

Chapter 10

Carbon Dynamics in Coral Reefs



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Abstract Coral reefs show high organic and inorganic carbon production and create unique landforms on tropical coastlines. The balance between organic and inorganic carbon production is determined by benthic organisms such as corals, macroalgae, and seagrasses, and also by reef hydrodynamics, which in turn determine CO₂ sinks and sources within the ecosystem. Many studies have shown that net organic carbon production in coral reef ecosystems is almost zero (balanced), with net positive calcification resulting in reefs acting as CO₂ sources. However, the relationships among productivity, benthic organisms, and hydrodynamics have not been well documented; more detailed information is required from both field observations and coupled physical–biological models. Reef sediments have low organic carbon content (median, 0.35% dry weight), approximately 50% those of tropical and subtropical seagrass beds (median, 0.67%) and 5% those of mangrove forests (median, 6.3%). Sedimentation rates do not vary significantly between these three ecosystems, so organic carbon input and decomposition in the surface sediments are key factors controlling organic carbon burial rates. Coral reefs provide calm conditions that enhance sedimentation of fine sediments, which facilitates the development of seagrass beds and mangrove forests. Seagrass meadows and mangrove forests in turn trap fine sediments from terrestrial sources and prevent high-turbidity water from reaching coral reefs. Coral reefs, seagrass meadows, and mangrove forests are thus interdependent ecosystems; to effectively store and export blue carbon in tropical coastal areas, it is necessary to maintain the health of these ecosystems.

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10.1 Introduction

Coral reefs are not explicitly included as part of the blue-carbon ecosystem, so you might wonder why coral reefs are included as a chapter in this book. In the tropics and subtropics, coral reefs often overlap seagrass beds and mangrove forests (Fig. 10.1) and are therefore strongly linked to blue-carbon ecosystems. Often there is also hydrodynamic connectivity or interaction among these tropical coastal habitats (Guannel et al. 2016).

This chapter briefly explains the general characteristics of coral reefs in terms of carbon-cycle components such as primary production and calcification. The resultant CO₂ sinks and sources, and carbon storage and export in coral reefs are then

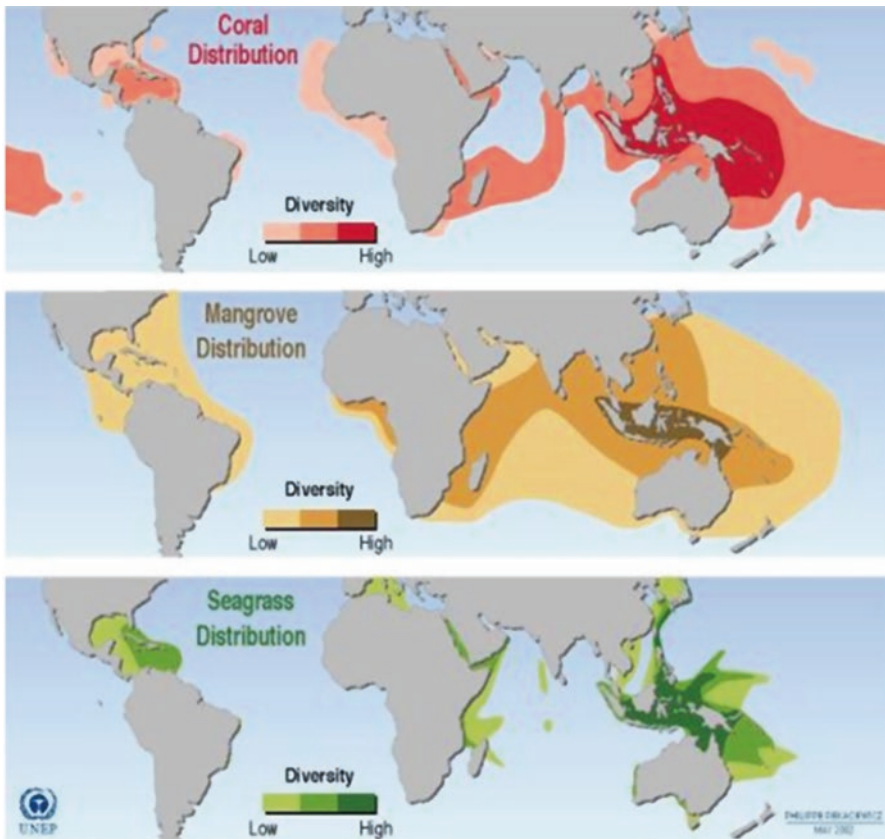


Fig. 10.1 World distribution of coral reefs, mangrove forests, and seagrass beds. The areas with high diversity for each ecosystem overlap, especially around Indonesia, Malaysia, Papua New Guinea, and the Philippines. (Source: <https://www.grida.no/resources/7766> (credit: Hugo Ahlenius))

addressed. Finally the relationships between coral reefs and other ecosystems, especially with seagrass beds and mangrove forests, are discussed to highlight the necessity of regarding these connected ecosystems together as a blue-carbon ecosystem.

10.2 Carbon Cycling, Storage, and Export in Coral Reefs

10.2.1 *Basic Carbonate-Chemistry Changes Due to Calcification and Primary Production*

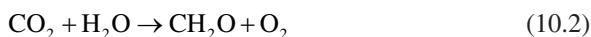
We first briefly explain the basics of carbonate chemistry alterations due to calcification and photosynthesis to provide the background necessary to understand this chapter. For further reading, please refer to Gattuso et al. (1999) or Zeebe and Wolf-Gladrow (2001).

The calcification reaction, which releases CO_2 , is commonly expressed by the following equation:



The reverse of Eq. (10.1) is the reaction for the dissolution of CaCO_3 .

Photosynthesis fixes CO_2 and is expressed by the following equation:



The reverse of Eq. (10.2) is the reaction for aerobic respiration and decomposition.

There is a so-called “0.6 rule” for seawater, where about 0.6 moles of CO_2 is liberated (not the expected 1 mole) when 1 mole of CaCO_3 is produced by Eq. (10.1) (Ware et al. 1991; Frankignoulle et al. 1994). In contrast, 1 mole of CO_2 is fixed when 1 mole of organic C (CH_2O) is produced by Eq. (10.2). Therefore, when the rate of photosynthesis is greater (less) than 60% of the calcification rate, CO_2 is fixed (liberated) and the system acts as a sink (source) of CO_2 . The value 0.6 in the 0.6 rule is due to the buffering capacity of seawater, and it changes with ocean acidification (the trend of increasing CO_2 in seawater). This value, termed Ψ (Frankignoulle et al. 1994), is 0.6 when pCO_2 (partial pressure of CO_2) in seawater is 350 μatm , salinity is 35, and water temperature is 25 °C, but it rapidly increases to 0.78 when pCO_2 reaches 1000 μatm under the same conditions. Ψ also changes with temperature (see Fig. 10.2). At constant pCO_2 , Ψ decreases as water temperature increases. For example, seawater at higher latitudes generally has higher Ψ values and lower buffering capacity.

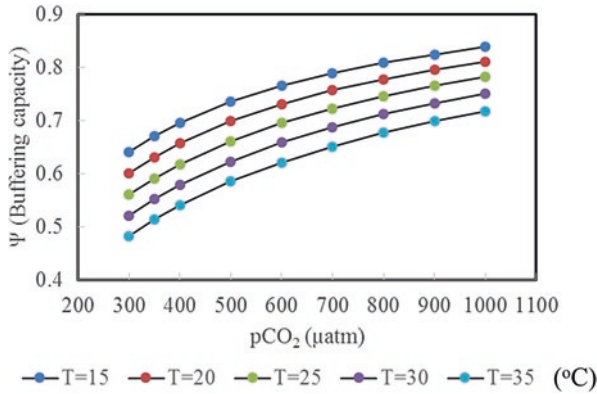


Fig. 10.2 Buffering capacity of seawater as a function of pCO₂ at varying water temperatures (salinity = 35 and the total alkalinity = 2300 μmol kg⁻¹)

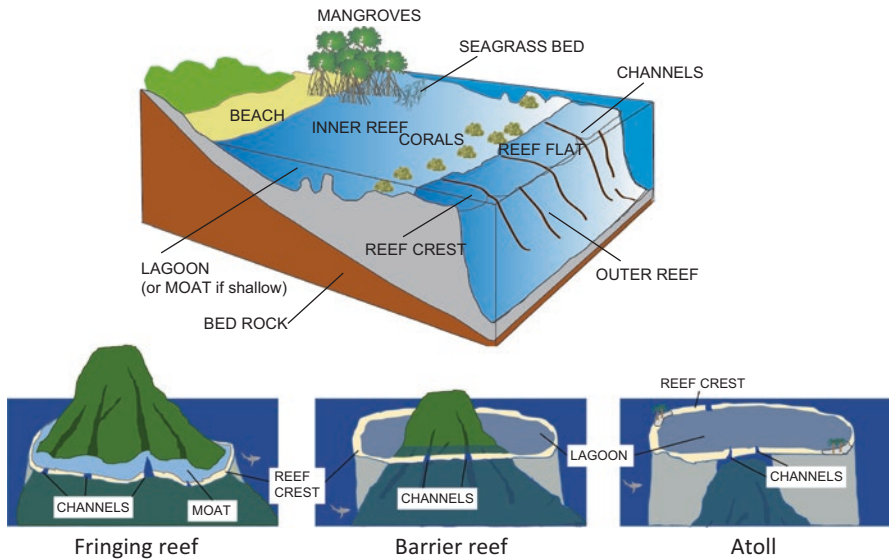


Fig. 10.3 General reef geomorphology and types (fringing reef, barrier reef, and atoll)

10.2.2 Calcification and Primary Production in Coral Reefs

One conspicuous characteristic of coral reefs is the huge production of CaCO₃ by which tiny corals build the world’s largest living structures, such as the Great Barrier Reef in Australia, which is visible from space. Coral reef environments can be roughly divided into three parts: reef flat with reef crest, inner reef, and outer reef (upper panel in Fig. 10.3). The reef flat with reef crest is the shallowest part of a coral reef and is covered with either corals or macroalgae. Incoming wave energy is

effectively dissipated at the reef crest or reef flat. The inner reef is therefore calmer compared to the outer reef, and often has a lagoon (or “moat” when it is shallow [typically shallower than 5 m]), which can harbor corals, seagrasses, and mangroves. The outer reef is a high-energy environment and often covered with corals or coralline algae that are resistant to the high wave energy.

There are three major types of coral reefs: fringing reefs, barrier reefs, and atolls (lower panel in Fig. 10.3). A fringing reef develops right beside an island, whereas a barrier reef has a relatively deep lagoon between an island and the reef flat. Atolls are rings of reefs without a central island; sometimes the reef itself becomes exposed to air and forms a low-lying island.

The coral/algal reef flats display a wide range of calcification rates (5–126 mol $\text{CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ or 0.5–12.6 kg $\text{CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$; Gattuso et al. 1998). The value gets progressively higher as the water depths decrease over the reef flat zone (shallowest part of coral reefs) independent of domination by corals or coralline algae (Sorokin 1993). On average, the shallow seaward reef flat zone produces 40 moles (or 4 kg) of $\text{CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$. Considering the “0.6 rule” explained in Sect. 10.2.1, net primary production on the “average reef” would have to exceed 24 moles (or 288 g) $\text{C m}^{-2} \text{ year}^{-1}$ to act as a CO_2 sink. Gross primary production (GPP) on reef flats is quite high, varying from 79 to 584 moles (or 948–7008 g) $\text{C m}^{-2} \text{ year}^{-1}$ (Gattuso et al. 1998), but community respiration is also high and net primary production is thought to be close to zero. In this case, calcification overwhelms the net primary production on the reef flat, and the reef flat is believed to act as a source of CO_2 .

10.2.3 CO_2 Sinks and Sources in Coral Reefs

The debate on whether coral reefs act as a sink or source of atmospheric CO_2 began in the 1990s. Gattuso’s group (Gattuso et al. 1993, 1996b; Frankignoulle et al. 1996) reported that most coral reef flats are sources of CO_2 to the atmosphere. Their study sites were the Tiahura barrier reef (Moorea, French Polynesia) and Yonge Reef (northern Great Barrier Reef). Both sites are classified as barrier reef flats. Gattuso et al. (1996b) reported that the Tiahura reef supported abundant corals on the seaward side and abundant macroalgae on the back reef area, whereas the Yonge Reef flat was mainly dominated by a single community characterized by the coral species *Acropora palifera*. In contrast, Kayanne’s group (Kayanne et al. 1995) reported that coral reef flats act as sinks for atmospheric CO_2 . Their study site was the Shiraho reef (Ishigaki Island, Japan), which is a fringing reef flat. The dominant coral species around the monitoring site were *Montipora digitate*, *Porites cylindrica*, and *Heliopora coerulea* (Kayanne et al. 2002), and algal turf and brown algae were on the offshore side of the reef crest (Kayanne et al. 1995). Since Kayanne et al. (1995) indicated that coral reef flats are a net sink for atmospheric CO_2 , there have been many comments and papers published regarding the CO_2 sink–source issue (Buddemeier 1996; Gattuso et al. 1996a, 1997; Kayanne 1996; Kraines et al. 1997; Ohde and van Woesik 1999; Bates et al. 2001; Bates 2002; Kayanne et al. 2005),

and the debate has been reviewed extensively (Gattuso et al. 1999; Suzuki and Kawahata 2004). Here we summarize the points of the debate and list some of the more recent literature published after those reviews.

Table 10.1 summarizes the CO₂ sinks and sources in coral reefs, separately listing reef flats and lagoons. Positive CO₂ flux values indicate sources and negative values indicate sinks. Although the values vary widely, the majority of reef flats studied acted as sources of CO₂, with a median CO₂ flux value of 2.2 mmol m⁻² day⁻¹. The majority of relatively deep lagoons also act as sources of CO₂ with a median value of 0.7 mmol m⁻² day⁻¹. These values are relatively small and comparable to the CO₂ flux for open ocean in most of the subtropical and tropical areas where coral reefs exist, which typically exhibit fluxes of -1 to 1 mol m⁻² year⁻¹ (or -2.7 to 2.7 mmol m⁻² day⁻¹, Takahashi et al. 2009). Some reefs absorb CO₂ from the atmosphere, but many researchers insist that the reef flats absorbing CO₂ are mainly fringing reefs (see Fig. 10.3 and Sect. 10.2.2). The hypothesis is that fringing reefs receive substantial amounts of nutrients from adjacent lands, conditions more favorable for the growth of seagrasses or macroalgae than corals. With the reef area covered by these autotrophs, net primary production exceeds calcification and the system overall absorbs CO₂. Gattuso et al. (1997) tested this hypothesis by measuring community metabolism and air-sea CO₂ fluxes on a fringing reef at Moorea. The results showed that this reef flat was a sink for CO₂ up to 10 mmol m⁻² day⁻¹, whereas the neighboring barrier reef flat was a CO₂ source (Gattuso et al. 1993, 1996b; Frankignoulle et al. 1996). These contrasting results from the fringing reef and the barrier reef of Moorea led to the concept that “algal” reefs absorb CO₂ whereas “coral” reefs emit CO₂ to the atmosphere.

More recently, different views have been offered regarding the air-sea CO₂ flux in coral reefs resulting from long-term or continuous monitoring at the same sites. For example, Kayanne et al. (2005) showed that the Shiraho fringing reef became a source of atmospheric CO₂ following coral bleaching¹ in 1998, although the reef was a CO₂ sink during other non-bleached periods. Massaro et al. (2012) presented continuous CO₂ data covering 2.5 years in southern Kaneohe Bay, Hawaii, a semi-enclosed tropical coral reef ecosystem. They showed that local climatic forcing strongly affected the biogeochemistry, water-column properties, and air-sea CO₂ gas exchange. Large drawdowns of CO₂ following storms occasionally caused the bay waters to switch from a CO₂ source to a sink. These results indicate that even the same reef can dynamically shift from sink to source depending on reef conditions (e.g. coral and macroalgal coverage) as well as on external forcing (e.g. storms and subsequent supply of nutrients). These kinds of dynamic features can be more important than the static sink-source views of coral reefs under rapidly changing reef conditions due to global climate change and local environmental changes.

¹ Coral bleaching: Corals have symbiotic algae called zooxanthellae inside their tissue. When corals are stressed from high water temperature or other causes, they release or digest their zooxanthellae and lose their color, making the white coral skeleton visible. This phenomenon is called coral bleaching.

Table 10.1 Summary of air–sea CO₂ flux data for coral reefs

Country (region)	Air–sea CO ₂ flux	Reference	Year
	(mmol CO ₂ m ⁻² day ⁻¹)		
Reef flats (including moat or shallow lagoon)			
Barrier reef in Moorea, French Polynesia	1.5	Gattuso et al.	1993
Barrier reef in Moorea, French Polynesia	1.8	Frankignoulle et al.	1996
Yonge Reef, N. GBR ^a , Australia	5.1	Frankignoulle et al.	1996
Barrier reef in Moorea, French Polynesia	31.0	Gattuso et al.	1996b
Yonge Reef, N. GBR, Australia	182.0	Gattuso et al.	1996b
Fringing reef in Moorea, French Polynesia	–10	Gattuso et al.	1997
Rukan-sho atoll, Okinawa, Japan	Neutral	Ohde & Van Woesik	1999
Hog Reef Flat, Bermuda	3.3	Bates et al.	2001
Xisha Islands, China	1.5	Dai et al.	2009
Nanwan, South China Sea, Taiwan	–0.56	Jiang et al.	2011
Yongxing Island, South China Sea	4.7	Yan et al.	2011
Luhuitou Reef, Hainan Island, China	9.8	Yan et al.	2011
Shiraho Reef, Ishigaki, Japan	0.0	Watanabe et al.	2013
Shiraho Reef, Ishigaki, Japan	–1.9	Watanabe et al.	2013
Heron Reef, southern GBR, Australia	2.5	Cyronak et al.	2014
Rarotonga, fringing reef in South Pacific	8.8	Cyronak et al.	2014
Coroa Vermelha, Brazil	0.3	Longhini et al.	2015
Heron Reef, southern GBR, Australia	172.8	McGowan	2016
Luhuitou Reef, Hainan Island, China	1.5	Yan et al.	2016
Median	2.2		
Lagoons (moderate to deep lagoons) or open ocean surrounding reefs			
Fanning Island	46.7	Smith & Pesret	1974
Christmas Island, Kiribati	–2.6	Smith et al.	1984
Rim and terrace reefs, Bermuda	–0.03	Bates	2002
Palau	1	Watanabe et al.	2006
Kaneohe Bay, Hawaii, USA	3.97	Fagan & Mackenzie	2007
Yongshu Reef atoll, Yongxiang Island reef flat, and Luhuitou Fringing reef, South China Sea	0.4	Yan et al.	2011
Southern Kaneohe Bay, Hawaii, USA	4.93	Massaro et al.	2012
Kaneohe Bay, Hawaii, USA	4.0	Drupp et al.	2013
Mamala Bays, Hawaii, USA	0.06	Drupp et al.	2013
Lady Elliot Island, southern GBR, Australia	–1.82	Shaw & McNeil	2014
Median	0.70		

Positive values indicate a net CO₂ flux from the reef to the atmosphere

^aGreat Barrier Reef

More studies are needed for the mechanistic understanding of CO₂ dynamics in coral reefs. It is recommended that future works incorporate following points.

1. Measurements should include reef metabolisms (ecosystem primary production, respiration, calcification, and carbonate dissolution) and organic-matter flux along with air–sea CO₂ fluxes.
2. The benthic condition of reef areas of interest should be quantitatively monitored. The biomass balance between corals, macroalgae, and seagrasses can be especially important.
3. Monitoring should include terrestrial loads such as submarine ground water or river water inputs to the reefs, their chemistry (e.g. nutrients and carbonate chemistry), and their advection in the reef, together with hydrodynamic features of the reefs (e.g. residence time of seawater).
4. The reef as a CO₂ sink or source should be addressed by comparison with the CO₂ in the open ocean impinging on reefs, and not necessarily directly with atmospheric CO₂. The reason is simple: the open ocean is not necessarily in equilibrium with atmospheric CO₂, and the capacity of a coral reef as a CO₂ sink or source should be discussed relative to CO₂ levels in the source water (mainly open ocean seawater in many cases). This would require adequate monitoring of conditions offshore of the reefs as well.

Achieving these points will require a combination of hydrodynamic–biogeochemical modeling as well as the appropriate fieldwork to properly constrain the models. These topics are discussed in more detail in Sect. 10.4.

10.2.4 Carbon Storage in Coral Reefs

Coral reef sediments are known to contain small amounts of organic carbon (OC). Table 10.2 compiles data for the OC content of reef sediment. For example, Sorokin (1993) reviewed OC contents in reef bottom sediments and reported values ranging from 0.09% to 0.6% (% dry weight). The OC in reef sediments rarely exceeds 1%, and the mean and median values from previous studies are 0.46% and 0.35%, respectively. The low OC content of reef sands is thought to reflect background OC

Table 10.2 Summary of organic carbon content, burial rate, and sedimentation rate in reef, seagrass, and mangrove sediments

Ecosystem	Organic carbon content			Organic carbon burial rate			Sedimentation rate		
	(% dry weight)			(g cm ⁻² year ⁻¹)			(g cm ⁻² year ⁻¹)		
	Mean	Median	<i>n</i>	Mean	Median	<i>n</i>	Mean	Median	<i>n</i>
Coral reefs	0.46	0.35	11	11.04	12.82	4	0.26	0.26	4
Seagrass meadows	0.73	0.67	6	65.76	83.00	3	0.12		1
Mangrove forests	8.7	6.3	14	149.98	139.00	9	0.28		2

contained in carbonates mainly originating from corals, foraminifera, and calcareous algae, which typically have values less than 0.2% to 0.4% (Miyajima et al. 1998).

Table 10.2 also summarizes the OC content of seagrass bed and mangrove forest sediments. Please also refer to Chaps. 2 and 3 for discussions of OC in seagrass beds (Miyajima and Hamaguchi 2018) and mangrove sediments (Inoue 2018), respectively. OC in seagrass sediments shows large variability, ranging from 0.1% to 11% (Kennedy et al. 2010). Most tropical and subtropical seagrass beds have a relatively low OC content of 0.6% or 0.7%; the median of the values surveyed here is 0.67%, which is about twice that of coral reef sediments (0.35%). Coral reef sands vegetated by seagrasses have OC contents 2–5 times those of unvegetated reef sands, possibly from the accumulation of detrital OC in seagrass beds (Miyajima et al. 2015). OC in mangrove sediments also shows large variability, ranging from 0.6% to 36% (Bouillon et al. 2003; Breithaupt et al. 2012). The median of values surveyed here is 6.3%, which is close to the median mangrove sediment OC content of 7.0% reported by Breithaupt et al. (2012) and about 18 times the OC content of reef sediments.

The differences between OC concentrations in coral reef, seagrass meadow, and mangrove sediments can be explained in terms of the supply and preservation of organic carbon in each ecosystem. The sedimentation rates compiled from previous studies are not very different across these ecosystems (Table 10.2): $0.26 \text{ g cm}^{-2} \text{ year}^{-1}$ for coral reefs, $0.12 \text{ g cm}^{-2} \text{ year}^{-1}$ for seagrass beds (although only limited data are reported), and $0.28 \text{ g cm}^{-2} \text{ year}^{-1}$ for mangrove forests. The OC burial rates, however, are much higher in mangroves and in seagrass beds than in coral reefs; the median values are $12.8 \text{ gC m}^{-2} \text{ year}^{-1}$ for coral reefs, $83.0 \text{ gC m}^{-2} \text{ year}^{-1}$ for seagrass beds, and $139 \text{ gC m}^{-2} \text{ year}^{-1}$ for mangrove forests. This difference results not only from the supply of organic matter, but also from the differences in decomposition and preservation of organic matter in the sediments. In coral reef sediments, the top several centimeters of sediments are usually supplied with oxygen (Werner et al. 2006; Yamamoto et al. 2015) mainly through pore-water advection due to highly permeable sediments with relatively large grain size (Werner et al. 2006). This oxygen supply can facilitate carbon mineralization in the surface sediments (Miyajima and Hamaguchi 2018). This mechanism can help maintain low OC content in reef sediments when the supply of organic matter is not too high.

10.2.5 Carbon Export from Coral Reefs

Coral reefs can export organic matter from primary production, either to their internal sediments or to the open ocean. As explained in Sect. 10.2.2, coral reefs have high GPP as well as respiration, but many reef flats are slightly autotrophic and show positive net primary production (NPP) (for example Gattuso et al. 1993, 1996b; Kayanne et al. 1995, 2005; Ohde and van Woesik 1999; Hata et al. 2002). Positive NPP means that OC can be either stored within the ecosystem or exported to adjacent systems such as the open ocean. Note that the pCO_2 decrease due to NPP

can often be offset by net calcification in coral reefs, which increases $p\text{CO}_2$. Corals release the excess primary production as mucus, either as dissolved organic carbon (DOC) or particulate organic carbon (POC) (Wild et al. 2004; Tanaka et al. 2008). According to Wild et al. (2004), much of the mucus released into seawater efficiently traps organic matter from the water column, which is rapidly carried to the lagoon sediment and filtered through the lagoon sands. Mucus transports energy to the lagoon sediments and then the sediments rapidly recycle the organic matter to nutrients, thus serving as a mechanism for retaining energy and nutrients within the reef ecosystem.

Some portion of the excess production can be transported offshore of the reef. Delesalle et al. (1998) studied the organic carbon and carbonate export for Tiahura reef, French Polynesia, and reported an offshore transport of about 47% and 21% of the excess organic and inorganic carbon production, respectively. Hata et al. (1998) studied the organic carbon flux around a barrier reef in Palau in the western Pacific. They estimated that 7% of carbon from GPP on the reef flat is deposited in the lagoon, 4% is exported to the open ocean, and 0.6% is transferred below the thermocline (150-m depth) of the inshore open ocean (Fig. 10.4). Hata et al. (2002) simultaneously studied organic carbon fluxes and community production rates on the Shiraho coral reef for a week. They found that 6–7% of GPP and a majority of NPP (almost 100%) were exported offshore as POC and DOC, and about 14–20% of the POC and 0.2% of GPP exported from the reef flat reached 1 km offshore and 40-m depth.

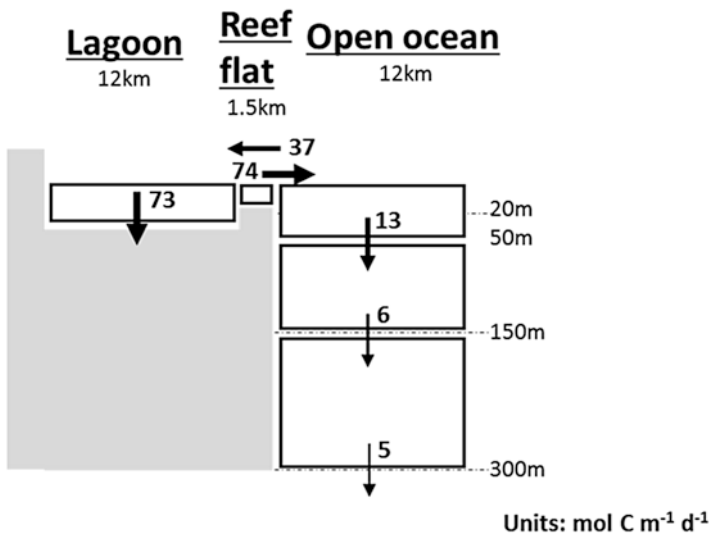


Fig. 10.4 Organic carbon flux around a coral reef (based on Hata et al. 1998). The organic carbon flux from the reef flat to the open ocean is estimated at $74 \text{ mol C m}^{-1} \text{ day}^{-1}$, which is about 7% of the gross primary production (GPP) of the reef. The net export of organic carbon from the reef flat is $37 \text{ mol C m}^{-1} \text{ day}^{-1}$, which is about 4% of the GPP, and about $6 \text{ mol C m}^{-1} \text{ day}^{-1}$ is carried to a depth of 150 m (below the thermocline) in the inshore open ocean, which is about 0.6% of the GPP

Carbon export studies from coral reefs are obviously limited and need a more integrated approach in the future. First, the carbon fluxes should be studied together with in-reef productivity measurements to understand their interrelationships. Seasonal variations as well as tidal effects on the carbon export should also be examined; a higher carbon flux can be anticipated during spring tide compared to neap tide. Characterization of the organic matter will also be required. The C/N ratios of the organic particles captured in sediment traps have been reported (Delesalle et al. 1998; Hata et al. 1998, 2002), but it will be necessary to know the fatty acid composition or isotopic signatures of the particles to determine the origins of the organic matter (Hata et al. 2002).

10.3 Relationships Between Coral Reefs and Other Tropical and Subtropical Coastal Ecosystems

As noted in the Introduction, the distribution of coral reefs overlaps with those of mangroves and tropical/subtropical seagrasses (Fig. 10.1), and we can expect close linkages among these ecosystems. Mangroves and seagrass beds interrupt freshwater discharge, are sinks for organic and inorganic materials as well as pollutants, and can generate an environment with clear, nutrient poor water that promotes the growth of coral reefs offshore (Fig. 10.5 and references such as Moberg and Folke 1999; Hemminga and Duarte 2000; Duke and Wolanski 2001; Unsworth and Cullen

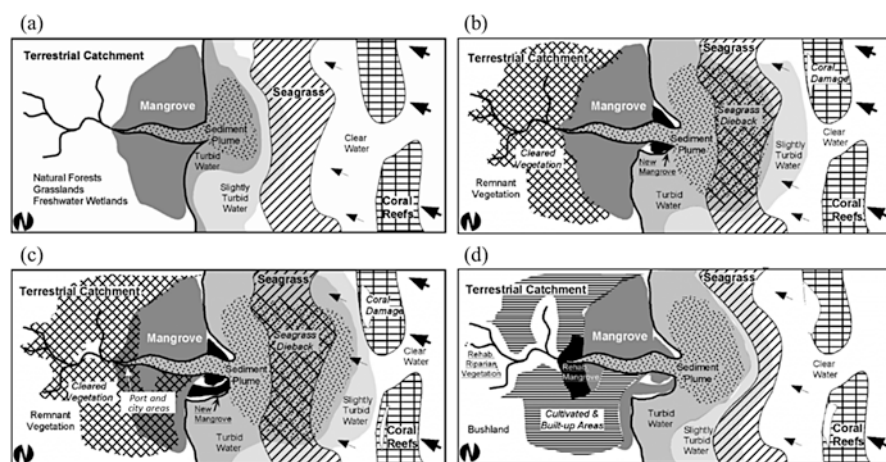


Fig. 10.5 Conceptual illustration showing the turbid waters and sediment plume from (a) an undisturbed terrestrial catchment, (b) a disturbed terrestrial catchment for a rural area only, (c) a terrestrial catchment including rural, port, and city areas disturbed by clearing mangrove vegetation, and (d) a catchment in a port and city area rehabilitated from the conditions in (c) with mangroves and riparian vegetation. Arrows indicate prevailing wave direction and relative strength. Figures are after Duke and Wolanski (2001) with slight modifications

2010). Coral reefs in turn dissipate wave energy and create favorable conditions for the growth of seagrasses and mangrove ecosystems (Birkeland 1985; Ogden 1988). Here we briefly summarize the physical and biogeochemical relationships between coral reefs and associated landscapes such as seagrass meadows and mangrove forests. We also explain the shift of reef flats from coral communities to macroalgal communities (“phase shift”) and the implications of this shift to changes in biogeochemical cycles.

10.3.1 Relationship Between Coral Reefs and Seagrass Beds

Lamb et al. (2017) showed recently that when seagrass meadows are present in a reef ecosystem there is a 50% reduction in the relative abundance of pathogens potentially capable of causing diseases in humans and marine organisms. Their field surveys showed that disease levels in more than 8000 reef-building corals located adjacent to seagrass meadows were lower by a factor of two compared to corals at sites without adjacent seagrass meadows.

Biogeochemical interactions between seagrasses and corals have recently been proposed. Unsworth et al. (2012) found that 83% of seagrass meadows in the Indo-Pacific have a positive NPP and can increase seawater pH, which could buffer coral reef calcification against future ocean acidification. Future laboratory and field work should quantify the buffering capacity of seagrass relative to ocean acidification.

Coral reefs in turn serve as physical buffers against oceanic currents and waves, creating a suitable environment for seagrass beds over geologic time (Moberg and Folke 1999). However, as Saunders et al. (2014) suggested, this shelter effect can be threatened by increases of water depth in the lagoon (or moat) from sea-level rise. They indicate that the rates of carbonate accretion typical of modern reef flats (up to 3 mm year⁻¹) will not be sufficient to maintain suitable conditions for reef seagrasses in the future. These climate change (i.e. ocean acidification and sea-level rise) impacts on connected coral reef–seagrass landscapes should be considered when planning conservation efforts.

10.3.2 Relationships Between Coral Reefs and Mangrove Forests

Mangrove forests act as natural filters to trap fine sediments and improve water clarity (Fig. 10.5; Duke and Wolanski 2001). Mangrove forests typically occur in turbid waters where the turbidity mainly comes from a terrestrial catchment. When the catchment still has natural forests, grasslands, or freshwater wetlands, mangroves can filter the turbid water, and any remaining slightly turbid water does not reach

that far into the coastal areas, permitting the co-existence of offshore seagrass meadows and coral reefs (Fig. 10.5a). If a river catchment includes disturbances in rural areas from clearing vegetation for grazing and agriculture, the turbid waters and sediment plume can extend far offshore, resulting in seagrass dieback (Fig. 10.5b). Mangroves can be largely unaffected by these disturbances, or even become established on new depositional banks, achieving a net gain in areal extent. In cases where even the mangrove forests are cleared, slightly turbid water can extend farther toward reef areas (Fig. 10.5c). Seagrass dieback occurs in turbid waters and coral damage in slightly turbid water. In the Great Barrier Reef, there has been a shift from pristine conditions (Fig. 10.5a) to disturbed conditions (Fig. 10.5b, c) within the last 200 years, since European settlement. Rehabilitation of upstream ecosystems is considered the only way of restoring downstream marine ecosystems (Fig. 10.5d). The maintenance of healthy mangrove forests can therefore be seen as a prerequisite for keeping coral reefs (and seagrass meadows) productive, and thus they should be rehabilitated or conserved together as a connected seascape.

Mangrove forests can enhance the biomass of coral reef fishes. Mumby et al. (2004) showed that mangroves in the Caribbean strongly influence the community structure of fish on neighboring coral reefs, and the biomass of some commercially important fish is more than doubled when the adult fish habitat is connected to mangroves. More recently, Serafy et al. (2015) pointed out that at a regional scale in the Caribbean, a greater expanse of mangrove forest generally functions to increase the densities on neighboring reefs of those fishes that use these shallow, vegetated habitats as nurseries.

10.3.3 Relationships Between Corals and Macroalgal Communities: Phase Shift

Several reefs around the world have been degraded and shifted from a coral-dominated phase to a macroalgae-dominated phase. This phase shift has been reported in Caribbean reefs and was attributed to increased nutrient loading as a result of changed land-use and intensive fishing, which reduced the numbers of herbivorous fish species (Scheffer et al. 2001).

The phase shift toward macroalgae could influence the carbon cycle in the reefs. For example, Haas et al. (2013) found that macroalgae released more DOC than hermatypic corals, but the exudates from macroalgae and corals had different impacts on neighboring ecosystems. Coral exudates increased the net planktonic microbial community production and enhanced autotrophic benthic microbial community production, thus shifting toward a net autotrophic system. In contrast, macroalgal exudates stimulated heterotrophic organic carbon consumption rates by the planktonic and benthic microbial community, thus there was an overall shift toward a microbial community metabolism that was substantially more heterotrophic.

10.4 Directions for Future Study of Blue–Carbon Dynamics in Coral Reefs and Connected Ecosystems

Modeling can be a strong approach to understanding blue-carbon dynamics in coral reefs under both current and future conditions. Considering the large spatiotemporal variability of carbon dynamics caused by the heterogeneous distribution of benthic organisms and the resultant biogeochemical cycles in coral reefs, it is difficult to accurately represent blue-carbon dynamics solely from field data. Recently biogeochemical models have been coupled with hydrodynamic models for coral reefs (Zhang et al. 2011; Falter et al. 2013; Watanabe et al. 2013; Nakamura et al. 2017). For example, Watanabe et al. (2013) developed a carbonate-system dynamics model driven by coral and seagrass photosynthesis and calcification, and described the air–sea CO_2 fluxes under various hydrodynamic and benthic conditions. They clarified that the status of the fringing reef studied as a CO_2 sink or source was greatly influenced by neap and spring tides (Fig. 10.6). During neap tide, the tidal exchange becomes sluggish and the seawater residence time inside the reef increases, which allows the effects of reef metabolism to remain more within the reef.

The model by Watanabe et al. (2013) did not consider the feedback from water quality to coral metabolism, so Nakamura et al. (2017) further refined the model by

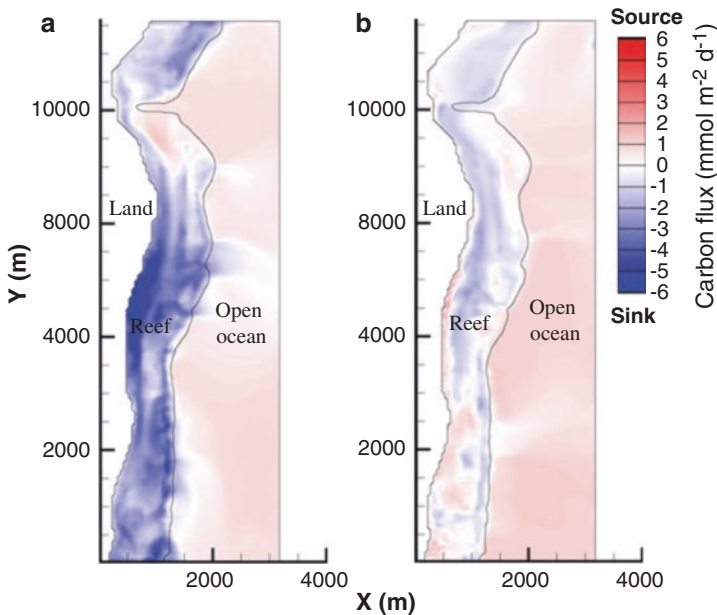


Fig. 10.6 Spatial distribution of CO_2 sinks and sources around a coral reef at Ishigaki Island, Japan during (a) neap tide and (b) spring tide, simulated using a carbonate-system dynamics model coupled with a three-dimensional hydrodynamics model (Watanabe et al. 2013). (Source: Watanabe et al. 2013 with slight modifications)

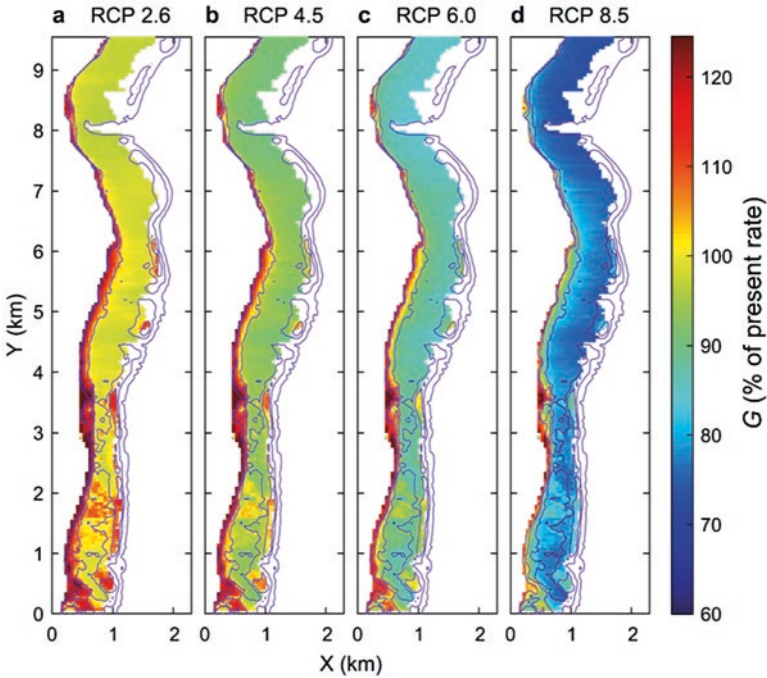


Fig. 10.7 Spatial distribution of coral polyp calcification rates (G , %) of inner-reef corals relative to the present rate under various future Intergovernmental Panel on Climate Change (IPCC) climate-change scenarios for the year 2100 around a coral reef at Ishigaki Island, Japan (Nakamura et al. 2017). (a) CO_2 421 ppm and sea level rise (SLR) 0.4 m (IPCC representative concentration pathway [RCP] 2.6); (b) CO_2 538 ppm, SLR 0.47 m (RCP 4.5); (c) CO_2 670 ppm, SLR 0.48 m (RCP 6.0); (d) CO_2 936 ppm, SLR 0.63 m (RCP 8.5). (Source: Nakamura et al. 2017)

incorporating these feedback interactions so that, for example, the modeled coral could respond to ocean acidification (OA). They also incorporated the effects of seawater flow over the reef on mass transfer in the model. Higher bottom velocity and hence higher bottom shear stress induces higher mass transfer velocity, which in turn enhances diffusive material exchange between corals and ambient seawater. Using their model, they examined coral calcification of inner reef corals under present conditions and under various future OA and sea-level-rise (SLR) scenarios in the year 2100 (Fig. 10.7). In general, calcification rates decreased as a result of OA, but increased in some nearshore reef flat areas because of enhanced mass exchange due to SLR. The more efficient water exchange due to SLR supplies more dissolved oxygen to corals and enhances respiration, which increases ATP synthesis and therefore increases calcification rates in the model.

Many things need to be improved or added for such ecosystem models to be applied to the analysis of blue-carbon dynamics (Fig. 10.8). First, it will be necessary to properly model organic matter production and decomposition. This is critically important to understanding whether the carbon produced within the blue-carbon

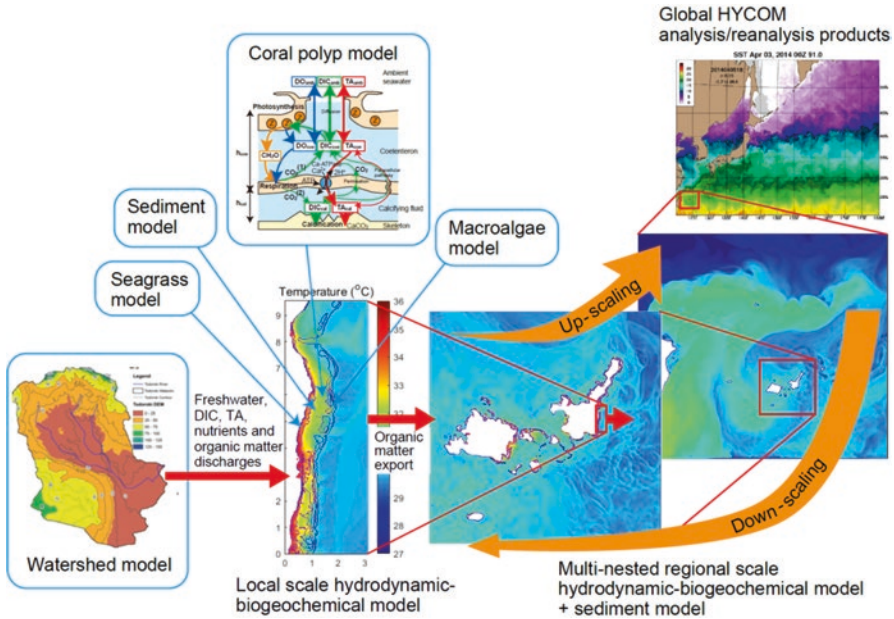


Fig. 10.8 Integrated model for describing blue-carbon dynamics at local and regional scales around a coral reef at Ishigaki Island, Japan. A coral polyp model, sediment model, seagrass model, and macroalgae model (and eventually mangrove model) are incorporated into a local-scale hydrodynamic- biogeochemical model coupled with a watershed model which calculates green carbon flux. The model system calculates the local, reef scale primary production, calcification, and mucus release rate and then calculates dissolved and particulate organic carbon exports to the open ocean. A regional scale hydrodynamic model, which is downscaled from analysis/reanalysis products of global HYCOM (Hybrid Coordinate Ocean Model) using multi-nesting approach, is coupled with biogeochemical and sediment models to track the fate of organic C exported from the local scale model

ecosystem can be exported outside the system (i.e. to the deep layers of the open ocean or within reef sediments) (Abo et al. 2018; Kuwae et al. 2018). An initial simulation of DOC exports using the carbon dynamics model (Fig. 10.8) from a fringing coral reef is shown in Fig. 10.9. Second, interactions between sediment and water-column should be modeled. Carbon burial and sequestration in the sediments can be the key factor determining blue-carbon dynamics (Endo and Otani 2018; Inoue 2018; Miyajima and Hamaguchi 2018). Third, the model should properly address seagrass, macroalgae, and mangrove biogeochemical carbon cycles. Fourth, modeling should incorporate terrestrial carbon (so called “green carbon”) dynamics in the coastal area, including the dynamics of suspended solids. The transport and accumulation of green carbon in coastal areas should be evaluated together with blue-carbon dynamics to quantify the relative importance of these carbons and to highlight the importance of the blue carbon. Fifth, regional three-dimensional models should incorporate horizontal and vertical carbon exports in the open ocean. Export of dissolved inorganic carbon, DOC, or POC from coastal ecosystems to the

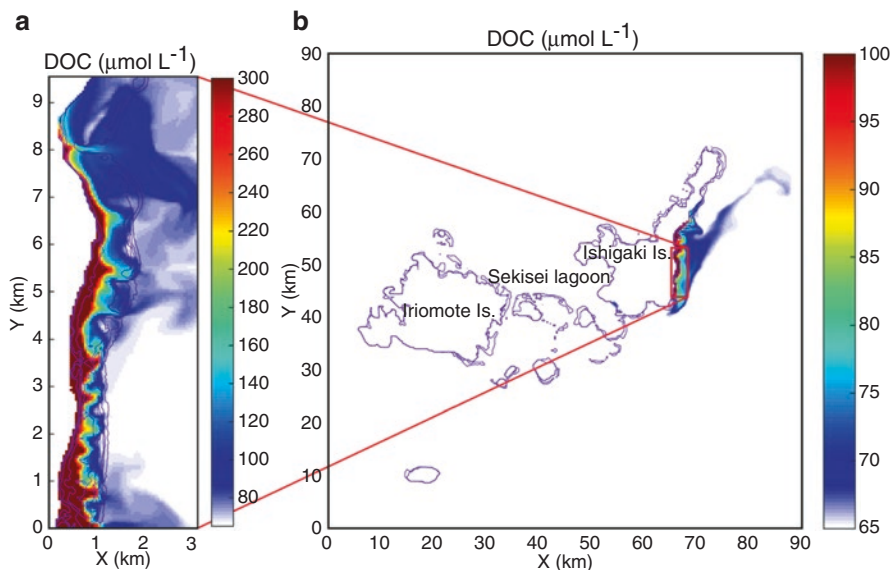


Fig. 10.9 Example of spatial variations in DOC around coral reefs at local and regional scales around a coral reef at Ishigaki Island, Japan

interior of the open ocean can be considered long-term storage of blue carbon, but is difficult to quantify solely from observations. We should therefore model the blue-carbon exports to the ocean interior, which can be validated from sediment-trap observations. All of these considerations can be challenging given the different time scales and models used, but they could be achieved through transdisciplinary approaches involving specialists in hydrology, geochemistry, oceanography, marine ecology, and ecological modeling.

Finally, field and experimental data are indispensable for verifying a blue-carbon dynamics model. The fate of organic matter should be assessed experimentally through decomposition experiments and empirically using sediment traps. Sediment organic carbon contents and sedimentation rates should be measured across different reef environments with and without mangrove forests and seagrass meadows.

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