seasonal difference in SST was 3 °C at both sites, the seasonal difference in Sr/Ca values differed significantly (~40%). Zinke et al. (2015) have utilized Sr/Ca records to demonstrate that the sea surface temperature increases (marine heatwave) in the southeast Indian Ocean are caused by the Western Pacific Warm pool during strong La Niña periods.

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As the Sr/Ca concentration in seawater varies in different oceans and various unresolved issues whether Sr^{2+} simply replaces Ca^{2+} in the aragonite lattice or resides in discrete strontianite (SrCO$_3$) domains, and biological and kinetic effects, as well as growth and calcification rates, affect the incorporation process (reviewed in Mertz-Kraus et al. 2009), most students take a very prudent approach to consider site-specific relationship between coral skeletal chemical and isotopic compositions and environmental variables and all other circumstantial evidence to reconstruct paleotemperature away from sole dependency on Sr/Ca or other chemical or isotope proxies. It is noted that correlation "*a*" and "*b*" does not mean that there is a direct relationship of cause and effect involving both "*a*" and "*b*." Therefore, many detailed observations on coral calcification and incorporation of trace elements are being studied using newly developed observation and analytical tools to understand their cause-and-effect relationships.

It also should be noted that water temperature retrieved based on coral skeleton proxy (ies) is often expressed as sea surface temperature (SST) in the literature. Usually, SST refers to the state of the upper mixed layer of the ocean typically covering a few tens of meters thick. However, the depth distribution of temperature in the surface (mixed) layer is not invariant with depth. In tropical surface waters, coral grows at variable depths from just 1–11 m below sea surface or deeper depth relative to mean low tide level depending on species and location. Coral skeleton records water temperature at their growing depth. The temperature at the sea surface at zero-meter depth could be higher than at 2 m depth as much as 2 °C (thermal skin layer) at daytime and largely subject to solar radiation, wind speed, and mixing of the subsurface. In the Gulf of California, the water temperature difference between 4 and 6 m depth was observed to be about 1.0 °C (Ward et al. 2004, 2006). Therefore, attention should be given to the coral growing depth and depth profile of local hydrography to infer paleowater temperature from temperature proxy(ies) records in coral skeleton.

^{88}Sr/^{86}Sr

Strontium has four stable isotopes ^{84}Sr (0.56%), ^{86}Sr (9.86%), ^{87}Sr (7.00%) and ^{88}Sr (82.58%) in nature (Meija et al. 2016a). Among them, ^{87}Sr is produced from the ^{87}Rb

($t_{1/2} = 48.8 \times 10^{19}$ year) via radioactive decay. Its isotopic composition is usually expressed in Eq. (6.80).

$$\delta^{88/86}\mathrm{Sr} = \left({}^{48}\mathrm{Sr}/{}^{86}\mathrm{Sr}_{\mathrm{sample}}/{}^{48}\mathrm{Sr}/{}^{86}\mathrm{Sr}_{\mathrm{standard}} - 1\right) \times 1000 \qquad (6.80)$$

where standard material is NIST SRM 987.

The temperature dependence (0.033‰/°C) of $\delta^{88/86}$Sr in coral (*Pavona clavus*) is sixfold stronger than that of inorganically precipitated aragonite (0.005‰/°C) (Fietzke and Einsenhauer 2006). A nonlinear relationship between temperature and $\delta^{88/86}$Sr was found in tropical surface coral *Acropora* sp. (Krabbenhöft 2011) as shown in Eq. (6.81).

$$\delta^{88/86}\mathrm{Sr} = 0.001 \times T^2 - 0.039 \times T + 0.692,\ r^2 = 0.47 \qquad (6.81)$$

Similar temperature dependence of $\delta^{88/86}$Sr (0.026‰/°C) in deep-sea coral (*Lophelia pertusa*) was also found (Rüggeberg et al. 2008). Raddatz et al. (2013) found that there is a constant offset of −0.196‰ in cold coral compared to $\delta^{88/86}$Sr in seawater of 0.386‰; therefore, they suggested that the offset value may be used to infer the seawater values.

^{90}Sr

The concentrations for fallout ^{90}Sr radionuclide ($t_{1/2} = 28.79$ years) have been decreased substantially from the early 1960s to the present (Hong et al. 2011), and dissolved ^{90}Sr concentrations in surface waters of the Pacific and Indian Oceans were about 0.1–1.5 Bq/m^3 at the year 2000. The mean effective half-lives for ^{90}Sr were estimated to be 12–20 years (Povinec et al. 2005). Since there is no fractionation of ^{90}Sr/^{88} or ^{89}Sr in coral skeleton relative to its composition in seawater (Moore et al. 1973) and the Sr/Ca ratios in corals relative to seawater constant $K_{\mathrm{D(sr)}} = 1.040 \pm 0.008$ for *Montastraea annularis* (Benninger and Dodge 1986), ^{90}Sr activity concentrations in the annual bands faithfully reflect the ^{90}Sr activity concentration in the parent seawater. By comparing ^{90}Sr activity concentrations in the coral skeleton with the time between Bermuda and Florida corals, Purdy et al. (1989) found that coastal waters of the Florida Keys are fed with ^{90}Sr-incorporated particle-laden terrestrial runoff adjacent land, and the flux of the coastal waters varied seasonally due to the variable Loop Current intrusion. ^{90}Sr activity concentrations in corals up to 1979 from the Pacific and Indian Oceans (Galapagos, Oahu, Fanning, Tawara, Fiji, Tonga, Great Barrier Reef, Cocos, Mauritius) were also utilized to obtain an insight on the basin-scale ocean circulation including Indonesian Throughflow and El Niño events (Toggweiler and Trumbore 1985).

6.6.14 Yttrium

Yttrium is incorporated into the suspended sediments in the river and desorbs from the suspended sediments in a low-salinity estuarine environment, and then mixes conservatively along the freshwater-seawater salinity gradient in the coastal ocean, therefore, it can be utilized as a tracer for the input of terrestrial material into the sea. Y/Ca in the Fajardo coral (*Montastraea faveolata*) were from 1.04×10^{-3} to 0.41 µmol/mol and varied seasonally and interannually within the amount of river discharge over fifty years (Moyer et al. 2012).

6.6.15 Molybdenum (Mo) Isotopes

Molybdenum (Mo) has six naturally occurring stable isotopes of ^{92}Mo (14.6%), ^{94}Mo (9.2%), ^{95}Mo (15.9%), ^{96}Mo (16.7%), ^{97}Mo (9.6 %), and ^{98}Mo (24.3%) and one radioactive isotope, ^{100}Mo (9.7%) (natural abundance in parentheses) in nature (Meija et al. 2016a): ^{100}Mo is a singly occurring primordial radioactive isotope ($t_{1/2} = {\sim}7 \times 10^{18}$ year). Mo isotopic data are generally reported in terms of $\delta^{98/95}$Mo (Eq. 6.82).

$$\delta^{98/95}\mathrm{Mo}(‰) = \left[\left({}^{98}\mathrm{Mo}/{}^{95}\mathrm{Mo}\right)_{\mathrm{sample}}/\left({}^{98}\mathrm{Mo}/{}^{95}\mathrm{Mo}\right)_{\mathrm{standard}} - 1\right] \times 10^3 \qquad (6.82)$$

There is no internationally accepted reference material available yet, but NIST SRM 3134 has been widely used (Brand et al. 2014). Mo is highly soluble and unreactive under oxic conditions but is easily incorporated into sediments under highly euxinic conditions; therefore, Mo is increasingly used as a proxy for changing redox conditions in the oceans. In the modern oxic oceans, Mo is present as the conservative oxyanion molybdate ($\mathrm{MoO_4}^{2-}$) at relatively high concentrations (~10^7 nmol/kg). The modern open-ocean seawater is enriched with heavy isotopes ($\delta^{98/95}\mathrm{Mo}_{\mathrm{SRM\ 3134}} = +2.34$‰) relative to the dominant input from rivers ($\delta^{98/95}\mathrm{Mo}_{\mathrm{SRM\ 3134}} = +0.7$‰). This seawater enrichment is attributed to the isotopic fractionation (−3‰) in the slow Mo adsorption on particulate manganese oxides under widespread oxic conditions and the Mo deposition in euxinic conditions (0 to −0.7‰) (Chen et al. 2015). Therefore, Mo isotopic composition is useful to track the redox conditions of the oceans. Coral samples taken from Bahamas and Florida showed Mo concentration of about 0.02 ppm and their $\delta^{98/95}$Mo values of about + 2.00 to +2.19‰ that is slightly lighter than the modern mean oxic ocean (Voegelin et al. 2009). This could mean that MoO_4^{2-} in oxic seawater is principally incorporated directly as an impurity in the crystal lattice (Kendall et al. 2017).

6.6.16 Cadmium (Cd)

Sea surface temperature in the Gulf of Panama was 24.8 °C and 28.3 °C, and Cd concentrations in the coral skeletons were 2.5 and 1.9 μg/g in upwelling and non-upwelling periods, respectively (Matthews et al. 2008). Cd is depleted at the ocean surface via biological activity and enriched at depths by decomposition and dissolution of sinking organic and inorganic materials. During upwelling events, Cd-rich cool deep water is pulled to the surface and bathes surface-ocean-dwelling corals that incorporate these fluctuating Cd concentrations in seawater at their aragonite skeletons. This temporal variation in Cd concentration in coral skeleton has been used to reconstruct the past upwelling events and wind regime in a large scale. Cd distribution coefficient was estimated to be ≈1.3–1.7 directly comparing Cd concentration in the coral skeleton and ambient seawater (Matthews et al. 2008). The molar ratio of Cd/Ca in coral skeletons of colonies of *Acropora* sp., *Stylophora pistillata*, and *Montipora verrucosa* cultured in the laboratory under controlled environmental conditions at different salinities showed a decreasing trend with salinity (Pretet et al. 2014).

6.6.17 Iodine (I) and Iodine Isotopes

Iodine content was reported to be about 1.0–1.5% in tropical surface-ocean-dwelling carbonate gorgonian corals (Sugimoto 1928) and to account for about 23% of the skeletal weight in some proteinaceous antipatharian (black) corals (cited in Prouty et al. 2018). The iodine isotope occurs as stable ^{127}I and the long-lived radioisotope ^{129}I ($t_{1/2} = 15.7 \times 10^6$ year). Both are naturally occurring; however, military (e.g., bomb testing) and industrial nuclear activity (e.g., nuclear waste reprocessing) have significantly increased the marine $^{129}I/^{127}I$ ratio since the late 1940s (Hong et al. 2011). The concentration of ^{129}I was about 0.94–1.83 × 10^7 atoms L^{-1} and 89.8 × 10^7 atoms L^{-1} ($^{129}I/^{127}I = 362 \times 10^{-11}$) near Japan in the North Pacific and as much as before and after the Fukushima Daiichi Nuclear Power Plant accident in March 2011, respectively (Suzuki et al. 2013). Surface ocean dwelling coral skeletons at the coasts of the Pacific Ocean and the South China Sea has recorded the ^{129}I input from the 1962 global fallout, Chernobyl accident and the discharge of nuclear fuel reprocessing plants (Bautista et al. 2016). Guam coral recorded 129I/127I as much as 157 × 10^{-12} in 1955 (Chang et al. 2016). Chang et al. further simulated basin-scale ocean circulation, using Marshall Islands (the US Proving Grounds) as a point source of ^{129}I and time series $^{129}I/^{127}I$ recorded in coral over 60 years, to show that water from the Marshall Islands took about 4 years to get to Hainan Island, but it takes only a year to arrive at Okinawa via Philippine coast and to the east of Hawaii Islands for about 10 years. Deep-sea coral recorded $^{129}/^{127}I$ value of $<0.5 \times 10^{-12}$ in the pre-atomic period and continues to rise as much as about 18 × $^{129}I/^{127}I$ at 300 m depth of the Gulf of Mexico (Prouty et al. 2018). Prouty et al. further suggested that the $^{129}I/^{127}I$ records of the deep-sea coral can be also utilized to trace the arrival time of ^{129}I or bomb-produced ^{14}C-laden particulate organic matter from the surface ocean to their inhabiting water depth of 300 m.

6.6.18 Barium (Ba) and Barium Isotopes

Barium is known to substitute Ca into the lattice of the aragonite skeleton because there is a solid solution between orthorhombic $BaCO_3$ (witherite) and $CaCO_3$ (aragonite). In tropical surface coral *Favia fragum* incubation experiments, Gonneea et al. (2017) found that (i) Ba inclusion was linear across the concentration window from 73 to 450 nmol/kg; (ii) distribution coefficient, $D = (Ba/Ca)_{coral} / (Ba/Ca)_{seawater}$, was around 1.4–1.9 and was lower than chemically precipitated non-biogenic aragonite; (iii) D was negatively correlated with temperature, $D = (2.514 \pm 0.190) - (0.02865 \pm 0.01487) \times T(°C)$; and (iv) distribution coefficients did not depend upon calcification rates. In the cold-water corals, similar values of D of 1.8±0.4 (2sd) and a strong linear correlation in Ba/Ca molar ratio between skeleton and seawater were also observed (Hemsing et al. 2018). Ba/Ca in coral skeleton has been used to reconstruct the Ba content of seawater.

In the ocean, dissolved Ba is usually depleted in surface waters and enriched in deep waters similar to that of dissolved silicic acid. Hence, variations in Ba/Ca mole ratios in coral skeletons reflect both the intensity of subsurface upwelling and temperature as deep water is cooler than the surface water. Using these features of the ocean, Lea et al. (1989) were able to reconstruct temporal variations in the upwelling events off Galapagos over the last 20 years. As river water contains about four times more Ba than seawater, skeleton Ba/Ca ratio of Galapagos coral *Pavona clavus* was reported to be from 3 to 80 μmol/mol from the various locations and coral species (*Porites* and *Montastraea*) and has been used as a climate proxy of river discharge, river sediment transport, upwelling or groundwater discharge and indirectly rainfall, sea surface temperature, and other climate variables (Gonneea et al. 2017). Similarly, Ba/Ca ratio in coral skeleton was used to trace the sediment load and river flow in Madagascar catchments (Grove et al. 2012) and

Ishigaki Island (Sowa et al. 2014). In the coastal waters, weathering rocks and minerals release barium (Ba) into the drainage catchment, and it adsorbs to suspended sediments (clay minerals), which are then transported to coastal waters via rivers. As salinity increases, Ba desorbs from the suspended sediment due to the higher ionic strength of seawater in the estuary. Ba diluted by seawater is thought to follow a conservative mixing pattern in the ocean and thus can act as a tracer for riverine sediment input into the ocean. Corals collected from a shelf edge in Fajardo, Gulf of Panama, exhibited a strong coherence between Rio Fajardo river discharge and coral (Moyer et al. 2012) as many studies across the Caribbean and Indo-Pacific regions (e.g., Maina et al. 2012).

Ba Isotopes

Stable barium isotopes are ^{134}Ba (mole fraction, 0.0242), ^{135}Ba (0.0659), ^{136}Ba (0.0659), ^{137}Ba (0.1123), and ^{138}Ba (0.7170) in nature (Meija et al. 2016a). Ba isotope data are usually expressed as Eq. (6.83).

$$\delta^{13x/134}\mathrm{Ba}(‰) = \left[\left({}^{13x/134}\mathrm{Ba}_{\mathrm{sample}}\right) / \left({}^{134x/134}\mathrm{Ba}_{\mathrm{SRM3104a}}\right) - 1\right) \times 10^3 (\text{where } x = 7 \text{ or } 8) \tag{6.83}$$

Significant variation has been found in natural samples. For example, $\delta^{138/134}$Ba concentrations in the dissolved Ba in the Atlantic exhibited relatively enriched at the sea surface (~0.6‰) and depleted to ~0.3‰ at 4000–5000 m depth. A monotonic decrease in $\delta^{138/134}$Ba with depth in the deep water results from conservative mixing between North Atlantic Deep Water (+0.45‰) and Antarctic Bottom Water (+0.26‰) (Bates et al. 2017). There are large Ba isotopic fractionations between modern seawater and corals. In surface water-dwelling corals of *Porites* sp., *Acropora* sp., *Stylophora* sp., and *Montipora* sp. in the Mediterranean Sea, the Ba isotopic composition of their skeletons exhibits $\delta^{137}/^{134}$Ba values of +0.16 to +0.41‰ that is identical or lighter than that of the ambient Mediterranean surface seawater (+0.42) (Pretet et al. 2016). Similarly, cold-water coral (CWC) also shows isotope fractionation of Ba between seawater (SW), $\Delta^{138/134}\mathrm{Ba}_{\mathrm{CWC-seawater}}$ is −0.21‰, indicating that cold-water coral skeleton also preferentially incorporates the lighter isotopes (Hemsing et al. 2018). Hemsing et al. further showed that this fractionation likely does not depend on temperature or other environmental variables and suggested that cold-water coral aragonite skeletons could be used to trace the Ba isotope composition in ambient seawater.

6.6.19 Rare Earth Elements (REEs)

Rare earth elements, as defined by the International Union of Pure and Applied Chemistry (IUPAC), are a set of 17 chemical elements in the periodic table, specifically the 15 lanthanides (atomic number 57–71) as well as scandium (atomic number 21) and yttrium (atomic number 39). Despite their name, rare earth elements are relatively abundant in Earth's crust (ppm level), except promethium (Pm) which is radioactive and extremely rare. Weathering of different rock types results in river waters having a different REE composition. In seawater, REE concentrations are about 0.4–175 pM with higher at the sea surface and minimum at subsurface and increase again with depth toward the seafloor (e.g., Osborne et al. 2015). The main attraction of using REEs is that they form a coherent group whose chemical properties change systematically across the series, such as a gradual decrease in ionic radius with increasing atomic number. REE-carbonate ion complexes are the dominant species in seawater. The increased complexation from La to Lu leads to a decrease in the proportions of free REE (III) ions that results in fractionation, whereby the light REEs (LREEs) are preferentially adsorbed to surfaces as the heavy REEs (HREEs) are preferentially retained in solution. Cerium only undergoes redox reaction and precipitated as a consequence of its oxidation to Ce(IV) (Sholkovitz and Shen 1995). Sholkovitz and Shen analyzed REE contents in coral collected from Bermuda and the Pacific Ocean. REE concentrations in the coral skeleton (lattice-bound fraction) exhibited about 0.9–61 pmol/g, and their distribution coefficient was from 1 to 3 except Ce. A time history of impacts of coastal development of road construction, port, and river dredging in the past was revealed through REEs recorded in coral, *Porites lutea*, in Nha Trang Bay, Vietnam (Nguyen et al. 2013).

6.6.20 Neodymium (Nd)

Among REEs, neodymium deserves special attention due to their temporal and spatial variability of isotopic composition in the ocean. Neodymium has seven isotopes in nature: ^{142}Nd (27.1%), ^{143}Nd (12.2%), ^{144}Nd (23.8%), ^{145}Nd (8.3%), ^{146}Nd (17.2%), ^{148}Nd (5.8%), and ^{150}Nd (5.6%) (Meija et al. 2016a). Usually, ^{143}Nd/^{144}Nd ratio is reported as εNd in Eq. (6.84), where CHUR stands for Chondritic Uniform Reservoir and represents a present-day average earth value of 0.512638. Water masses bathing landmasses of different Nd isotopic composition acquire a characteristic Nd isotopic signature; therefore, the Nd isotopic signature of seawater may provide its provenances, advection, and mixing process of water masses.

$$\varepsilon\text{Nd} = \left[\left({}^{143}\text{Nd}/{}^{144}\text{Nd}\right)_{\text{sample}}/\left({}^{143}\text{Nd}/{}^{144}\text{Nd}\right)_{\text{CHUR}} - 1\right)\right] \times 10^4 \quad (6.84)$$

Based on the mass balance considerations and solid-state nuclear magnetic resonance (NMR) spectroscopy observations, Nd and other REEs are suggested to be incorporated as a form of authigenic phosphate mineral (apatite) into coral skeleton (Mason et al. 2011; Struve et al. 2017). Archived records in coral could be used to track the past changes in the water circulation in the ocean (Copard et al. 2011). Copard et al. reported Nd concentrations in deep-sea corals retrieved from 500 to 2700 m depth were 6 to 111 ppb and εNd values were −12.7 to −10.7 in seawater in the Mediterranean Sea (−13 to −11). van de Flierdt et al. (2010) also demonstrated that deep-sea corals are reliable archives for seawater Nd isotopes using a worldwide collection of five different genera, provided that coral samples are cleaned by removing ferromanganese coatings and any lithogenic phase. As deep-sea corals continuously live longer than 4265 years (Roark et al. 2009), they possess a great potential for paleoceanographic studies.

6.6.21 Lead (Pb) and Lead Isotopes

Aragonitic coral skeletons incorporate Pb from seawater; therefore, Pb archived in coral skeleton has been utilized for tracking time variation of ambient seawater Pb concentration. Corals near Bermuda were subject to study on the Pb concentrations from 1780 to 2000 utilizing seawater collected over the last 20 years (Kelly et al. 2009). The distribution coefficient of Pb in coral from seawater, $D_{\text{Pb}} = [\text{Pb/Ca}]_{\text{coral}}/[\text{Pb/Ca}]_{\text{seawater}}$, was estimated to be about 2.8–3.6 (*Diploria strigosa*) and 3.6 (*Diploria labyrinthiformis*). Pb concentrations varied from 5 to 60 nmol Pb/mol Ca corresponding to seawater concentration of 15–200 pmol/kg in seawater with a peak in 1930–1940. Lee et al. (2014) also reported the surface water Pb concentrations in the Indian Ocean from 1945 to 2010 using corals growing in the region. Overall coral Pb/Ca increased in coral skeleton from about 7–38 nmol Pb/mol Ca from 1972 to 1995 in Chagos, about 4–9 nmol Pb/mol Ca in Sumatra, and about 20–45 nmol Pb/mol Ca at Singapore Strait (Jong Island). Chen et al. (2016a) reported that Pb/Ca ratio in coral skeleton increased from 10 to 16 nmol/mol in the 1950s to more than 30 nmol/mol by 2000 in the western South China Sea. Lu et al. (2015) utilized non-destructive synchrotron radiation micro-X-ray fluorescence (SR μ-XRF) analysis with multi-element, submicron meter-scale resolution, atto-gram (10^{-18}) sensitivity to obtain the historical lead input to the coastal waters from 1900 to 2010 using surface water living black corals in the northern South China Sea.

Lead Isotopes

Four stable lead isotopes (abundance in percentage) of ^{204}Pb (1.4%), ^{206}Pb (24.1%), ^{207}Pb (22.1%), and ^{208}Pb (52.4%) are known in nature (Meija et al. 2016a). Among the four lead isotopes, only ^{204}Pb is not radiogenic; the ^{206}Pb isotope is the final product of the radioactive decay of ^{238}U with halftime ($T_{1/2}$) of 4.468×10^9 years. ^{207}Pb is the product of the decay of ^{235}U ($T_{1/2} = 7.04 \times 10^8$ years), and ^{208}Pb results from the decay of ^{232}Th ($T_{1/2} = 1.40 \times 10^{10}$ years). Half-lives are taken from Meija et al. (2016b). The content of ^{204}Pb in rock and minerals remains constant in time, while the contents of the radiogenic isotopes increase with different rates because the radioactive decay of the mother radionuclides continues. Scientists estimates the age of the Earth to be 4.57×10^9 years old by assuming the lead isotopic composition of the Canyon Diablo iron meteorite is that in the earliest Earth, utilizing the current mean stable Pb isotopic compositions in sedimentary, volcanic, and igneous rocks (Stacey and Kramers 1975).

Past changes in seawater Pb isotopes archived in coral or bottom sediments have been utilized to track the time evolution of continental weathering, ocean circulation, and anthropogenic Pb pollution via the atmosphere. Kelly et al. (2009) reported that ^{206}Pb/^{207}Pb and ^{208}Pb/^{207}Pb varied from 1.19 to 1.21 and 2.45 to 2.49, respectively, in corals near Bermuda. Both Pb concentrations and Pb isotopic ratios reached their maximum in the 1880s due to the atmospheric Pb emission from Upper Mississippi Valley Pb ore. ^{206}Pb/^{207}Pb and ^{208}Pb/^{207}Pb continue to decrease to 1.17 and 2.44, respectively, in the year 2000. Lee et al. (2014) determined characteristic isotope signatures of corals in the Indo-Pacific Ocean to be around 1.15 of ^{206}Pb/^{207}Pb and 2.41 of ^{208}Pb/^{207}Pb at Chagos Island. At Sumatra, ^{206}Pb/^{207}Pb of coral skeleton decreased from 1.18 to 1.15 with time and ^{208}Pb/^{207}Pb decreased from 2.485 to 2.440 with time, and at Singapore Strait, ^{206}Pb/^{207}Pb and ^{208}Pb/^{207}Pb increased from 1.18 to 1.19 and 2.46 to 2.475 with time, respectively. Lee et al. attributed their Pb input from India, Indonesia, and combined input from southern China, Indonesia, and Austral and local sources at Chagos Island, Sumatra, and Singapore Strait, respectively. Similarly, Chen et al. (2016a) determined Pb/Ca and ^{206}Pb/^{207}Pb ratio of coral *Porites lutea* to delineate the natural and atmospheric deposition of lead at coastal waters in central Vietnam for the last 170 years.

Recent advancement in analytical instruments (e.g., TIMS) measuring ^{204}Pb in the relatively small size of the sample (about 3 ng Pb) opens new revenue on the various unresolved environmental issues. Using over 10,000 specimens of deep-sea corals, *Desmophyllum dianthus* (0.8–2.4 km depth), collected from the south of Tasmania, Wilson et al. (2017) reported that typical Pb concentrations for the cleaned deglacial coral skeleton were 6–20 ppb (Pb/Ca = 3–10 nmol/mol), and values for $^{206}Pb/^{204}Pb$, $^{207}Pb/^{204}Pb$, and $^{208}Pb/^{204}Pb$ were found to be about 18.0–19.0, 15.60–15.72, and 15.55–15.75, respectively. They were further able to reconstruct the millennial timescale of ocean mixing between a radiogenic endmember transported from upstream within the Antarctic Circumpolar Current and a non-radiogenic endmember potentially supplied from Australia through glacial to interglacial periods. As detailed Pb isotopic compositions in the oceanic water columns become available recently in part of the recent GEOTRACES program, deep-sea coral will provide a new powerful tool to deciphering deep ocean processes (e.g., Bridgestock et al. 2018).

6.6.22 Uranium (U)

The variation of uranium concentration of seawater is determined by variations in the inputs (riverine delivery) and output (removal via a microbial reduction in marine sediments) fluxes into the ocean. Uranium occurs in two redox states of U(VI) and U(IV) in natural waters. Under oxygenated conditions, U(VI) is abundant as the uranyl ion (UO_2^{2+}) and forms a suite of aqueous carbonate complexes dominated by uranyl tricarbonate ($UO_2(CO_3)_3^{4-}$) at pH ~ 8. In the absence of oxygen, U(VI) is reduced to poorly soluble U(IV) and subsequently precipitates as uraninite in sediments (UO_2). U/Ca mole ratios are about 0.86 to 1.03 μmol/mol for the skeleton of a coral (*Porites cylindrica*) and decrease with water temperature (e.g., Eq. 6.85 in Armid et al. 2011) and showed a marked seasonal pattern of water temperature, pH, carbonate ion, and salinity (Lazareth et al. 2016). Therefore, it may be used as a proxy for paleo-seawater temperature. The mode of U incorporation into coral skeletons appears to be dependent upon pH and the carbonate activity in the calcifying fluid. Some suggested that U is incorporated as $UO_2(CO_3)_3^{4-}$ substituting for CO_3^{2-} in the aragonite lattice (DeCarlo et al. 2015). The abundance of uranyl tricarbonate ion is dependent upon both pH and carbonate ion concentration [CO_3^{2-}] in seawater. DeCarlo et al. found that the U/Ca ratio of aragonite precipitated from seawater decreased with increasing carbonate concentration in the calcifying fluid and was independent of pH and temperature. They further suggested that its temperature dependence arose indirectly. The U/Ca ratio was inversely related to the Mg/Ca ratio in both tropical and cold-water coral skeletons. And that was attributed to the environmental variables other than temperature, the controlling biology, or the growth rate of the coral (Eq. 6.85, Sinclair et al. 2006).

$$\begin{aligned} \mathrm{U/Ca}(\mu\mathrm{mol/mol}) = {} & (1.488 \pm 0.0484) \\ & - (0.0212 \pm 0.00189) \\ & \times T(^{\circ}\mathrm{C})\left(r^2 = 0.78\right) \qquad (6.85) \end{aligned}$$

U Isotopes

Uranium has three isotopes of ^{234}U (0.005%), ^{235}U (0.72%), and ^{238}U (99.27%) in nature (Meija et al. 2016a). The isotopic composition is usually expressed as in Eq. 6.86, where $^{238}U/^{235}U$ is the atom ratio.

$$\delta^{238}\mathrm{U} = \left({}^{238}\mathrm{U}/{}^{235}\mathrm{U}_{\mathrm{sample}}/{}^{238}\mathrm{U}/{}^{235}\mathrm{U}_{\mathrm{standard}} - 1\right) \times 10^3 \quad (6.86)$$

The standard reference material ($U_{standard}$) is U metal CRM-112a (also named SRM-960 or NBL-112a, CRM-145 for the solution form). ($^{238}U/^{235}U$) is the atom ratio (Tissot and Dauphas 2015). ^{238}U is preferentially reduced from U (VI) to U(IV) relative to ^{235}U, leaving the residual U(VI) with a lower $\delta^{238}U$ value compared with reduced uranium in sediments. Therefore, if the volume of anoxic water or anoxic seafloor is increased, the remaining seawater U(VI) decreases in both its concentration [U] and $\delta^{238}U$ (Lau et al. 2016). Lau et al. estimated the reduction of [U] and $\delta^{238}U$ values from ~3 ppm and −0.15‰ to ~0.3 ppm and −0.77‰ across the end-Permian extinction period as the areal extent of bottom water anoxia increased. $\delta^{238}U$ value of modern seawater is −0.39‰ (Tissot and Dauphas 2015). Chen et al. (2016b) observed a significant U isotope fractionation in aragonite precipitation but not calcite precipitation at pH ~ 8.5. Therefore, coral aragonite can be used to track the changes in the volume of anoxic water and areal extent of anoxic seafloor through geologic time (Chen et al. 2017).

6.6.23 Plutonium (Pu) Isotopes

Plutonium isotopes had been introduced largely from atmospheric nuclear testing since 1945 and occasional accidents in the nuclear industries (Hong et al. 2004). The concentrations for fallout $^{239+240}Pu$ nuclides have been decreased substantially from the early 1960s, and at the year 2000, dissolved $^{239+240}Pu$ concentrations in surface waters of the Pacific and Indian Oceans varied from 0.1 to 5.2 mBq/m^3. The mean effective half-lives for $^{239+240}Pu$ were estimated to be 7–12 years, respectively (Povinec et al. 2005). By comparing $^{239+240}Pu$ activity concentrations in the coral skeleton between Bermuda and Florida corals, Purdy et al. (1989) found that coastal waters of the Florida Keys are fed with particle-laden terrestrial runoff from adjacent land, and the flux of the coastal waters varied seasonally due to the variable Loop Current intrusion. Pu distribution coefficient, $D = (\mathrm{Pu/Ca})_{\mathrm{coral}}/(\mathrm{Pu/Ca})_{\mathrm{seawater}}$, was estimated to be 1.8 ± 1.2; thus, Pu may be incorporated preferentially relative to Ca into the coral skeleton (Benninger and Dodge 1986).

^{240}Pu/^{239}Pu Atom Ratio

The atom ratio of ^{240}Pu/^{239}Pu in fallout is variable and depends upon the specific weapon design and test yield. Average ^{240}Pu/^{239}Pu atom ratio is 0.18, 0.035, and 0.21–0.36 of the global stratospheric fallout (USSR), fallout from Nevada test, and close-in tropospheric fallout from the US Pacific Proving Grounds. Coral Pu records showed that in the western North Pacific Ocean, the magnitude of local Pu deposition from close-in fallout in the 1950s was larger than Pu deposition from global fallout in 1963 observed elsewhere, and the atom ratio of ^{240}Pu/^{239}Pu shows the mixing of two end members: close-in and global fallouts with time (Buesseler 1997). The utility of source-specific atom ratios of plutonium isotopes in ocean circulation has been reviewed (Hong et al. 2011). By analyzing Guam coral, Lindahl et al. (2011) estimated as much as 70% of total Pu in the 1981–1999 growth bands originated from remobilized Pu brought via the North Equatorial Current, and the contribution from US Pacific Proving Grounds increases recently (1984 onwards) as much as 54%–72% along the North Equatorial Current and its extension of Kuroshio Current (Lindahl et al. 2012).

6.7 Discussion and Summary

We have collated various chemical proxies developed up to the present in their atomic number order in the preceding sections; some were established many decades ago and some were reported in relatively recent years (Table 6.3).

Earth climate including ocean chemistry and their biota have experienced significant changes since its formation largely due to variation in Earth's orbits, plate tectonics, solar radiation, and volcanic eruption. Geologic times over the last 4.5 billion years were termed as eons, eras, periods, and epochs based on various climate changes including the emergence of new biological organisms and extinction of some organisms. In the context of climate change or ocean chemistry, it is also true that the proxies which are seen were not made of things that do appear and often reflect more than one variable thus require careful analysis to extract the exact relationship between a proxy and environmental or biological variable(s). Climate proxies embedded in the characteristics and constituent compositions of annual layers in corals represent some evidence to the extent of our knowledge. As we understand more about coral calcification, we can see more about the past climate and environmental variabilities, such as the atmospheric compositions, tropospheric aerosol loads, volcanic eruptions, ground air and sea surface temperatures, precipitation and drought patterns, seawater chemical compostion, oceanic primary productivity, ice-sheet extent, solar activities, etc.

Surface ocean acidification, rising air and ocean temperature, and ocean deoxygenation are major global climate and environmental changes that pose a significant threat to humans in our time. Sea surface temperature (SST) has been rising over the last century caused partly by human activities, and the rising SST has caused poleward expansion in reef-building coral species in temperate regions. For example, well-observed seawater temperature records and coral occurrence around the coastal waters off Japan islands during the last 80 years yielded the speed of northward extension of 10–14 km year^{-1} in the East China Sea that is far greater than that for other biological species (Yamano et al. 2011; Takao et al. 2015). As the coral habitat is dependent upon the water temperature, the geographical current and fossil coral reef occurrence data and current SST data were utilized to derive paleotemperature during the last interglacial episode (LIG, ~125,000 years ago) when the subtropics were warmer than the tropics (Lauchstedt et al. 2017). During LIG, sea surface temperature was higher as much as 0.5–1 °C than that of the pre-industrial period (Fischer et al. 2018). It is important to note that global warming changes are largely derived from the human emission of CO_2 into the atmosphere.

The increased CO_2 concentration in the atmosphere results in the acidification of the surface ocean. The effect of ocean acidification on the ocean surface-dwelling scleractinian corals that form calcium carbonate reefs hosting a major habitat for high marine biodiversity may be significant. As opposed to the initial assessment of the vulnerability of coral due to the increasing ocean acidification, some corals are able to maintain their calcification rates to control carbonate chemistry in their extracellular calcifying fluid despite that the ambient water becomes acidic (Comeau et al. 2017a, b; McCulloch et al. 2017). And the role of organic matrix in calcification of corals has yet to be discovered (DeCarlo et al. 2018). Therefore, it is extremely important for scientists to pull all the necessary scientific data and theories and to advance working models and continue to refine them by employing new observations and new measurements to better prepare the climate in the future. Interpretation of proxy records embedded in coral skeletons would be one of starting points for this effort.

It may be useful at this stage to reflect how the coral calcification process in days, weeks, and years is related to the ambient seawater environment and its variation. As tropical surface reef-building corals usually inhabit about 2–20 m

Table 6.3 Selected chemical proxies collated in Sect. 6.6. These and other proxies need to be carefully assessed in the context of given coral calcification processes and variations in their growing environmental conditions to reconstruct the past climate or environmental changes

Climate (environmental) conditions	Proxies (tracers)
Water temperature	Li/Ca, δ^{13}C, δ^{18}O, Δ_{47}, F/Ca, Mg/Ca, $\delta^{44/40}$Ca, Sr/Ca, $\delta^{88/86}$Sr, Ba/Ca, U/Ca
Seawater carbonate ion concentration ($[CO_3^{2-}]$)	B/Ca, F/Ca
Seawater pH	δ^{11}B
Seasonality	δ^{13}C, δ^{18}O, Na/Ca, Mg/Ca, S/Ca, Sr/Ca
Upwelling of subsurface water	δ^{15}N, P/Ca, Cd/Ca, Mn/Ca, Ba/Ca
Terrestrial input (river runoff, precipitation, soil erosion, sediment flux, groundwater discharge)	Mn/Ca, Fe/Ca, Sr/Ca, Ba/Ca, Mn/Ca, Zn/Ca, Pb/Ca, Y/Ca, REEs
Photosynthetic efficiency of coral	δ^{13}C
Sea level (continental ice (glacial) volume)	δ^{18}O
Seawater triple oxygen isotope composition	Δ^{17}O
Seawater composition, continental weathering, crustal weathering dolomitization, hydrothermal activity	δ^{26}Mg, δ^{34}S, $\delta^{53/52}$Cr, $\delta^{88/86}$Sr, $\delta^{13x/134}$Ba (deep-sea coral), Pb and Pb isotopes, εNd
Seawater redox conditions, volume of anoxic water, and extent of anoxic sea floor	$\delta^{98/95}$Mo, δ^{238}U
Pollution, wastewater, sewage, population increase, military and civilian nuclear industry	δ^{15}N, P/Ca, V/Ca, Fe/Ca, Ni/Ca, Cu/Ca, Zn/Ca, Pb/Ca Δ^{14}C, ^{90}Sr, ^{129}I, ^{206}Pb/^{207}Pb, ^{208}Pb/^{207}Pb, Pu isotopes, ^{240}Pu/^{239}Pu

below the sea surface, they draw nutrients from the ambient seawater for their symbiotic flagellate (zooxanthellae) or food particles using tentacles and secrete aragonite skeleton extracellularly, although corals appear to actively modify seawater in this extracellular calcifying fluid to precipitate aragonite due to the Raleigh fractionation (Fig. 6.2). As corals live at a fixed depth, the chemical composition of the coral skeleton is largely determined by the chemical composition of seawater at that depth. Coral living depth is usually within the surface mixed layer that may be characterized as high temperature, low salinity water due to rainfall, and low nutrient depending upon locations. In the fringing reef, river water flows in with terrestrial particles and organic matter as well as nutrients. On the other hand, the subsurface water is usually cold and rich in nutrient or nutrient-like metals such as Cd and Zn, etc.

In the ocean basin scale, however, wind speed or direction changes, the depth of the surface mixed layer also changes, and so does the chemical composition of seawater adjacent to coral. One of the most notable examples in the tropical region is the sudden changes in the trade wind from time to time. In the Indo-Pacific warm pool region (the west of the Pacific Ocean) where its warm water may extend down to 200 m depth below the sea surface, trade winds blowing from the east bring heat and moisture to the region and are uplifted to the high altitude to form cumulative clouds that subsequently rained out. This rain fuels the terrestrial ecosystem and agriculture and drinking water in the Asia-Pacific region. On the other hand, dry air subsides and results in desert climate in the eastern end of the Pacific Ocean (Equatorial South America). However, prevailing southerly winds along the coast bring nutrient-rich subsurface water to sustain high fisheries productivity due to the shallow surface water (Fig. 6.3).

When the trade winds weaken or reverse and subsequently westerlies moved in, the Warm Pool region becomes dry and warmer and receives more UV radiation as water vapor in the air becomes thinner (Fig. 6.4). This phenomenon is called El Niño Southern Oscillation. In some regions in the west, drought threatens agricultural industry and drinking water availability. And torrential rain devastates previous arid lands in equatorial South America and makes fisheries collapsed along the coast as the surface mixed layer thickens and the subsurface water upwelled lacks nutrients because it is still the same nutrient-depleted surface mixed layer water. This change in the tropical climate features subsequently changes the rest of the climate system over the entire globe, including the Arctic and the Antarctic.

The horizontal distribution of sea surface temperature across the Pacific is shown here as an exemplary case (Fig. 6.5). Corals populate across the entire tropical ocean, and they faithfully record the temperature and other changes including contaminant input in seawater substrate where they depend upon. Therefore, if we expand our database on coral samples across the ocean basins both surface warm-water-dwelling and cold-water-dwelling in the deep sea, our knowledge on the changing climate and environment will deepen and will enable us to prepare better for future climate change.

As we glimpsed over the preceding sections of this chapter, interpreting temporal variations in proxies archived in coral skeleton has helped to deepen our understanding on the interdependence of proxies in the ocean. For example, the oxygen isotopic ratio between ^{18}O and ^{16}O of $CaCO_3$ coral skeleton (δ^{18}O) is related to the δ^{18}O of seawater and temperature at the time of its precipitation. Seawater temperature, in turn, depends on solar irradiance, abundances of atmospheric

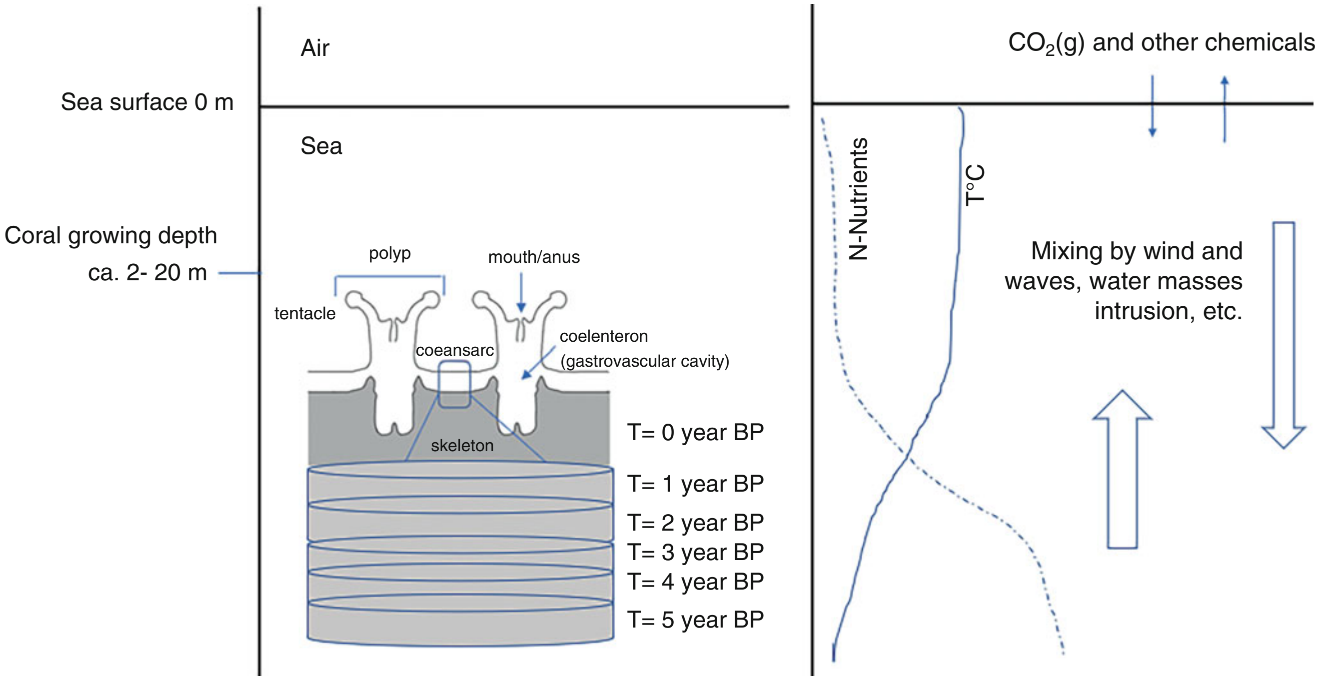

Fig. 6.2 Schematic diagram of the surface reef-building coral in relation to water depth

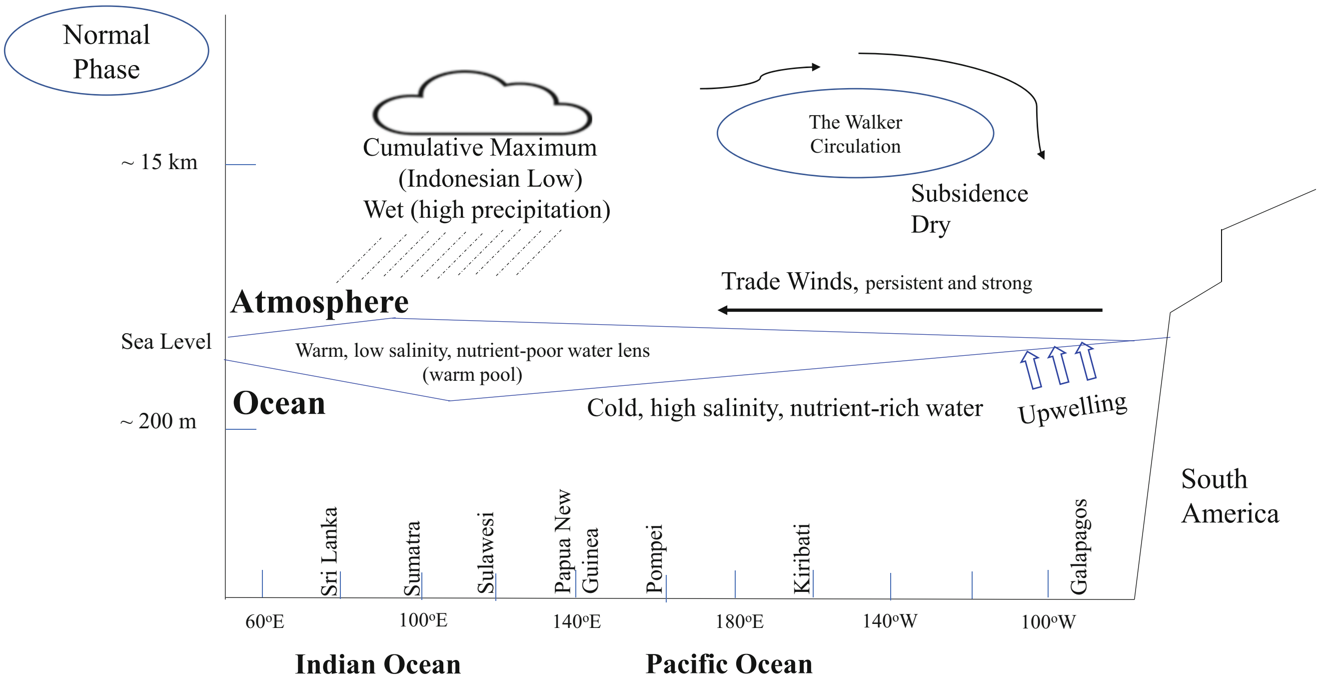

Fig. 6.3 Schematic diagram of the atmospheric and ocean system during normal period at the tropics (scales are arbitrary, redrawn using Cole et al. 1995)

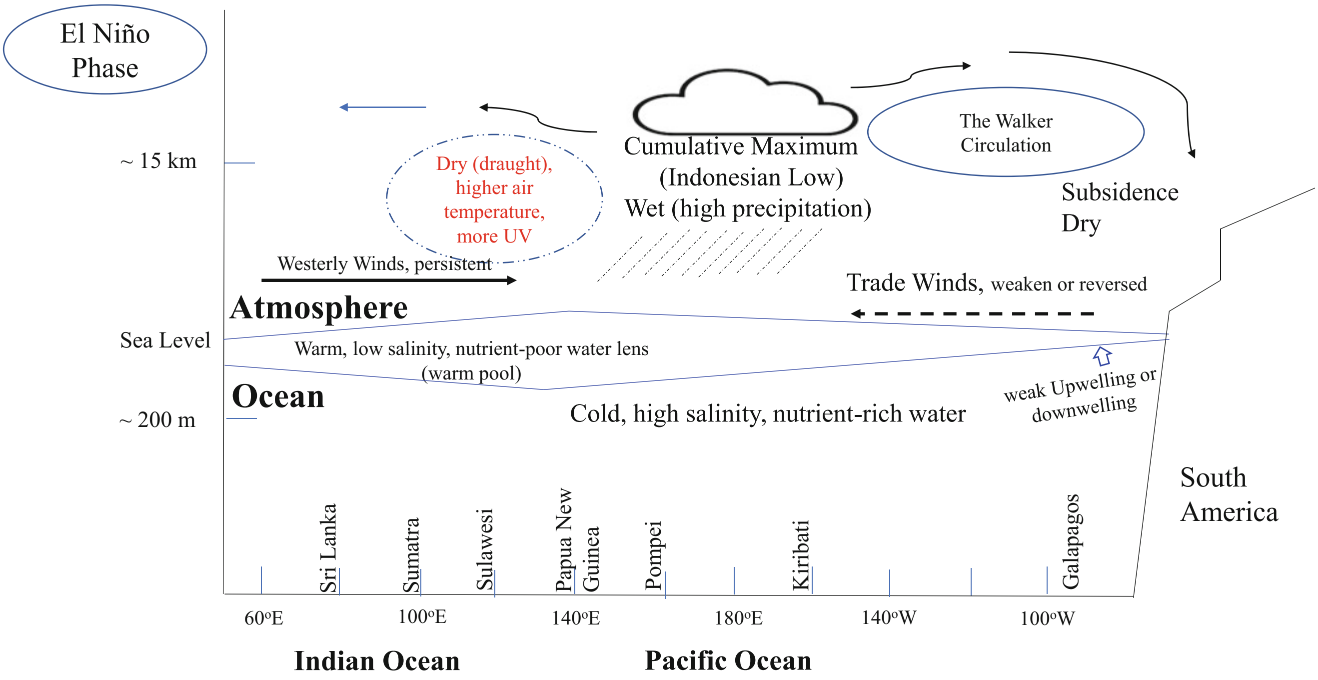

Fig. 6.4 Schematic diagram of the atmospheric and ocean system during the El Niño period at the tropics (scales are arbitrary, redrawn using Cole et al. 1995)

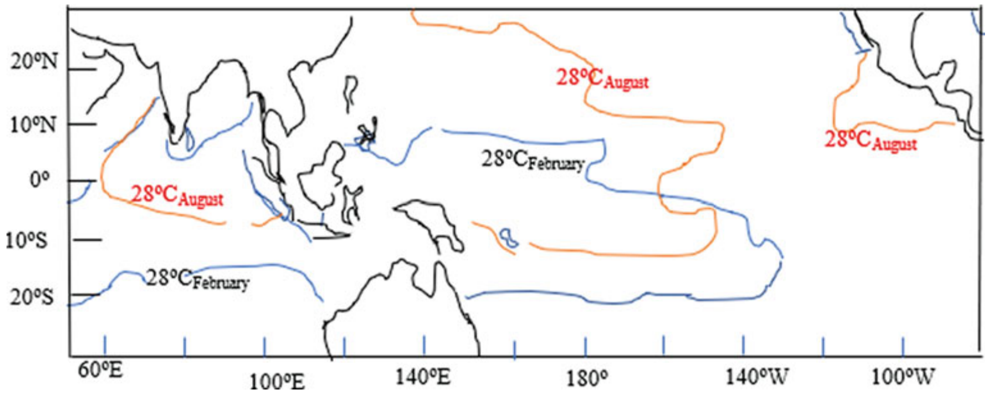

Fig. 6.5 Sea surface temperature (28 °C isotherms) in August during the normal year (blue line) and the El Niño year (red line). Redrawn using De Deckker (2016)

greenhouse gases, albedo and intrusion of subsurface cold water or oceanic waters of different temperature, etc. And δ^{18}O content of seawater is related to the evaporation and the rainfall; hence, salinity, global ice volume on the continent, sea level, ocean circulation, etc. can be inferred. Recently, owing to the increasing atmospheric CO_2 due to human activities and advancements in the understanding of the biomineralization process of coral animals in the molecular level with sophisticated observation instrument and sensitive analytical tools and techniques, coral skeleton geochemistry and climate proxies have been increasingly drawn more attention from both climate scientists and the public amid grave concerns over global climate change in recent decades.

The reef coral thriving in the Indo-Pacific Warm Pool region ($>30 \times 10^6$ km^2)is of significance for the utility of the coral skeleton as a climate proxy. The pool plays a role in the heat and water engines of the Earth due to piling up warm surface water over 28 °C (heat engine) and extensive evaporation and rainfall due to atmospheric convection (steam engine). (De Deckker 2016). The variability of the El Niño occurrence (Figs. 6.3, 6.4, and 6.5) is a notable one in shaping global climate. This warm pool region is also the place of North Equatorial Current Bifurcation, the formation of Kuroshio and Mindanao currents, and Equatorial Counter Current, Indonesian Throughflow. This warm pool dynamics dictates local ocean dynamics that determine the various features of the ocean including biological productivity and hence the local economy (Cabrera et al. 2015). In addition, The Proving Grounds in the tropical North Pacific is a unique and important asset for coral paleoclimatology as they continue to release the stored radionuclides to the ocean. A time average feature of the ocean and atmospheric dynamics may be only recovered from the high-resolution archives such as corals living at the sea surface and at depths. Corals living in the Indo-Pacific Warm Pool region as well as in the other parts of the ocean, therefore, have a huge potential to contribute to the advancement of our knowledge on climate change and its impacts on marine biological productivity that our lives are dependent upon.

Studies on coral skeleton proxies are continuously evolving with the aid of the advancement on the understanding of coral calcification process and concurrent development of analytical capability using a sufficiently small amount of coral skeleton enough to provide high-resolution time-series data. A recent example of new proxy development and analytical standard reference materials is given below for the illustrative purpose for further studies.

Developing a New Proxy: An Example

Although an in-depth review of the validity and accuracy of proxies developed so far is beyond the scope of this chapter, it may be still useful to provide a few thoughts for the benefit of starting laboratories to analyze rich climate archives embedded in the annual growth bands in corals. Preliminary observation on the proxy concentration with respect to Ca and the paleoenvironment data such as water temperature at the time of coral skeleton formed usually proves to be applicable to well-defined regions, but extrapolating this relationship to a wider area usually poses a significant deviation. Students conventionally refer to this deviation from the established relationship terms as "vital effect." The so-called vital effects are originated from the fact that we do not know enough how corals calcify aragonite mineral at sea and the sensitivity of skeletal composition to processes occurring at the site and time of calcification. Biomineralization models to address the calcification process by coral animal have been greatly advanced recently.

Typically metal/Ca ratios are first calibrated with modern instrumental records in the case for temperature (or metal concentration in seawater) to establish a coral specific metal/Ca-temperature relationship using the currently living coral collected in a well-defined seawater environment at sea or corals culturing in the controlled water tanks and then applied to the older skeleton of the same coral, or in some cases to fossil corals, in order to reconstruct past SST (or other variables, such as the concentration of metal in seawater) at the time of coral skeleton formed.

However, problems arise because SST is not the only factor that influences coral skeleton Sr/Ca ratio. The biomineralization process affects Sr/Ca ratios and can do so independently of any changes in temperature. These biological influences are known as "vital effects" and are obvious in the comparison between coral and abiogenic aragonite precipitation experiment at laboratory (DeCarlo et al. 2016). According to DeCarlo et al., these Sr/Ca vital effects arise because corals accrete their skeleton within an isolated calcifying space. As aragonite crystals nucleate from the fluid within this space, the elemental composition of the fluid changes. The site of calcification is microns or less in size and yet inaccessible to human observation due to its location beneath the polyp.

Elemental ratios that are elevated in aragonite relative to the fluid (e.g., Sr/Ca) become progressively lower in the fluid as precipitation proceeds. This is known as Rayleigh fractionation. At a given temperature, the Sr/Ca ratio of the aragonite will monotonically decrease as precipitation proceeds, in response to changes in the Sr/Ca ratio of the calcifying fluid. Fluctuations in calcifying fluid carbonate ion concentration [CO_3^{2-}] likely drive variations in the amount of aragonite precipitation and thus cause fluctuations in the magnitude of the Rayleigh fractionation vital effect (Cohen et al. 2009; Gagnon et al. 2013). Accurate coral-based temperature proxies must therefore account for this process in order to isolate the temperature component of geochemical variability in the skeleton. Vital effects on coral skeletal geochemistry are linked with biomineralization process. Corals nucleate and grow the aragonite crystals that form their skeleton within an isolated space located between the calicoblastic epithelial cells where seawater transport into this space supplies the elements for crystallization. Corals modify the carbonate chemistry of the incoming seawater to induce aragonite precipitation. The modified seawater from which the aragonite crystals precipitate is referred to as the extracellular calcifying fluid (ECF). As calcification proceeds in an isolated (or semi-isolated) space, there are implications for interpreting compositional variations in coral skeleton. Changes in the extent of precipitation from an isolated calcifying fluid would lead to the variability of element ratios in coral skeletons as a result of Rayleigh fractionation.

DeCarlo et al. (2015) did not find correlation between Sr/Ca and U/Ca in experimentally precipitated abiogenic aragonite, in which Sr/Ca is controlled by temperature and is insensitive to [CO_3^{2-}], whereas U/Ca is controlled by [CO_3^{2-}] but is insensitive to temperature. However, positive correlations between coral Sr/Ca and U/Ca ratios were found in the coral skeleton excreted from live corals cultivated in water tanks. Therefore, DeCarlo et al. (2016) hypothesized that the correlations between Sr/Ca and U/Ca in coral skeletons must be derived from processes occurring during biomineralization. DeCarlo et al. (2015) developed a forward biomineralization model that successfully predicts Sr/Ca and U/Ca ratios of coral skeleton. Seawater exchange, alkalinity pumping, and aragonite precipitation modify the elemental composition of the ECF (Fig. 6.1). Together, these processes influence the Sr/Ca and U/Ca ratios of the skeleton via Rayleigh fractionation and [CO_3^{2-}] changes in the ECF. This combination of factors produces a positive correlation between coral skeleton Sr/Ca and U/Ca ratios at a single temperature, such that a given coral Sr/Ca ratio does not correspond to a unique temperature. Since U/Ca is sensitive to Rayleigh fractionation—through variations in [CO_3^{2-}]—but not to temperature, a single U/Ca ratio can serve as a benchmark with which to investigate variability in other element ratios independent of vital effect driven by Rayleigh fractionation. Comparing Sr/Ca ratios that correspond to a single U/Ca ratio should, therefore, isolate the temperature component of the Sr/Ca signal. DeCarlo et al. (2016) were able to derive the following relation (Eq. 6.87).

$$T(^\circ\mathrm{C}) = -10 \times \left(\mathrm{Sr} - U_{\mathrm{parallel}} - 9\right) + 28.1, \qquad (6.87)$$

where $\mathrm{Sr\text{-}U_{parallel}} = - \overline{\mathrm{Sr/Ca}} - 1.1107\ \mathrm{U/Ca}$ and where overbar indicates means of Sr/Ca and U/Ca. The Sr-U proxy for temperature was developed from the advancement of the knowledge that (i) coral Sr/Ca ratios are sensitive to temperature, but that influence is subordinate to vial effects, and (ii) vital effects are originated mainly from the Rayleigh effect in the extracellular calcifying fluid, while (iii) U/Ca ratio records vital effects but is insensitive to temperature. DeCarlo et al. (2016) suggested that Sr-U thermometry has doubled its accuracy as much as 0.5 °C than those derived from Sr/Ca only.

It is also worthy to note that δ^{18}O-SST and Sr/Ca-SST relations derived from coral skeleton records were employed to correct a systematic temperature instrumental error (Pfeiffer et al. 2017). Combining records that have been drawn from different areas and that use different types of indicators into a consistent picture has been emerged employing the various statistical treatments to overcome the limitations inherent to individual proxies (e.g., Juillet-Leclerc et al. 2009). New discoveries in the measurements of various proxies and continued refinement on the calcification models and empirical shreds of evidence are currently undergoing.

Determining Proxy Concentration in Coral Skeleton

The coral skeleton grows about 1 cm year^{-1} and as low as less than 5 μm year^{-1} for surface reef-building corals and deep-sea corals, respectively. Climate studies often require monthly or weekly variation data much less than a year. Therefore, sample size becomes necessarily small as much as ~1 mg and ~1 μg for surface reef-building corals and deep-sea coral skeleton, respectively. Although a non-destructive synchrotron radiation micro-X-ray fluorescence (SR μ-XRF) analysis with multi-element, submicron-meter-scale resolution, atto-gram (10^{-18}) sensitivity was recently demonstrated for metal analysis in coral skeleton (Lu et al. 2015), most analyses do employ cleaning, extraction, digestion, and derivatization to determine the proxy concentration; therefore, processing losses, contamination, or interference have evidently occurred. It is of paramount importance to give extensive efforts to ensure the measurement reliability.

Many proxies presented in the previous section were made possible to gain their utilities in climate and environmental proxies upon solving their respective analytical challenges. Also, measuring coral proxies across the ocean basins is an enormous task due to the vast area of the ocean and the laborious burden to take the sample in remote and harsh habits at depth; therefore, many laboratories in the world have been engaged to collect coral skeletons from many parts of the world and subsequently generate proxy data over many years and decades. Various measurements made in different laboratories or at different times should be comparable. One way to ensure each measurement value should be compared is to establish a linkage to a specified material with known concentrations of interest by employing standard reference materials (Taverniers et al. 2004). Some selected reference materials for coral skeleton analyses are listed in Table 6.4. The composition of the reference materials should be as close as possible to that of the samples. It is also a good practice to develop laboratory working coral skeleton reference material for the individual laboratories to train newcomers or new analytical methods. For example, DeCarlo et al. (2016) obtained external precision (one relative standard deviation) using repeated measurements of a secondary coral standard treated as a sample. And they standardized their element ratio measurements to the JCp-1 coral standard (Table 6.4). It is important to note that samples, reagents, measurement standards, and reference materials must be stored to ensure their integrity. Samples must be stored in such a way that cross-contamination is not possible. The laboratory should guard against their deterioration, contamination, and loss of identity. The laboratory environment should be sufficiently uncrowded, clean, and tidy to ensure the quality of the work carried out is not compromised. The quality of reagents and other consumable materials must be appropriate for their intended use. Where the quality of a reagent is critical to a test, the quality of a new batch should be verified against the outgoing batch before use, provided the outgoing batch is known to be still serviceable. Metallic impurities would be of special concern for coral analysis.

Table 6.4 Selected analytical reference materials used for measurements of isotopes and chemical elements of coral skeletons. References are given in the text

Element and isotope	Reference material
CaO, Ba, Fe, K, Mg, Mn, Na, P, Sr	GSJ CRM JCp-1 coral (*Porites* sp.)[a]
^{6}Li, ^{7}Li	NIST SRM 8545 (LSVEC)
	IRMM-016 (lithium carbonate, isotopic, solid)
Li	NIST SRM 924a (lithium carbonate salt)
B	NIST SRM 3107
^{10}B, ^{11}B	NIST SRM 951 (boric acid), IAEA-B-7 (limestone)
^{13}C, ^{12}C	Calcite (PDB), NBS 18 (carbonate)
^{14}C	NBS Oxalic Acid I (NIST-SRM-4990), NIST SRM 422c
^{15}N	Air 2, USGS32
^{16}O, ^{17}O, ^{18}O	VPDB, VSMOW, SLAP
F	NIST SRM 120c (phosphate rock)
Na	NIST SRM 351a (sodium carbonate)
Mg	NIST SRM3131A
^{24}Mg, ^{25}Mg, ^{26}Mg	NBS SRM 980, DSM3, JCP1
P	NIST SRM 3139a, **NIST SRM 84L**
S	NIST SRM 3154
^{32}S, ^{34}S	NBS SRM 127, IAEA-S-4
Ca	NIST SRM 3109a
^{40}Ca, ^{42}Ca, ^{43}Ca, ^{44}Ca, ^{46}Ca, ^{48}Ca	NIST SRM 915, IAPSO, USGS EN-1
V	NIST SRM 3165
Cr	NIST SRM 3112a
^{50}Cr, ^{52}Cr, ^{53}Cr, ^{54}Cr	NIST SRM 979, NIST SRM 3112a
Mn	NIST SRM 3132
Fe	NIST SRM 691
Ni	NIST SRM 3136
Cu	NIST SRM 3114
Zn	NIST SRM 3168a
Sr	NIST SRM 3153a
^{84}Sr, ^{86}Sr, 87Sr, ^{88}Sr, ^{88}Sr	NIST SRM 987
^{90}Sr	NIST SRM 4239
Y	NIST SRM3167a
Mo	NIST SRM 3134
^{92}Mo, ^{94}Mo, ^{95}Mo, ^{96}Mo, ^{97}Mo, ^{98}Mo, ^{100}Mo	NIST SRM 3134
Cd	NIST SRM 3108
I	NIST SRM 3232
^{129}I	NISTSRM 4249d
Ba	NIST SRM 31094a
^{134}Ba, ^{135}Ba, ^{136}Ba, ^{137}Ba, ^{138}Ba	NIST SRM 3104a
REEs	REE-1 CRM (Natural Resources Canada)
Nd	NIST 3135a
Pb	NIST SRM 981
^{204}Pb, ^{206}Pb, ^{207}Pb, ^{208}Pb	NIST SRM 981
Natural U radioactivity	NIST SRM 4321c
^{229}Th	NIST SRM 4328c
^{230}Th	NIST SRM 4342a
^{210}Pb	NIST SRM 4337
^{226}Ra	NIST SRM 4965
^{228}Ra	NIST SRM 4339b
^{232}U	NIST SRM 4324b
^{239}Pu	NIST SRM 4330c
^{240}Pu	NIST SRM 4334i

[a] Geological Survey of Japan, National Institute of Advanced Industrial Science and Technology (AIST)

Concluding Remarks

The coral animal is a part of the marine ecosystem that is part of ocean, and ocean, in turn, is a part of earth system. Therefore, the product of a coral animal, aragonite skeleton, reflects naturally the interaction of coral animal with its surrounding environment. The resulting physical manifestation between coral organisms and their habitat of the marine environment is what we do see as a coral skeleton. Deciphering hidden information in the coral skeleton, therefore, requires an interdisciplinary approach encompassing coral biology, ocean physics and chemistry, climatology, and numerical modeling. It also requires developing working hypotheses based on the earlier observations and theories and test them with articulated observation tools and further revise the hypothesis with new information. Human activities are increasingly influencing the chemistry of the sea surface notably, acidify the surface ocean by emitting CO_2 into the atmosphere. Due to the pressing need to estimate the effect of surface ocean acidification on the calcification of corals, scientists are increasingly paying attention to understand the coral calcification process in molecular and genetic levels; therefore, the so-called "vital effect" will be better constrained in the near future. New metal isotope proxies have been entered into the existing pool of proxies, thanks to the advancement of the analytical instruments for small-size samples and concurrent new measurements in the oceanic waters and biogeochemical models to interpret the past changes in the sea. It may be apparently more difficult to decipher the meaning of proxies embedded in coral in the context of the ocean and climate change compared to other physical proxy depositories such as ice core, bottom sediments, but as the apparently complex coral biomineralization process is being uncovered recently and climate and ocean modeling is rapidly advancing, coral proxy studies will be greatly benefited from these developments and subsequently contribute to advancing our scientific knowledge on ocean changes and global climate. After all life form appeared as a result of interaction among nutrition, genetics, and biochemistry of corals; therefore, coral skeleton will offer many aspects of environmental and climate information to us, particularly in the Indo-Pacific Area.

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7 Synthesis and Future Perspectives on the Coral Reefs in the Western Pacific Region

Jing Zhang, Gi Hoon Hong, R. John Morrison, and Thamasak Yeemin

Abstract

Being one of the older marine organisms, corals have existed on this planet for more than several hundreds of millions of years and serve as an important component in global marine ecosystems. Coral reefs provide services covering a variety of social and economic aspects affecting the life and welfare of millions of people in the Western Pacific Region. Coral reefs also protect marine environments in low latitude zones that help to reduce the impacts from global climate changes. However, the future of coral reefs in the Western Pacific Ocean and particularly tropical and subtropical areas relies on the behavior of human beings at regional scales, as well as the interactions with changes in global climate. Uncertainty exists in the predictions on how coral reefs will cope with the complex interactions between various external forcings on this planet over the next century.

Keywords

Western Pacific Ocean · Coral reefs · Multiple stressors · Ecosystem sustainability · Future development

7.1 Introduction

The oceanic waters adjacent to the low latitude member states of the sub-commission of the UNESCO International Oceanographic Commission for the Western Pacific Region (IOC/WESTPAC) are characterized by the extensive development of shallow coral reefs. The coral reefs in the region cover about 300×10^6 km^2 of ocean surface area and have been estimated to provide, annually, ecosystem services ranging from 570 billion to ~33 trillion US dollars (Wilkinson 2000; Veron et al. 2009). Thus, the coral reefs in the Western Pacific Region are of paramount importance in the regional economies and welfare of human society. These coral reefs have developed in the oceans of this planet over hundreds of millions of years, starting from early Mesozoic Era (250–220 Mya). The term "Anthozoa" (i.e., corals) include three classes, Octocorallia, Hexacorallia, and Ceriantharia, in which Hexacorallia is composed of coral reef builders, the stony corals (Scleractinia), sea anemones (Actiniaria), and zoanthids (Zoantharia) (https://en.wikipedia.org/wiki/Anthozoa). The modern corals include ca. 6323 species worldwide (Appeltans et al. 2012). In the Indo-Pacific Region, reef building corals have more than 600 species, and the number of coral species that form symbiosis with zooxanthellae accounts for >75% in the world (Veron et al. 2009 and 2015; DeVantier et al. 2020), most of which are distributed in shallow waters of tropical and subtropical regions of the global ocean. In the Western Pacific Region, coral reefs can be found between 40° N and 40° S, where they contribute to ecosystems as individual reefs making archipelagoes, groups of atolls/lagoon-islands spreading all over the tropical waters, and reef flats adjacent to the coasts and/or islands (Chin et al. 2011).

Coral reefs have been incorporated into the entire range of anthropogenic activities since the beginning of human settlements. For example, coral reef ecosystems have been exploited for food items such as fish, holothurians, and seaweeds; they have been mined for use as construction

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materials, such as road fill sand, bricks, house-building and/or making cement, etc. These activities can be traced back to thousands of years ago, well before the modern era. Skeletons of some rare coral species have been used historically for decoration, jewelry, and/or currency for trade and industry. This may have accelerated their disappearance and extinction on this planet. Pearls were harvested from pearl-rearing oysters inhabiting in the coral reefs (http://www.sustainablepearls.org/pearl-farming/ecology/coral-reefs/). In modern societies, coral reefs have become even more valuable resources as sustaining pillars of regional economies, through tourism and fisheries. However, anthropogenic perturbations super-imposed by the large magnitude of climate variability have impaired the functions of coral reefs in many low latitude maritime countries over the last 500 years worldwide, including the tropical Western Pacific Ocean (Bellwood et al. 2004; Hoegh-Guldberg et al. 2007). Although detailed discussions of the anthropogenic forcings on the coral reefs would include a lengthy list of human activities, some of the more important issues are commented on below:

- In coastal areas, coral reefs serve as protection and buffering zones against damage caused by the oceans, such as tropical storms and strong waves (e.g., surges). They help to minimize serious coastal erosion on the adjacent land mass. This nearshore land is often the best agricultural area in these tropical locations.
- Coral reefs help to maintain the high level of biodiversity of marine ecosystems, particularly in the Western Pacific Region, where they provide habitats for many precious and rare biological species with rich genetic resources located close to both coastal and open ocean waters through system connectivity. Damage to coral reefs has induced an irredeemable impact on the function of marine ecosystems.
- Coral reefs play an important economic role for maritime countries that can be linked to the wealth of society. The most direct benefits include tourism and fisheries. The renewable resources in tropical areas rely on the health of coral ecosystems. In many tropical and subtropical countries, deterioration of coral reefs has become a barrier to economic progress.

Sound and sustainable management strategies should start from a comprehensive scientific understanding of the coral reef ecosystems. Here our purpose is intended to serve as a reference guide for college students, postgraduate fellows, coral reef park managers, and relevant administrators in the Western Pacific Region. In the broad Western Pacific Region from north to the south, six tropical countries (i.e., Indonesia, Malaysia, Papua New Guinea, the Philippines, Solomon Islands, and Timor-Leste) are of concern in the Coral Triangle Initiative on Coral Reefs, Fisheries and Food Security (CTI = CFF, http://www.coraltriangleinitiative.org/), where nearly 30% of the world's coral reefs and 75% of all known coral species are found (Burke et al. 2012).

In this monograph, we try to revisit the major issues resulting from changing climate and anthropogenic perturbations on coral reefs in the Western Pacific Region. As in other tropical and subtropical marine environments, coral reefs in the Western Pacific Ocean have suffered from increased external forcings, such as global warming, sea level rise, and surface ocean acidification, which together with the land-use changes and direct (e.g., coral mining) and/or indirect (e.g., illegal fishing) exploitation activities have created much uncertainty regarding the fate and destiny of coral reefs. Based on an understanding of the nature and impact of the identified changes, plus an analysis of existing data and knowledge, we summarize the major findings of coral reef studies in the Western Pacific Region and raise a number of issues for consideration in future developments.

7.2 Function of Coral Reefs in a Sustainable Anthropocene

Large-scale environmental perturbations caused by the changes in climate and prolonged anthropogenic activities may shift coral reefs from healthy symbiotic coral regimes to barren rocky surfaces (Fig. 7.1). There exist synergistic and antagonistic effects with regard to the situation of multi-stressors (driving forces) and interactions of external forcing and coral reef, which amplifies the uncertainty of prediction for the responses of coral ecosystem to the changing external pulse. The synergistic effect can impair the resilience of coral reefs against the external forcings, while antagonistic character will visually make the systems not sensitive to the environmental changes. For example, removal of herbivores (e.g., fish and sea urchins) via overfishing, through diseases, or through excessive nutrient loadings allows macro-algae to overgrow the reef, and the coral symbiont zooxanthellae became unable to synthesize food for corals. Thus corals eventually die and the coral reefs became barren rock. Such "regime and/or phase shifts" have been observed in coral reefs in the Atlantic, Indian, and Pacific Oceans (Kleypas and Yates 2009). In fact, the so-called regime/phase shifts occur in processes of a multiple-step fashion, and the ecosystem may undergo several quasi-stable stages where each transit condition with resistance as resilient ability of system can be regarded as separate "regime" and/or "phase" for a given time and at specific space dimensions.

In a natural ecosystem, coral reefs rely on the food and energy from autotrophic endo-symbiotic zooxanthellae (e.g., dinoflagellates) and capturing planktonic prey through heterotrophic feeding. In coastal waters adjacent to human

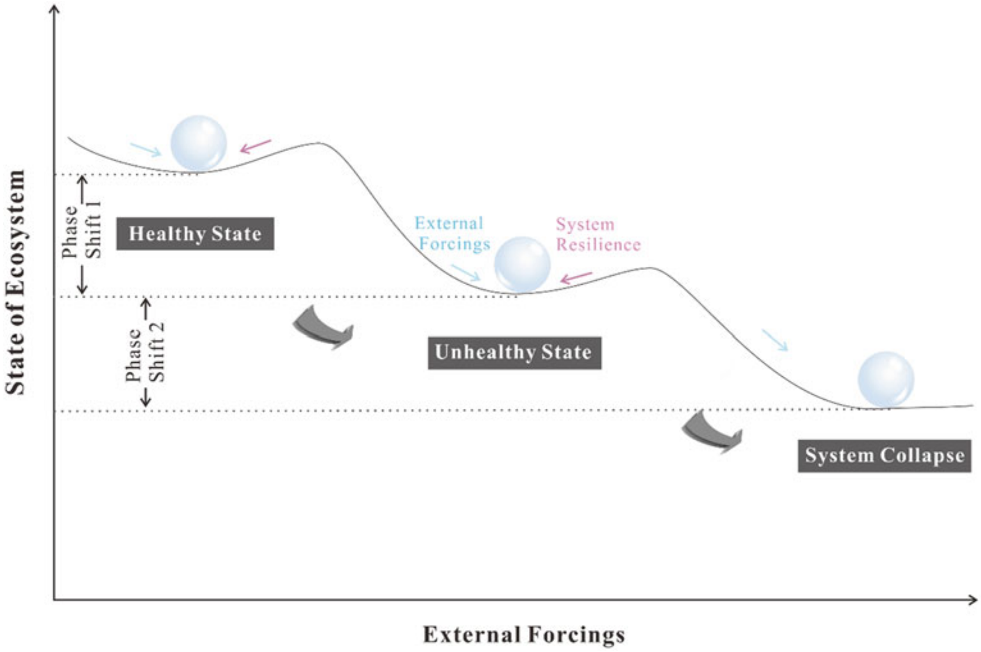

Fig. 7.1 Conceptual illustration of regime and/or phase shifts for coral reefs under the perturbation of combined external forcings and system resilience, with illustrations of different and/or intermediate phases/ regimes of state of ecosystem along with the combined stressors. In reality, there exist several/different intermediate phases/regimes between original state and system collapse, for example, the regime/ phase shifts from a dominance by hard corals to turf and macro-algae and even to rocky landscape, while the figure shows a simplified case. In the case of interactions among multi-stressors, the synergistic effects can amplify the impacts of external pulses, while antagonistic behaviors tend to increase visually the resilience of coral reefs. Note that in the figure, temporal scale is not included

settlements, over-enrichment of nutrients often occurs, and this promotes blooms of macro-algae to outcompete reef building corals for habitats and other limiting micronutrients (e.g., trace elements). The proliferation of macro-algae favors herbivorous swimmers and benthos over omnivorous species. The species compositions of swimmers and benthos (e.g., fish) are consequentially followed. Some of the sea urchins, such as black long-spined species (*Diadema antillarum*), can eat coral-smothering algae in reef systems (https://www.sciencedaily.com/releases/2001/07/010730081053.htm), but incursion of sea urchins due to overfishing (i.e., removing sea urchin predators) facilitates rapid grazing of crustose coralline algae (O'Leary and McClanahan 2010). This can remove and/or retard coral recruits and erode the coral surface and hence push the coral-zooxanthellae symbiosis towards bleaching and rocky collapse. Incursion of coral-eating starfish (e.g., crown-of-thorns starfish, *Acanthaster* sp.) due to pollution and agricultural runoff may occur (Pratchett et al. 2017). Coral diseases often occur in nearshore and eutrophic coastal waters, resulting in coral bleaching and reproductive system and genetic damage, driving the whole system from an autotrophic to a heterotrophic status.

In the coastal environment, land resources-related drainage of pollutants is usually the critical factor that initiates water quality deterioration and promotes eutrophication and, in certain circumstances, the hypoxia and even anoxia of benthic systems. Coastal eutrophication can be characterized by changes in turbidity, nutrients as well as dissolved organic carbon in the water column, and an increase in harmful algal blooms with accumulation of some kinds of biotoxins in organisms. The blooms of algae can be either indigenous through competition for limiting nutrients or invasive species that are related sometimes to shipping activities (e.g., discharge of ballast water and leach of ship hull coatings).

Although large-scale changes such as global warming, sea level rise, and surface ocean acidification are considered as the important (negative) external forcings on the sustainability of coral reefs in the Western Pacific Ocean and in other oceanic tropical and subtropical sectors, they all are of large/worldwide, slow, and persistent nature. For example, the rate of sea level rise is a few millimeters per year in the tropical Western Pacific Region countries; pH of surface seawater has been reduced by 0.1–0.2 units over the last several hundreds of years. On the other hand, anthropogenic perturbations, such as eutrophication and dumping of wastes, are local or regional in nature with small areal scale and high temporal frequencies. In the coastal environment, sea level, surface temperature, and seawater pH experience large-scale daily as well as seasonal variability. Sea level in coastal areas can be a difference of several meters between high and low tide periods, and sea water pH values can differ by 0.5–1.0

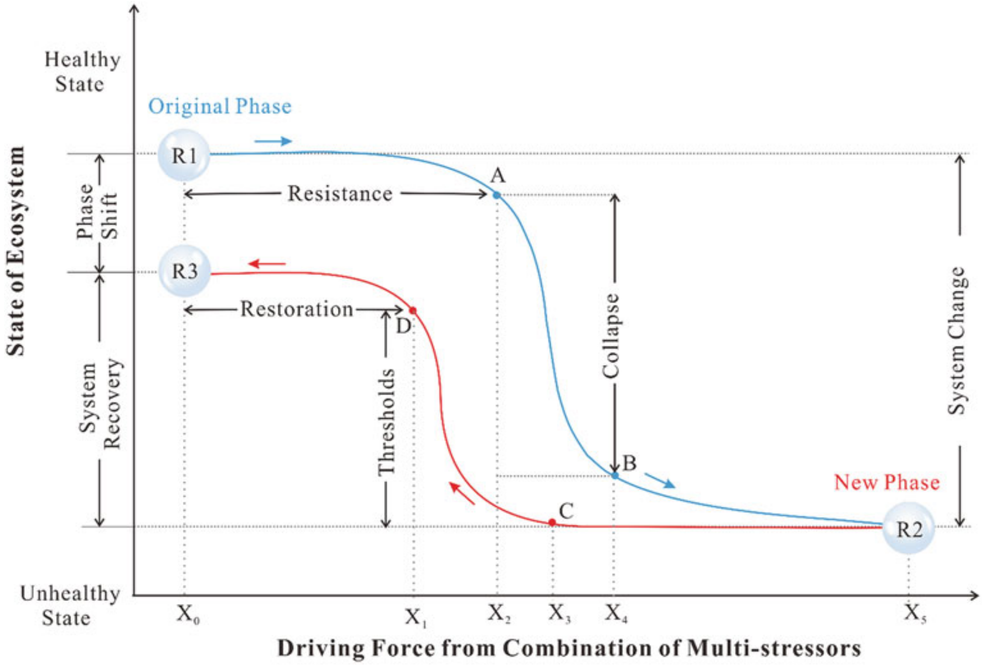

Fig. 7.2 Resistance, hysteresis, and threshold of system transformation of coral reefs. Under the impact of driving forces, original coral reefs (R1) may illustrate resilience (X_0–X_2) before collapse (X_2–X_4) to a new phase (R2). While recovery of coral reefs may be more difficult and suffering, there is threshold (X_1–X_3) before the reefs can reach the observed recovery and system stability (i.e., restoration in X_0–X_1). It is unexpected that the changes in coral reefs are irreversible, and hence there is still phase/regime shift between original status (R1) and system recovery (R3). Note that in the case of combination of multiple stressors, there exists lag/delay of system response, such as X_5–X_3. In the stage X_2–X_4, the synergistic effect can induce cascading consequences of system response. In the stage of X_3–X_1, the system response can be delayed and/or there is a lag related to the antagonistic effects

unit between day (photosynthesis dominance) and night (respiration dominance) time. These magnitudes in changes are far greater than those of the slow warming and surface ocean acidification in the ocean basin scale. Thus, the fringing reefs may have adapted to higher variability of the change in sea level, sea surface temperature, and seawater pH and hence be more resistant to the external perturbations than the coral reef ecosystems (e.g., atolls) in the open ocean situation.

Another important aspect of coral reefs is the hysteresis effect in the structure and function of ecosystems. Between different regimes, there are usually barriers and/or obstacles, because of the nature of system resilience (Fig. 7.2). In this case, release of external forcings and/or removal of anthropogenic perturbations does not necessarily mean that the ecosystems will immediately return and/or shift back to its original state. Sometimes, the full recovery of a damaged ecosystem will never happen (Wilkinson et al. 2005). What is more common is that changes in ecosystems can be slow and often irreversible, and the consequences can be delayed (lag) and even unexpected based on state-of-the-art knowledge. Therefore, new regimes/phases often emerge due to the complexity of interactions among the constituents of the coral reef system that we do not yet fully understand. Moreover, it should be kept in mind that the complex interactions between driving forces and system behaviors include synergistic and antagonistic effects of external pulses and cascading consequences of coral reefs, which in combination will result in a lag of recovery of coral reefs (Ellis et al. 2019). In the case of synergistic effect, the impact of individual stressors is amplified, while antagonistic behavior will make the system more resilient against the combined external pulses. For example, increased levels of ultraviolet radiation can damage photosynthetic cells, which in combination with thermal stress can accelerate and exacerbate the coral bleachings (Radice et al. 2020). Nevertheless, elevated $p\mathrm{CO}_2$ and low pH associated with upwellings are considered stressors with negative effects on the reef metabolism; coral calcification is autotrophy-enhanced process with photosynthetic drawdown of seawater CO_2 concentrations that elevates Ω_{ar} and hence favorable for organismal $CaCO_3$ deposition (Yeakel et al. 2015).

7.3 Coral Reefs in the Western Pacific Region and Comparison to Other Areas

Coral reefs are found in the low latitude zones of the Western Pacific Ocean and the adjacent coastal seas, covering wide areas in tropical and subtropical climate (i.e., between 40 °N and 40 °S), and illustrate a spectacular landscape on this plant, in comparison to Indian Ocean and Atlantic Ocean (Fig. 7.3). As coral reefs are increasingly important for the human society in the broad Indo-Pacific Region in terms of economic value, cultural heritage, and aesthetic status, wise management is urgently needed in the current phase of climate change response and rapid expansion of various economic activities centered around the coral reefs (e.g., tourism).

Globally, the total area of coral reefs has decreased by almost a half from 62 million hectare (ha, 1 ha = 10^{-2} km^2) in 1977 to 28 million ha in 2001 that is equivalent to 280×10^3 km^2, i.e., a reduction of ca. 50% in the last quarter of the twentieth century (Spalding et al. 2001; De'ath et al. 2012). The unit ecosystem service value of coral reefs has been estimated to be on average US $352,249 per ha/year (i.e., $36,794 to $2,129,122/ha/year) in 2007 dollar value (Costanza et al. 2014). The services provided annually by coral reefs include food (e.g., 5–15 tons of sea food/km^2), 150×10^3 km long shoreline protection from storms and erosion, about 15% of gross domestic product (GDP) in the world, and largely untapped sources of natural products with enormous potential as pharmaceuticals, nutritional supplements, enzymes, pesticides, cosmetics, and other novel commercial products. The total area of coral reefs in the Western Pacific Region is more than 134,860 km^2 and accounts for close to the half of the world area of the coral reefs. Moreover, the Indo-Pacific Region as a whole accounts for more than 90% of the global shallow coral reefs as shown in Spalding et al. (2001) and also in Table 7.1. It should be noted, however, that most of coral reefs are claimed within the Economic Exclusive Zones (EEZs) of individual countries, one or another, in the tropical and subtropical climate region. Given the fact that the claimed EEZs by different countries in the Western Pacific Ocean have conflicts of political interests and differences in economic demands, the reef areas and associated populations shown in Table 7.1 may have overlaps, and hence interpretation should be with caution.

Tropical and subtropical areas of the Western Pacific Region include a human population of ca. 1 billion of people, including mainland and island countries (Spalding, et al. 2001). Most maritime countries in this region rely on the services provided by coral ecosystems (e.g., coral reefs) as an important component of their GDP and national treasuries, based on fishery, tourism, pharmacology and manufacturing industry (e.g., natural products), and richness in biodiversity due to the structural complexity of their habitats (hotspots) generating multiple ecological niches for thousands of associated biological species, from microbial communities to the top predators (Roberts et al. 2002). This biodiversity (species) richness and heritage favor reef stability and provide benefits to human society (Rabosky et al. 2018). Such services have become indispensable to the daily life of millions of people in the coastal areas of the Western Pacific Ocean.

It has been reported that about 727 hermatypic coral species in 13 families are found in the Western Pacific Ocean (Bellwood et al. 2005), as the area is the most important on this planet for coral ecology and landscape (Roberts et al. 2002). In particular, East Indies Triangle (i.e., Indonesia, Malaysia, New Guinea Island, and the Philippines) is known to be the area of a global maximum for species diversity for several marine taxa, including fishes, corals, lobsters, and snails, and those species diversity is found to be decreased away from the triangle (Reaks et al. 2008). In most areas of the Western Pacific Region, coral reefs have exhibited various impairment symptoms depending on the type of external perturbations, locations, and temporal scales. Some important and negative impairment syndromes of coral species which hence lead to loss of ecosystem function in the Western Pacific Ocean can be summarized as below:

- Coral bleaching can be related to different forcing factors, such as changes in sea surface temperature, UV radiation and inhibition, overloading of sediments and change in turbidity, and nutrient (sewage) dumping by the local population.
- Coral diseases caused by bacteria and viruses are usually related to the deterioration of water quality, such as drainage of pollutants from adjacent land sources as well as the changes in seawater thermal conditions (e.g., temperature).
- Change from healthy corals to macro-algae-dominated systems and then rocky landscape can be a result of either over-enrichment of terrestrial nutrients (i.e., bottom-up) or overfishing of herbivores (i.e., top-down), or both.
- Release of predation pressure could decimate the coverage of live corals on the reef and consequently free space for algal growth (i.e., outbreaks of coral tissue-feeding crown-of-thorns sea stars).
- Loss of habitats provided by the coral reefs can also be a consequence of illegal fishing, mining and coral reclamation, as well as the damage by natural factors, such as the typhoon and tsunami and bleaching under high sea-surface temperature (SST).

In the Western Pacific Region, climate variability and anthropogenic perturbations have been recorded in the coral bands of reefs. For example, coral samples from Guam illustrate an increase of more than two orders of magnitude in the levels of $^{239+240}$Pu since the 1950s, resulting from atomic bomb tests in the subtropical Pacific Ocean. Moreover, the accumulation of radionuclides in corals showed a similar pattern to the worldwide $^{239+240}$Pu depositions from global fallout (Lindahl et al. 2011). In the subtropical Western

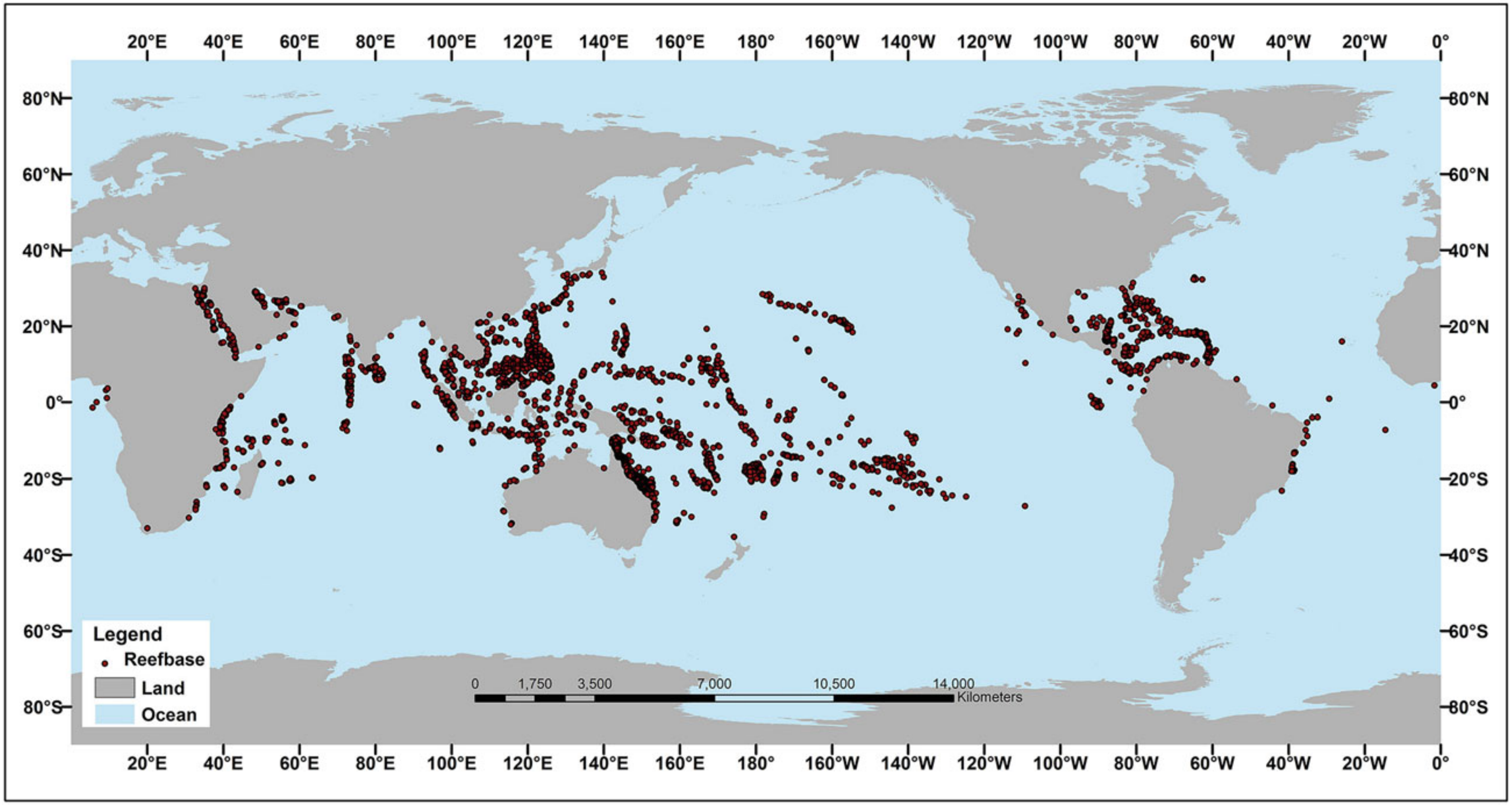

Fig. 7.3 A global view of the distribution of coral reefs in the region of 40 °N to 40 °S, seen from space. The figure is a composite image based on the data of satellite. In the figure, distribution of coral reefs in the Western Pacific Ocean is outstanding in comparison to other tropical and subtropical areas, such as Atlantic and Indian Oceans. This figure is from NOAA: "In what types of water do corals live? National Ocean Service website, web-site at https://oceanservice.noaa.gov/facts/coralwaters.html, renewed on 01/07/2020"

Table 7.1 Reef area (km^2) and population protected by coral reefs in the wider Western Pacific Ocean. Data are from Spalding et al. (2001) and Pendleton et al. (2016) with update from Burke et al. (2012)

Western Pacific Region	Reef area (km^2)	Population protected by coral reefs (inds.)
Australia	48,960	316,027
Bangladesh	50	1318
China	2450	1,212,378
Fiji	10,020	383,845
Indonesia	39,358	12,198,508
Japan	2900	623,273
Malaysia	2935	1,142,333
Philippines	22,484	12,963,66
Samoa	490	316,027
Singapore	13	78,342
Solomon Islands	5750	307,616
Thailand	2130	233,667
Tonga	1500	84,729
Vietnam	1270	1,581,789
Kiribati	2940	110,000
Marshall Islands	6110	65,000
New Zealand	150	No data
Palau	1150	6000
Papua New Guinea	13,840	750,000
Timor-Leste	350	15,000
Vanuatu	4110	42,000
American Samoa	220	1500
Commonwealth of Northern Marianas	88	33,000
Federated States Micronesia	4340	65,000
French Polynesia	6000	125,000
Guam	220	55,000
New Caledonia	5980	95,000
Wallis and Futuna	940	5000
Western Pacific Region Total	208,398	18,669,683

Note: According to Davey (2015), New Zealand in the strict sense does not have any coral reefs—rather it has coral colonies located in the northernmost islands (i.e., Kermadec Islands, Bay of Islands, etc.)

Pacific Ocean, anthropogenic lead concentrations in the reef-building corals have increased by more than fivefold in the twentieth century, and stable isotope ratios of lead (e.g., $^{206}Pb/^{207}Pb$ vs $^{208}Pb/^{207}Pb$) in corals provide clues as to the different sources, i.e., Australian mining Pb, Chinese loess, and lead deposition from gasoline exhausts via atmospheric depositions (Inoue and Tanimizu 2008).

In coastal areas of Thailand, coverage of hard corals (%) and related fish abundance are negatively correlated with the quality of ambient seawaters. Particularly, a reduction of coral coverage is observed when the area is affected by nutrient sewage inputs from adjacent land use (Reopanichkul et al. 2009). Along the coast of Thailand, corals are replaced by macro-algae where influx of nutrients and turbidity are both increased, and dissolved oxygen contents decrease due to the enhanced (high) level of sewage discharges from adjacent land-based sources.

In the Great Barrier Reef off the eastern Australia, it has been found that coral bleaching is regulated by a combination of thermal stress (i.e., sea surface temperature) and surface runoff from adjacent land-based activities, such as pollution (Furnas et al. 2005). In areas affected by flood plumes from river with higher nutrients and *Chl-a* levels (i.e., inshore), temperature and exposure time of thermal bleaching of corals have lower resistance compared to reef systems further offshore, and a reduction of 1 °C–2 °C of bleaching threshold was observed for the inshore reef systems affected by the surface runoff (Wooldridge 2009). Reduction of nutrient input (i.e., dissolved inorganic nitrogen, DIN) from adjacent land sources was reported to induce an increase of resistance of coral reefs to thermal bleaching (i.e., higher threshold) again.

7.4 External Forcings and Systems Response Threats to Coral Reefs in the Indo-Western Pacific Region

Threats to the health of coral reefs range from the sudden increase of sediment and nutrient loads to coastal areas resulting from human activities, surface ocean warming, and acidification due to the emission of greenhouse gases through industrial activities, to the underlying climate change resulting from the periodic orbital variations (e.g., Milankovich Cycle).

The deterioration of coral reefs is manifested by the suppressed growth and survival of hard coral colonies, coral reproduction and recruitment, and disturbance of the previous interactions of coral populations with other organisms (e.g., coralline algae, bioeroders, macro-algae and heterotrophic filter feeders, pathogens, and coral predators), which has been recognized an impact with negative consequences, for example, coverage and mortality, fecundity and recruitment, photosynthesis, symbiont, and calcification (Jones et al. 2015). An increase in nutrient supply (i.e., eutrophication) from the coastal cities and tourist industries may induce the blooming of crustose coralline algae and/or even macro-algae, forming mucous sheets enveloping the colony's surface and trigger or aggravate coral diseases (Bessell-Browne et al. 2017). This results in consequences of calcification, fecundity, and larval survival to decrease (Szmant 2002; Fabricius 2005; Costa et al. 2008). Increase in terrestrial sediment load to the adjacent coral reefs can increase water turbidity and reduce the underwater light field (e.g., photosynthetically available radiation and quantum yield), which can lead to declining coral cover and diversity and decreased recruitment of juveniles (Fabricius 2005; Cooper and Fabricius 2007). Drainage of pollutants, including sub-marine ground sources and discharge of ballast waters, may also induce lower symbiont zooxanthellae density, reduced recruitment, and increased possibility of infection by diseases (Laporiade 1997). Furthermore, eutrophication modifies the interactions between microbial loop and the main food chain in the reef areas, which alters the pathway of material flow and energy partitioning in the system, with proliferation of heterotrophic bacteria. In the case when hypoxic water develops, benthic system can be also negatively affected.

Coastal reclamation, including construction of airfields and resorts, as well as lime production using corals, can significantly damage and/or even destroy the whole adjacent coral reef (Maragos et al. 1996). Furthermore, different fishing activities, such as selective fishing on top-predators vs herbivores, may also affect the habitats through changing competition among corals, macro-algae, and turf algae (Walsh 2011). All the stressors mentioned above are related to human-designed/intended activities within the adjacent watersheds and/or even in the marine environment itself (e.g., overfishing and illegal fishing activities). Nevertheless, changes in food-web structure of coral reefs can affect the coral coverage and symbiont relationships, for example, an increase in biomass of filter feeders and grazers, resulting from land to sea gradients (i.e., inshore–offshore) created by the land-based human activities (Fabricius 2005; Kleypas et al. 2006).

Last but not the least, climate variability and a slow but consistent trend of warming/sea level rise and ocean acidification also have negative but not to be underestimated impacts in the Western Pacific Region. For example, calcification and growth rates of coral communities all decrease along with the increase of $p\mathrm{CO}_2$ and reduction of Ω_{arag}, i.e., the saturation of aragonite in surface seawater (Kleypas et al. 2006; Kleypas and Yates 2009). In the high CO_2 and SST oceanic waters, the combined effects of thermal and pH stressors make the system calcification more difficult because extra energy is required to maintain the function of H^+ and Ca^{2+} gradients in the cell. At the same time, respiration can be higher than the rate of system photosynthesis. Using $p\mathrm{CO}_2$ and SST as independent variables, the model prediction indicates that at $p\mathrm{CO}_2 = 450$ ppm (v/v), the calcification rates of corals in the Western Pacific Ocean can be reduced by 50% (Kleypas and Yates 2009).

7.5 Summary and Main Conclusions of This Study

The present book is composed of five cross-linked chapters based on the digestion of research data that is focused on the Western Pacific Ocean, covering broad interests and including anthropogenic environmental impacts on coral reefs, coral biology and reef ecology, biogeochemical cycle of coral systems, proxies to understand climate and anthropogenic processes, and tracers embedded in coral skeletons that can explain various aspects of research results in the science of coral reefs (Fig. 7.4). Although the mission of this monograph is largely scientific in nature and is contributed by the research community of the Western Pacific Ocean, the knowledge summarized within is equally applicable to the Indian and Atlantic Oceans and thus helpful in configuring research and designing management in other parts of the world. In this section, the major findings of this monograph will be discussed and synthesized below based on the snapshot of individual chapters.

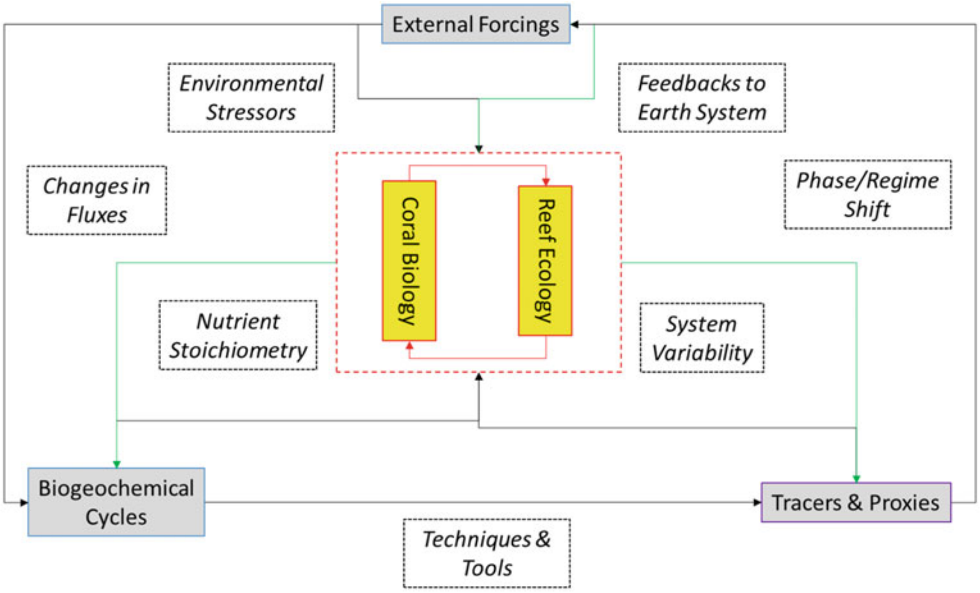

Fig. 7.4 Structure of present monograph, illustrating the cross-link of individual chapters that cover the major aspects of coral reefs study and challenges of coral reefs of Indo-Pacific Oceans. In the figure, five cross-linked chapters are indicated by shadow boxes; box with italic words illustrates the potential interactions between different chapters. Green arrows emphasize the impacts of coral reefs; otherwise, black color is used in the figure

7.5.1 Anthropogenic Impacts Become Dominant Issues for the Sustainable Development of Coral Reef Systems

Coral reefs are among the most important ecosystems globally. They provide food and construction materials for millions of people living in the tropics, but this use of the reef by humans comes at a cost. The major drivers of the many anthropogenic impacts on the coral reef environments in the Southeast Asia and Pacific Island region include increasing overall populations, increasing migration of people from inland to coastal areas, and issues relating to subsistence and low-income community's response to the global economic situation through their changing use of reef resources, e.g., increased reef gleaning. Pollution from small-scale and/or local developments can be linked to, for example, urbanization and industry, as well as impacts from other human activities including agriculture and aquaculture, tourism such as construction of resorts and diving facilities, mining, commercial fishing including marine and coastal mariculture. Relevant issues like land-use changes, coastal erosion, sedimentation, and eutrophication are recognized as being of major importance. Related impacts caused by coastal city expansion (e.g., building of ports and marinas, roads, industrial areas, waste management—including location of "landfills" and sewage treatment facilities) have received a good deal of attention, and we now have a reasonable understanding of the nature of their impacts. The significant impacts of shipping and trade activities (e.g., oil spills, reef collisions, waste disposal, antifouling materials) are also considered. The problem of plastics has come to the fore in recent years (Law 2017), with substantial quantities of plastic materials being found near most coastal population centers, and they are found in the bodies of a large number of coral reef organisms (Reichert et al. 2018). A comprehensive listing of the anthropogenic activities impacting on coral reefs, together with a review of the impacts from each type of activity, shows that the influence of anthropogenic activities can be dramatic in the absence of good legislation, management planning, and the effective implementation of both.

These direct impacts of humans can be enhanced by indirect effects of climate change (e.g., temperature, rainfall, acidification, sea level rise, and tropical storms) that are superimposed on the direct anthropogenic impacts. Hydrodynamic patterns around coral reefs are also altered by anthropogenic activities. The driving forces based on the impact types (e.g., hydrodynamics changes, sediment fluxes, nutrient flows, contaminant mobilization/transport/transformation) and the consequences for coral reefs of changes in these driving forces are discussed in the previous sections of this monograph.

Pollution can occur from many sources. These include small-scale developments, e.g., tourism and local industry (e.g., diving, construction of resorts and harbors), as well as impacts from large (watersheds)-scale human activities including agriculture, urbanization, extraction of resources (mining), commercial fishing, and marine and coastal mariculture. Pollution can also be from marine sector itself, such as those related to shipping activities, oil platforms and oceanic trade, for example, discharge of ballast waters may introduce alien species and external nutrients. Issues like land-use change, sedimentation, and eutrophication cause serious problems over wide areas of the region. Throughout the Western Pacific Region, coastal city expansion (e.g., building of ports, roads, industrial areas, housing and sites for waste management—including location of "landfills" and sewage treatment facilities) is problematic, often leading to pollution, sediment mobilization, displacement, and burial of reefs. Another problem for most governments in the Western Pacific Region is the significant impact of shipping activities and ship repairing in yard, including oil spills, reef collisions, waste disposal, and antifouling material handling and management, particularly in the Southeast Asia.

A comprehensive listing of the activities impacting on coral reefs, together with a review of the impacts from each type of anthropogenic activity, has been developed (Table 2.1 in Morrison and Aalbersberg, Chap. 2). This list, when complemented by commentary on the effects of climate change that are superimposed on the direct anthropogenic impacts, such as temperature, rainfall, acidification, sea level rise, and storms, provides a mechanism for developing a comprehensive picture of human impacts in any selected area. This information will assist environmental decision-makers in determining a priority order of actions that need to be addressed given local political and economic conditions.

7.5.2 Coral Biology Is Critical in Our Knowledge of Tropical and Subtropical Environments

Understanding coral biology is crucial for coral reef management under the crisis of global change. This monograph provides updated knowledge on several important aspects of coral biology with focus on the Western Pacific Ocean. The aspects include coral bleaching, coral diseases, coral genetics and sexual reproduction, developmental biology, and recruitment in corals. Studies on coral bleaching have focused on spatial and temporal variations of bleaching events, causes, mechanisms, and consequences of coral bleaching impacts. The severe coral bleaching events were observed in the years 1998 and then 2014–2017. Due to global warming and the transition to Anthropocene, coral bleaching is occurring more frequently in all El Niño–Southern Oscillation phases, increasing the annual coral bleaching in the next decades. The mechanisms in which the coral and its zooxanthellae are impacted by high temperatures and the initial cellular responses to the stress are intensively examined. Effects of coral bleaching on coral reef ecosystems include a decrease in net rates of calcium carbonate accretion and changes in primary productivity.

Coral diseases have the potential to significantly affect corals and their community structures. Several studies illustrated coral disease prevalence in Indo-Pacific reefs which is linked to local anthropogenic disturbances, such as eutrophication, sedimentation, land-based pollution, marine debris, and increased ocean temperatures. Several case studies of the identification and transmission of coral diseases are documented. Plastic waste can enhance microbial colonization by pathogens implicated in outbreaks of disease in marine ecosystems. The proposed prevention of coral diseases includes policy, management and good practice, technical methods, and coral genetic selection. The methods for the prevention and therapy of coral diseases are recently proposed.

Coral genetics have been intensively examined, particularly for research applications in molecular taxonomy and systematics as well as coral population genetics. The proposed integrative classification system will form the framework for more accurate biodiversity estimates and guide the taxonomic placement of extinct species. Molecular studies have been instrumental in refining species boundaries in the coral species complex and revealing hidden species diversity. Mitochondrial molecular phylogenies are congruent with groups based on gross morphology, therefore reflecting species-level differentiation. Population genetic studies based on genotypic information using molecular markers have clarified genetic diversity and connectivity, clonality, and species diversity, particularly cryptic species and coral population adaptations. Gene flow is also useful for investigating the expression of population dynamics. Population genetic studies are useful for estimating reproductive features and past events based on the extent of genetic differentiation in populations from different locations.

Advances in coral sexual reproduction, fertilization, hybridization, development, and recruitment are highlighted in this study. Coral spawning is often presented as synchronized phenomena. The important controlling factors include temperature, solar irradiance, wind, lunar cycles, and sunset times. Several coral species from some reef sites have lost their reproductive synchrony. Ultimately, such a synchrony breakdown reduces the probability of successful fertilization, resulting in the reduction of new recruits, which may drive coral populations to extinction. The *Acropora tenuis* had a mixture of gametes from more than six intraspecific colonies and could achieve stable fertilization rates of greater than 95%. Synchronous spawning occurs among many *Acropora* species, and crossing experiments have shown that some species can hybridize in vitro. Some products of interspecific hybridization may persist as the offspring of self-fertilizing F1 hybrids. The developmental biology of corals reveals that there are two major groups, the “complex” and the “robust.” One apparent difference between these two major groups is that before gastrulation the cells of the complex corals thus far described spread and flatten to produce the so-called prawn chip, which lacks a blastocoel. Understanding coral recruitment patterns for effective coral reef management is very important. Recruitment rates and juvenile abundance were lower on the more degraded reef. These patterns are likely a consequence of differential pre-and post-settlement mortality as a result of the high sedimentation rates and degraded conditions and possibly reduced larval supply.

7.5.3 Coral Reef Ecology Bridges System Functions and Adaptive Management Towards a Sustainable Development

The important information on coral reef biodiversity decline and extinction risk, coral reef recovery after disturbances, coral reef resilience, coral reef connectivity, coral reef bioerosion, coral reef refugia under global change, marine protected area networks, and passive and active restoration of degraded coral reefs is synthesized in this monograph. Coral reefs are critically important to the economic development of most tropical and maritime countries. The loss of vulnerable species from coral communities is occurring at an accelerating rate, particularly in the Western Pacific Region. Many coral species are impacted by anthropogenic perturbations, especially those in the coastal waters which are at risk. Coral reef recovery following severe disturbances depends on several complicated factors, including resistance and tolerance to external forcings, recruitment rate, reef connectivity, and local stressors. Some resilience factors have the potential to operate within the predicted annual frequency of thermal stress events, whereas others act over longer timescales. The resilience assessment involves assessing ecological factors that contribute to resistance and recovery, particularly bleaching-resistant coral species and coral recruitment and anthropogenic stressors that reduce resilience. Managers can use the resilience index to compare coral reef resilience levels among reef sites and times for global coral reef resilience assessment. The main goal of resilience-based management is to identify and prioritize management actions that enhance system resilience. Maintaining reef framework is also very important, particularly taking into consideration the bioerosion rate at a degraded reef. Reef-derived carbonate and organic matter, for example, in sediments, may dissolve chemically, at a rate correlated with the aragonite saturation state of the overlying seawater column. The biologically driven erosional processes are associated with the grazing activities of various fish and sea urchins, as well as the activities of various endolithic (internal substrate living, borers), including sponges, bivalves, worms, and microorganisms, such as cyanobacteria and fungi.

As global climate change potentially causes more frequent and severe coral bleaching events, identifying and conserving coral reef refugia is critically important. Coral reef refugia should be able to buffer regional changes in stressors related to environmental change, particularly seawater temperature (SST) and ocean acidity (pH) over decades while providing other conditions conducive to coral growth and reproduction, for a large complement of corals and associated species. Most coral reefs are in a type of marine protected areas (MPAs) that intensively require scientific data for management. Fifteen principles for integrating fisheries, biodiversity, and climate change objectives into MPA network design simultaneously were proposed. The establishment and management of MPAs and MPA networks should be based on adequate scientific information particularly to identify which areas serve as spawning, feeding, and nursery grounds and sink/source of juvenile fish/corals.

The achievements of passive and active coral reef restoration projects in the Western Pacific Region are necessarily considered for the improvement of coral reef management plans. Community involvement is very important to the success of coral reef restoration efforts, and it has the added benefit of raising awareness. The most effective and widely used method for active coral reef restoration is coral gardening. The coral gardening concept is a two-step process, i.e., the nursery phase dedicated to the development of large stocks of coral colonies in mid-water floating nurseries and the transplantation phase where nursery-farmed coral colonies, which have reached suitable sizes, are out-planted onto degraded reef areas. Integrating functional considerations into transplantation acts, such as in the use of allogenic and autogenic engineer species, could improve the impacts of restoration on coral reef biodiversity. The active coral reef restoration toolbox provided seven classes of novel avenues and tools, which include the improved gardening methodologies, ecological engineering approaches, assisted migration/colonization, assisted genetics/evolution, assisted microbiome, coral epigenetics, and coral chimerism. The guidelines for maximizing the adaptive potential of restored coral populations aimed to re-establish populations that are capable of sexual recruitment and genetic exchange. Coral larval enhancement also has the potential for increased scales of restoration on damaged reefs.

7.5.4 Biogeochemical Processes of Coral Reefs Play a Key Role in Understanding the Element Cycles and Connectivity Between Different Systems

Coral reefs in the Western Pacific Region are distributed over a wide range of different biogeochemical provinces. The coral systems can be found along water quality gradients including from reef flats in coastal (inshore) environments with, generally, a eutrophic character to the offshore barrier reefs and atolls which tend to be more oligotrophic in character. In coral reef systems, biogeochemical processes play a critical role in material flow and energy distribution among different compartments and for the maintenance of different metabolic functions. The successful symbiont relationship between coral (consumer) and zooxanthellae (producer) relies also on the sustainable provision of macro- and micronutrients. Many corals also have the ability to use heterotrophic pathways for food resources (i.e., dissolved and particulate organic matter), and hence the partitioning of material flow (nutrition) between autotrophic (i.e., photosynthesis by zooxanthellae) and external food uptake have a dramatic impact on the sustainable development of coral reefs in a changing marine environment. The influence of changing biogeochemical pathways induced by physical (i.e., hydrography and circulation), biological (e.g., food-web structure), and other factors (e.g., external forcings) on coral reefs can be in various aspects, for example, different concentrations for nutrients and their species ratio in autotrophic process, availability of dissolved and particulate organic matter in the water column as for heterotrophic food sources, and other pollutants and toxic materials with side effects such as pathogens and diseases. The responses of coral reefs to the abovementioned biogeochemical impacts include, but are not limited to, changes in the ratio between autotrophic and heterotrophic food resources for corals, calcification and growth rate, fecundity and coverage, as well as the connectivity between different reef systems (e.g., recruitment of juveniles). In the Western Pacific Region, degradation of coral reef systems has been observed almost everywhere across biogeochemical gradients (e.g., water quality as proxy) at low and mid-latitudes, from eutrophic coastal environment to oligotrophic open ocean waters (Williams et al. 2015).

In the oligotrophic waters from open and deep ocean, offshore coral reefs are facing low primary production, limited by nutrients and/or trace elements, where external forcings are linked to large-scale climate variability, such as warming and acidification. The sustainability of coral reefs in the offshore and open oceanic areas is heavily dependent on the biogeochemical processes (e.g., via upwellings) that regulate availability and supply of limiting chemical elements and the variability between new vs recycled nutrients and trace elements.

On the other side, in the nearshore environment, fringing reefs live in a condition affected by the human perturbations driven by land-based and in situ processes, imposed on the climate variability that is sometimes difficult to distinguish and separate, but together make the living situation more harsh than in the open and offshore systems. In this area, the challenge is how coral reefs can cope with the increased pollution and changes in habitats that both can be the driving forces for biogeochemical dynamics.

In addition to observations and laboratory simulations, a rather simple biogeochemical model can be developed to understand the behavior of coral and zooxanthellae symbiosis under the external forcings, such as availability of nutrients and increased temperature. The model outputs indicate that carbon transfer between zooxanthellae and the coral host and coral feeding rates both can be affected by the external nutrient concentrations and the temperature gradient. The implications include that changes in limiting nutrient species and global warming can have dramatic impacts on the sustainability of coral reefs. The potential of coupling a biogeochemical module into the 3-D hydrographic model is that responses of the coral ecosystem to environmental changes, such as the ocean warming, acidification, and coastal eutrophication, can be analyzed with fine resolutions in time and space.

7.5.5 Proxies Embedded in Coral Skeletons Are Powerful Tool to Track the Impact of Environmental and Climate Variabilities

Human pressures on coral reefs are reported to have increased significantly worldwide in recent decades, and their impact on the coral reefs are more pronounced in the Western Pacific Ocean including the Southeast Asia. For example, the Coral Triangle Region indicated that the level of threat from local activities (e.g., overfishing, destructive fishing, coastal development, watershed-based pollution) increased by about 40% from 1998 to 2007 (Burke et al. 2012). In addition to direct human activities, indirect environmental changes caused by global warming and surface ocean acidification together with low frequency natural climate variability and the associated changes arising from the consequences stemming from the species interactions among coral reef ecosystem constituents (e.g., proliferation of predators and diseases) also stress corals. Large-scale storm surges or tsunamis will, in some areas, physically destroy (e.g., kill corals, break corals, upturn corals) or disturb the health of coral reefs (e.g., partial bleaching, infestation with disease, silt-smothered live corals), for example, India, Indonesia, and Thailand after 2004 Indian Ocean earthquakes and tsunami (Kumaraguru et al. 2005; Wilkinson et al. 2005).

These environmental changes affect the chemical composition of the ambient seawater, where the coral grows. These seawater composition changes are often incorporated into the processes of calcium carbonate mineral aragonite precipitation as impurities or snapshots of isotopic variations within various constituents, since the entire processes of calcification are dictated by animal coral mediated thermodynamic principles. Therefore, deciphering environmental change indicators embedded in coral skeletons is dependent upon scientific reasoning and analytical capabilities. Many new tracers have been established recently, thanks to the advances in our understanding on the biology of aragonite skeletal formations in relation to the ambient seawater chemical and isotopic compositions and of the analytical instruments such as mass spectrometry and non-destructive analytical devices.

Corals generally precipitate their aragonite skeletons along the growth axis at a rate of about 1 centimeter a year. Therefore, a high-resolution sampling has to be made to provide signals at shorter than monthly intervals, which faithfully record seawater composition changes at the time of their growth. Dating of coral bands is available using visual or x-radiographs of annual growth bands; ^{14}C, ^{210}Pb, ^{228}Th, ^{230}Th, and artificial radionuclides of ^{90}Sr and ^{239}Pu isotopes; and amino acid racemization depending upon the purpose of the research project and amount of sample available. The exemplary tracers for long-term climate and environmental and short-term anthropogenic changes occurring in coral reefs ecosystem are Li, B, C, N, O, F, Na, Mg, P, S, Ca, V, Cr, Mn, Fe, Ni, Cu, Zn, Sr, Y, Mo, Cd, I, Ba, Nd and other rare earth elements (REEs), Pb, U, Pu, and their isotopes. As trace elements and their isotopes in the ocean receive major attention since 2010 through the ongoing GEOTRACES program (an international study of marine biogeochemical cycles of trace elements and their isotopes), the knowledge on the incorporation of trace impurities into coral skeletons will be greatly expanded in the coming decades. An extensive comparative study on the instrumental records and climate and environmental variabilities over the past 50–150 years led by another international program on the Future Earth Past Global Changes (PAGES 2k) for 2017–2020 will also greatly strengthen our ability to decipher climate and environmental changes that occurred in the ancient times before the modern instrumental records were available. This is particularly important for temperature estimation from a variety of geochemical proxies and their uncertainties, analytical issues associated with fossil corals, and novel proxies for global biogeochemical cycles (Zinke et al. 2018). Therefore, coral proxies will be very useful in coming decades for deciphering what happened in the past, and simultaneously they will provide us with critical knowledge and tools for the better stewardship of the fragile coral reefs facing multiple stressors both now and in the years to come. More detailed information embedded in coral skeletons will be added continuously to our knowledge base on the long-term variation in chemical composition of seawater and Earth climate as coral reefs were formed approximately 500 million years ago and continue to provide valuable information (Webby 1984).

7.6 Challenges for the Ecosystem-Based Management (EbM)

Given that the trends of increasing global warming, sea level rise, and ocean acidification will persist for the next century and/or even beyond, and various perturbations by human beings will also exert their influence on the coastal and terrestrial environment and adjacent marine waters, coral reefs in the Western Pacific Region will continue to face different external stressors in combination and will have to continue to cope with constraints arising from a changing environment (Fig. 7.5).

Managing coral reef ecosystems at the ecosystem level requires an integrated monitoring network and an operational strategy. Existing monitoring stations are usually confined to the coast, and the distribution of sites is limited to a few places covering the vast coral reef area. The data collection and transmission from monitoring stations to the home laboratory/office are often delayed. Moreover, in situ monitoring activity is limited to only a few relatively easily measured parameters, such as temperature, pressure (depth), salinity, and fluorescence of seawater. It is expected that the parameters of most interest in coral reef ecosystems, such as nutrients (index of eutrophication), dissolved oxygen (DO) (indicator of hypoxia), composition and abundance of pigments (information on the algae assembly and abundance), and turbidity (proxy of total suspended matter) in the water column will be designed, and monitoring stations will be added along the seawater chemical compositional gradients from nearshore to the offshore. Thanks to the advances in Internet and satellite communication technologies, more data transmission between monitoring sites and onshore laboratories will become two-way and real-time, which provides an opportunity for swift (response) actions to be initiated as required. The purpose of marine spatial planning (MSP) as a part of the integrated coastal zone management for a given community is to examine ecosystem services to the predetermined magnitude in terms of social, economic, and environmental benefits in a sustainable manner considering both current and future generations. Therefore, marine spatial planning should utilize an ecosystem-based approach (EbA). This marine spatial planning may be used to select the sites, their environmental variables, and frequencies of monitoring in a given coral reef ecosystem. The monitoring networks could be tied into an early warning observation system for marine disasters, including abrupt seawater compositional changes, algal blooms, storm surges, etc.

The observed data transmitted from the field to the onshore laboratory will need to be fed into numerical water circulation and/or biogeochemical models of a given coral reef ecosystem. In the past, observations on coral reefs usually included photographs and sampling for nutrients, alkalinity, pH, $p\mathrm{CO}_2$, composition of pigments, and taxonomy, whereas observations towards understanding food-web structure and interactions between different trophic levels and physiological time series did not receive sufficient attention. Therefore, observations on such ecosystem level variables and parameters should be promoted. Incubation and

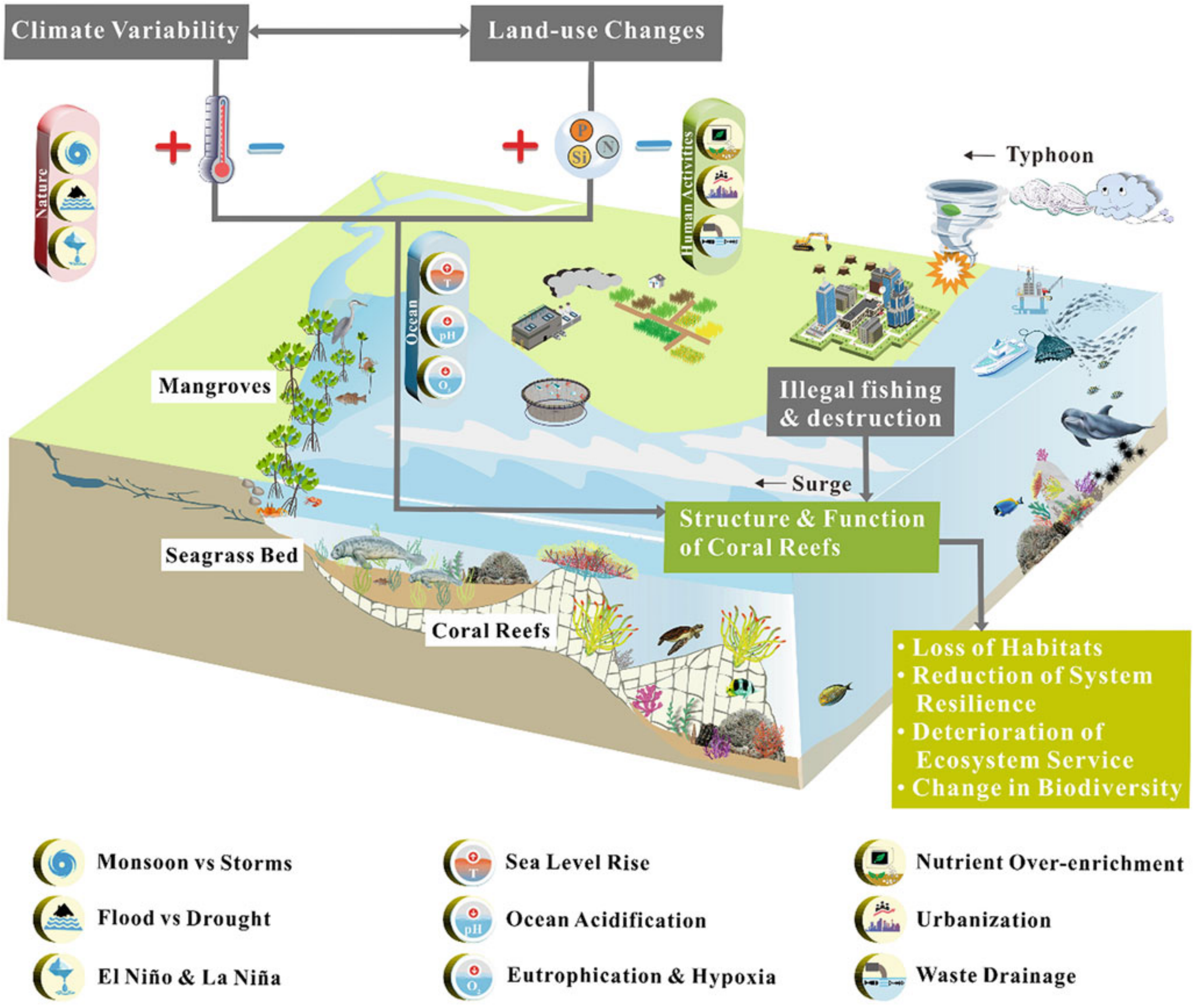

Fig. 7.5 Illustration of interactions between external forcings and responses of coral reefs, with applications for the Western Pacific Ocean at ecosystem management level. In the figure, the combined effects of natural and anthropogenic forcings may induce a number of syndromes from molecular to system levels, while responses of coral reefs are system specific

mesocosm experiments on the rate measurements and mechanism approaches should be encouraged in order to parameterize the biogeochemical processes and validate outputs of numerical simulations. Moreover, observations should be combined with continuous monitoring networks, and hence the spatial coverage of observational data can be integrated with the time-series information from monitoring sites in order to describe the biogeochemical field of targeted coral systems.

Currently, there is a gap in monitoring setups that allows understanding the relationship between examining external forcings (e.g., changes in water quality) and deciphering responses of coral reefs, for example, primary productivity and symbiosis between corals and zooxanthellae. In the landscape, resolution of satellite-based remote sensing is usually not high enough to collect and portray the patchy character of coral reefs, such as the temperature and distribution of pigments. There is also a challenge in remote sensing to examine the daily variability (e.g., day- and night-time differences) using the visible wavelength spectrum. In the tropics and subtropical areas, remote sensing using satellite data can be also a problem when the weather conditions (e.g., cloud coverage) are not suitable. Using the monitoring data, one can seldom extract information about the connectivity between different reef systems, such as the dispersal of larvae. At the molecular level, it is hoped that monitoring systems can provide information relevant to the studies on genetics and/or genomes of coral development.

Innovation of coral reef observing techniques is urgently required to address those challenges encountered by coral ecosystems in a changing climate, ranging from monitoring of multiple parameters in the field to the molecular and genetic studies in a well-equipped laboratory. In reality, the techniques currently used for in situ monitoring are limited to a few variables/parameters with limited precision and data logging. Therefore, new sensors for in situ monitoring are expected to be equipped with multi-sensor probes to observe coral physiological phenomena occurring in constituents of coral reef ecosystems and water quality with enhanced real-time data transmission capability (i.e., via satellites). The sensors are expected to become smaller in size, low energy consuming, more compact, and more robust for facilitating their use in harsh coastal environments. The question of what to "see" and what to "track" needs to be discussed when designing the monitoring network, and data transmission from sensors to shore laboratory should be warranted. In the onshore laboratory, biogeochemical variable/parameter determination (e.g., ICP-MS and HPLC-MS) needs to be closely coordinated with molecular/genetic analyses for samples of targeted biological species.

Numerical modeling is a powerful tool that allows diagnoses of condition of coral ecosystems and prediction of the response of reef ecosystems to external forcings, given that mechanisms are well understood and realized through parameterization. However, numerical models have been largely developed for hydrodynamics and sediment transport (cf. Storlazzi et al. 2011); biogeochemical models have recently become available to aid understanding of the causal relationship of essential key chemical elements and coral biology, which is affected also by the initial condition, boundary situations, as well as interactions with outside target ecosystems (Galli and Solidoro 2018). Developing numerical models requires comparison of model outputs with in situ observational/monitoring data to ensure validity of their parameterization of biogeochemical reactions occurring in corals and the ambient seawater. In the Western Pacific Region, application of numerical simulations to the biogeochemical processes occurring in the coral reefs is still in its infancy (Mayer et al. 2018), and upgrading this will need coordinate joint efforts of modeling as well as in process studies.

Study of marine ecosystems, including coral reefs, is usually multidisciplinary. The mission of a multidisciplinary research project in the Western Pacific Ocean is unlikely to overlap completely with the management needs of any specific country in this region. There is a need to match the scientific directions of projects with what is expected by any interested or concerned country in implementation. In the Western Pacific Region, there are several international research platforms to mobilize scientists from around the world to lend their expertise in research and educational facilities in their home laboratories or virtual team work, such as IOC/WESTPAC-CorReCAP Project established in 2008, Coral Triangle Initiatives, and NGOs among others. Such activities provide a collaborative environment in which regional scientists can come together to share and discuss research, as well as to get support for all steps of the research process, including designing, searching, writing, publishing, and even fundings. Publicly available high frequency and nonintrusive Earth observational information using electromagnetic waves (satellites) and data and knowledge produced by the existing projects supported by individual governments and/or inter-governmental organizations, e.g., Coral Triangle Initiative on Coral Reefs, Fisheries, and Food Security (CTI-CFF), can be coordinated by a team with a scientific advisory mechanism of the highest quality, with active participation of research scientists, educational agencies, management, and policy-making people. Any lack of research assets (e.g., a highly skilled academic work force, advanced research infrastructure, and a mature high-tech industry system) may be complemented by other participants through the network of distributed centers of excellences (Hellstrom 2018). The established international collaborations in this region will provide further opportunities for data sharing, exchange of expertise and research protocols, coordinating analytical facilities, etc. This kind of collaboration at the regional level will result in research networks on coral reefs across the whole Western Pacific Region, to face the need for capacity development to conduct multidisciplinary studies.

Finally, the successful and sustainable development of integrated coral reefs studies in the Western Pacific Ocean requires strong support from capacity building agencies in this region. National and international marine research initiatives require integrated multidisciplinary facilities with support for equipment and observations, as well as continued capacity building (Morrison et al. 2013). In addition to the infrastructure for research, the challenges of ecosystem-based management (EbM) in the Western Pacific Region include also the development of capability to synthesize the collaborative research results and to maintain the capacity built within the marine science community in the member countries. It is important to keep in mind that capacity building on the coral reef science should take into consideration technical and scientific skills and the ability to design research activities. This is particularly important in the Western Pacific Region, because capacity building needs to be developed for a wide range of religious belief and culture differences in this area. In order to reach the goal of high-quality coral reef studies in this region, the marine community, from the scientific to the social sectors, should reduce the overlap and duplication in capacity building activities and ensure to bring all efforts together with all existing relevant resources and infrastructure across the whole Western Pacific Region (Morrison et al. 2013).

7.7 Future Scientific Research Priorities on Coral Reefs

Coral reef ecosystems have developed over several hundreds of millions of years and are widely distributed in the tropical and subtropical marine environment and hence have survived episodes of climate variability and tectonic movements in geological time since Mesozoic Era. Coral reefs flourish in the tropical and subtropical ocean with very limited ranges of salinity, temperature, and sea level variability and are often exposed close to the thermal threshold of survival in the geological time. However, living in the current Anthropocene, coral reef stressors have been expanding due to global warming, with consequential sea level rise and ocean acidification. In urbanized coasts, coral reefs are subject to pollution (e.g., terrigenous and marine sediments, nutrients, heavy metals, organic contaminants, floating and submerged plastic litter, marine debris, and abandoned fishing net and gear, etc.) and human-made substrates, such as artificial rocky habitat, floating structures, piers and pilings, scoria deposits, and artificial islands (Heery et al. 2018). More than 20 million people in the Western Pacific Region depend on coral reefs for their livelihood (Pendleton et al. 2016). The future of coral reefs in the Western Pacific Ocean is largely subject to how human society in this area behaves in terms of protection of marine ecosystems and controls user communities against ambitions of exhausting marine resources.

Current major climate predictions indicate that in the very near future, greenhouse gas species (e.g., CO_2, CH_4, and N_2O) in the current atmosphere will continue to increase over the next several decades, suggesting that the global and large-scale climate trends, such as warming, sea level rise, and acidification, will continue. At the regional and local scales, superimposed perturbations may arise from urban activities and from open ocean operations. Effects of global climate change and CO_2 emissions, while relatively clear in trend direction, are quantitatively less certain at regional level, which makes it difficult to assess and predict the responses of coral reefs, often due to the lack of essential ocean observation and robust numerical models.

Over the last 10 years, several workshops and training courses have been conducted within the IOC/WESTPAC-CorReCAP Project by the participants from member countries in the Western Pacific Ocean. These activities have contributed to enhancing the knowledge and capacity of communities in this region on coral reef-related issues and to broadening the reach and scope of member countries' research programs. Some member countries are still experiencing numerous challenges in conducting scientific studies on coral reefs, ranging from limited material and financial resources, poor physical and communication infrastructure, and lack of scientific careers, scientific tradition, institutional support, and collaboration within the local scientific community due to economic constraints or small size of populations in some island states (Harris 2004). In this monograph, based on the multidisciplinary examination of current coral reefs of the Western Pacific Ocean, several priorities can be proposed for action that are also coming out from research experiences gained from activities at the regional level as well as through comparison with other global efforts. These include:

- Filling out of the knowledge gap with integrated monitoring and observational systems. Although studies on coral reefs are undertaken in most IOC-WESTPAC member countries, there is still lack of effective mechanisms for communication and data sharing in the Western Pacific Region. How to integrate local knowledge based on individual studies and update this kind of information to international forum and hence move forward coral sciences should be considered as one of the priorities in the future development.
- Innovation and updating of techniques and infrastructure in the network for coral science. Levels of research infrastructure are very different between countries of Western Pacific Region, hence updating and sharing the research facilities and exchange of expertise become a stumbling block in developing coral reef studies. It has been suggested that through coordinated research programs, people from different countries can have access to the state-of-the-art techniques and observational facilities, such as satellite observations, GIS, and molecular biology to match the growing research needs and update the laboratory facilities.
- Improvement of capacity building in coordinated coral reefs studies of Western Pacific Region. Sustainable development of coral reef studies to satisfy the requirement of ecosystem-based management is inseparable from the contribution of capacity building. There is a need to provide mechanisms for knowledge transfer, sharing the expertise, and updating the infrastructure within the network of coral reef studies. In this case, capacity building should strive to establish continuity and attract active PhDs and young scientists. Regionally targeted, mesocosm-level, or larger field experiments may be useful to study the combined effects of global stressors and local environmental stressors originating from human activities if funds are available. The future development of capacity building in this region should take into consideration differences in culture and language of the member countries.

We are quite optimistic noting that there are already a number of coordinated research programs on coral reefs in the Western Pacific Ocean, such as Coral Triangle Initiative (CTI) and IOC/WESTPAC-CorReCAP. Recent research data indicated the richness of coral biodiversity in the basin-wide biogeographic ranges of Western Pacific Ocean (Dietzel et al. 2021). Scientific evidences coming out from such research activities call for rethinking what declines in abundance mean for coral reef extinction risk in a global scale (Pennisi 2021). Because previous claims on coral extinction were based on studies from individual systems, there is a need to reexamine the actual status of coral reefs from perspective of biodiversity gradients taking into considerations classification for life history of species and population size in geographic ranges. Through the collaboration of existing regional and international level research programs and coordination of member countries in this region, coral reefs in the Western Pacific Ocean will be well maintained for the foreseeable future.

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Postscript

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This monograph is based on the research activities of coral reefs within the framework of a IOC/WESTPAC Sub-Commission, named “Coral Reefs under Climate and Anthropogenic Perturbations” (IOC/WESTPAC-CorReCAP) Project.

In May 26–29, 2008 the UNESCO/IOC-WESTPAC Sub--Commission adopted the CorReCAP as a new research project on its 7th assembly of national delegations at Kota Kinabalu of Borneo, Malaysia. Initially, IOC/WESTPAC-CorReCAP Project has 10 scientists in its steering committee in this region, which were later expanded to include more than 25 universities and/or research institutions from 13 member countries of IOC/WESTPAC Sub-Commission as shown in Fig. A.1.

For more than one decade, IOC/WESTPAC-CorReCAP has expanded its capacity through scientific workshops, summer schools and training courses, and collaborative observation activities within the regional network of the IOC/WESTPAC Sub-Commission (Table A.1). Those abovementioned activities promoted IOC/WESTPAC-CorReCAP in the region and elaborated the missions during the life time of this project, through activities including:

- Review the status/conditions of major coral reef ecosystems in the Western Pacific Ocean and identify critical issues of action that are required.
- Provide recommendations related to sustainability of coral reefs and undertake cost-effective implementation.
- Facilitate effective interactions/communications with other regional intergovernmental and nongovernmental organizations in research on coral reef systems.
- Promote capacity building on coral reef research and education within the IOC/WESTPAC Sub-Commission, and establish the coordination with other sub-commissions of UNESCO/IOC.

We would like to take this opportunity to acknowledge all the national delegates of IOC/WESTPAC Sub-Commission; their support made the implementation of this research project successful in the region. There are many people and colleagues in the scientific community of IOC/WESTPAC Region to whom we are grateful, who have provided venues and facilities so that we could organize workshops and training courses and make field trips and in situ observations but we could not name all of them here. Finally, we would also give our gratitude to the secretariat of IOC/WESTPAC Sub-Commission; the activities of this project were elaborated through the coordination of this office.

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Fig. A.1 Research network of IOC/WESTPAC-CorReCAP in the region through the secretariat of IOC/WESTPAC Sub-Commission at Bangkok of Thailand. In the figure the major focal points of research laboratories in the region are indicated

Table A.1 Major activities of IOC/WESTPAC-CorReCAP over last decade, including scientific workshops, training activities, and joint observations sandwiched in the middle

Date	Location	Activities
May 26–29, 2008	Kota Kinabalu (Malaysia)	Adoption of proposed CorReCAP Project by IOC/WESTPAC Sub-Commission
May 23–26, 2009	Shanghai (China)	First workshop of IOC/WESTPAC-CorReCAP Project
June 14–18, 2010	Koh Samui (Thailand)	First Summer School of IOC/WESTPAC-CorReCA Project (Topic: Effects of Sediments on Coral Reefs)
June 22–24, 2010	Phuket (Thailand)	Second workshop of IOC/WESTPAC-CorReCAP Project
March 28–31, 2011	Busan (Korea)	Third workshop of IOC/WESTPAC-CorReCAP Project
June 8–12, 2011	Sanya (China)	Second Summer School of IOC/WESTPAC-CorReCAP Project (Topic: Water Quality and Coral Reefs)
April 18–21, 2014	Nha Trang (Vietnam)	Third Summer School of IOC/WESTPAC-CorReCAP Project (Topic: Resilience of Coral Reefs)
April 22–23, 2014	Nha Trang (Vietnam)	Fourth workshop of IOC/WESTPAC-CorReCAP Project
March 28–30, 2016	Shanghai (China)	Fifth workshop of IOC/WESTPAC-CorReCAP Project
April 20, 2017	Qingdao (China)	Sixth workshop of IOC/WESTPAC-CorReCAP Project
June 5, 2018	Cebu (The Philippines)	Seventh workshop of IOC/WESTPAC-CorReCAP Project, focused on “Coral Reef Resilience to Climate Change and Human Impacts”
June 7, 2018	Cebu (The Philippines)	International workshop of enhancing young scientist network for coral reef research in the Western Pacific (under IOC/WESTPAC-CorReCAP Project)