

Chapter 3

Carbon Exchange Among Tropical Coastal Ecosystems

Steven Bouillon and Rod M. Connolly

Abstract Tropical rivers provide about 60% of the global transport of organic and inorganic carbon from continents to the coastal zone. These inputs combine with organic material from productive mangrove forests, seagrass beds, and coral reefs to make tropical coastal ecosystems important components in the global carbon cycle. Carbon exchange has been measured over multiple spatial scales, ranging from the transport and fate of terrestrial organic matter to the coastal zone, export of organic matter to the open ocean, exchange of leaf litter between mangroves and adjacent seagrass beds, to movement of carbon (at a scale of meters) between adjacent saltmarsh and mangrove habitats. Carbon is exchanged directly as particulate or dissolved material, or through migration of animals or through a series of predator-prey interactions known as trophic relay. This chapter first examines riverine carbon inputs to the tropical coastal zone, and how this material is processed in estuaries. The mechanisms and extent of carbon exchange among tropical coastal ecosystems are then discussed, showing their importance in ecosystem carbon budgets, and the implications for faunal and microbial communities.

Keywords Organic carbon · Mangroves · Seagrasses · Coral reefs · Tropical rivers

3.1 Introduction

Tropical coastal ecosystems are often highly productive, and can receive organic matter from a variety of sources, such as riverine inputs, local production by phytoplankton, or vegetated systems (mangroves, seagrasses). Tropical rivers have a disproportionately high importance in the global delivery of organic and inorganic

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carbon to the coastal zone (Ludwig et al. 1996a), but biogeochemical processing and local inputs from primary production in the coastal zone can greatly modify the quantity and composition of carbon. In-depth knowledge of carbon fluxes and transformations in the tropical coastal zone is therefore important for a finer constraining of global carbon budgets. Moreover, considering the rapid and global changes occurring in river flows and associated sediment and organic matter transport, coastal eutrophication and destruction of coastal ecosystems such as mangroves, seagrass beds, and coral reefs, understanding the functioning of these systems and their interactions is important to be able to correctly assess the health of estuaries and coastal systems and predict the impact of climate change or anthropogenic disturbance.

Organic matter differs substantially in biochemical composition and availability to consumers, depending on whether it is imported by rivers or produced locally by various primary producers (plankton, seagrasses, macroalgae, and mangroves). Exchange of organic matter across ecosystem boundaries thus has important consequences for the availability of organic matter and the relative importance of burial, mineralization, and consumption by fauna. It has often been proposed that organic matter exported from tidal wetlands such as mangroves and saltmarshes enhances secondary production in the coastal zone, thus contributing to fisheries production. The mechanisms involved now appear to be much more complex, however, and there is as yet little evidence for a direct trophic link between land-derived organic matter inputs and coastal zone fisheries in the tropics (e.g., see Lee 1995). Exchange of carbon has been studied over multiple spatial scales, ranging from the transport and fate of terrestrial organic matter to the coastal zone, export of organic matter to the open ocean, exchange of litter between mangroves and adjacent seagrass beds, to movement of carbon (at a scale of meters) between adjacent saltmarsh and mangrove habitats (Fig. 3.1).

This chapter attempts to summarize the available information on patterns of carbon movement and exchange, and to discuss the underlying mechanisms and consequences. We focus first on the riverine inputs of organic and inorganic carbon to the tropical coastal zone, synthesize available data on how this material is processed in estuaries, and explain how this differs from temperate estuaries. The second part of this chapter discusses the exchange of carbon among various tropical coastal ecosystems, its importance in understanding ecosystem carbon budgets, and the implications of carbon exchange for faunal and microbial communities.

3.2 Riverine Carbon Transport to the Tropical Coastal Zone

3.2.1 Fluxes, Composition, and Fate of Riverine Organic Matter

The global delivery of organic carbon (C) to the world's oceans is estimated to be in the order of 0.3–0.5 Pg C y^{-1} (1 Pg = 10^{12} g) (e.g., Ludwig et al. 1996a, 1996b, Schlünz and Schneider 2000), partitioned almost equally between dissolved and particulate organic carbon (DOC and POC). Riverine transport of inorganic carbon is globally estimated at approximately 0.3–0.4 Pg C y^{-1} (Ludwig et al.

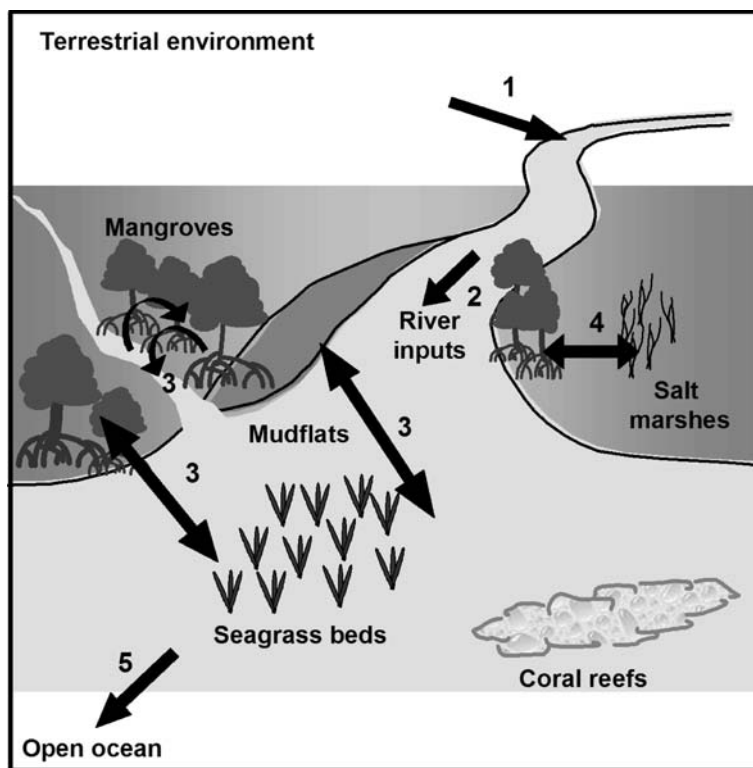


Fig. 3.1 Overview of some of the carbon exchange pathways considered in this chapter: (1) terrestrial inputs to rivers, (2) river inputs to the coastal zone, (3) exchange between intertidal and subtidal aquatic systems, (4) exchange between intertidal ecosystems, and (5) export towards the open ocean

1996a). The tropics are thought to be responsible for about 60% of these fluxes (Ludwig et al. 1996a, Table 3.1), and are therefore disproportionately important in the global terrestrial—marine carbon transport when considering their areal C fluxes. We can thus estimate that for both inorganic and organic carbon, about 0.2–0.25 Pg C is delivered annually to the tropical coastal zone. It should be stressed, however, that relatively few empirical datasets exist on carbon export in tropical rivers, and that these estimates are to a large extent based on extrapolations of data from a limited number of catchments themselves based on empirical models relating catchment characteristics to carbon export. Hence, errors in either underlying data on catchment characteristics or the relationship with carbon export can bias these estimates.

Considering that certain geographical areas are responsible for a major part of these C fluxes, they are particularly important in determining the overall estimates of riverine C transport. Milliman et al. (1999), for example, estimated that six islands in the Indo-Pacific were responsible for about 20% of the global riverine sediment flux, whereas they represent only about 2% of the terrestrial area draining to the

Table 3.1 Estimates of global riverine carbon transport, as dissolved organic carbon (DOC), particulate organic carbon (POC) and dissolved inorganic carbon (DIC), and the importance of the tropical zone in global carbon transport. These estimates are calculated from the data presented in Ludwig et al. (1996a). Note that DIC export is assumed to be equal to alkalinity export

Region	Flux (10^{12} g C y^{-1})			Flux ratios	
	POC	DOC	DIC	POC/DOC	DIC/(DOC+POC)
Tropical, Atlantic Ocean	45.3	59.1	74.6	0.77	0.71
Tropical, Indian Ocean	34.8	21.4	45.1	1.63	0.80
Tropical, Pacific Ocean	33.9	26.8	60.3	1.26	0.99
Σ Tropical zone (24°S–24°N)	114.0	107.3	180.0	1.06	0.81
Σ World	178.6	179.8	291.8	0.99	0.81
% of global transport in the tropics	63.8	59.7	61.7	–	–

global ocean, and this may suggest that such areas may be similarly important in terms of carbon delivery. In line with this, Baum et al. (2007) recently estimated that DOC export from Indonesia could be equivalent to as much as 10% of the global riverine DOC flux to the coastal zone. Data from a number of east African estuaries (Bouillon et al. 2007a, b, Ralison et al. 2008), indicate that the relative export of inorganic carbon (as compared to organic carbon) is more than 10 times higher than that predicted by the empirical model of Ludwig et al. (1996a). On a regional scale, it appears there is a substantial gap in data on the quantities and partitioning of carbon export. A further problem particularly relevant to quantifying carbon transport in tropical rivers is that (with some exceptions such as the Congo basin; Coynel et al. 2005), river discharge and associated carbon transport are often highly seasonal, with the majority of discharge often occurring in a very narrow time frame (e.g., Eyre 1998, Hung and Huang 2005).

Compositionally, organic carbon in rivers generally shows a strong link to the catchment vegetation and land use. In particular in turbid rivers where primary production is light-limited, organic matter from fringing vegetation, floodplains, and terrestrial soils (through runoff) dominates the river-borne organic matter pool. Nevertheless, not all vegetation types within a catchment contribute equally to riverine organic carbon inputs. In the Congo basin, for example, Coynel et al. (2005) found that forested sub-basins showed about three times higher area-specific fluxes of organic carbon than savannah-dominated basins. Similarly, a number of studies found a smaller contribution of C4-derived material (i.e., derived from tropical grasslands) in riverine organic matter than would be expected based on their relative cover in the rivers' catchment (Martinelli et al. 1999, Ralison et al. 2008). Inputs of organic carbon from (C4) grasslands appear to be more important during flood events or high flow periods (Martinelli et al. 1999) when there is sufficiently strong runoff to mobilize soils and organic matter.

The estimates of carbon transport above (see Table 3.1) refer to what is delivered by rivers to the tropical coastal zone, but do not take into account possible

changes occurring within estuaries, bays, and lagoons, and thus do not necessarily reflect what is actually delivered to the open ocean. In these coastal systems, a range of changes can take place which greatly modify the quantity and composition of organic matter pools. Organic matter can be removed through burial, consumption, or mineralization, and new inputs of organic matter can arise, in particular from the often very productive vegetated systems such as mangroves or seagrass beds. This will result in deviation from conservative behavior along the estuarine mixing gradient. Conservative mixing implies no loss or inputs along the estuarine gradient, and hence, a linear concentration gradient between freshwater and marine end-members (see also Chapter 12). Mixing scenarios can also be evaluated using $\delta^{13}\text{C}$ signatures, whereby conservative mixing follows the general equation (described here for dissolved organic carbon):

$$\delta^{13}\text{C} = \frac{\text{Sal}(\text{DOC}_F \delta^{13}\text{C}_F - \text{DOC}_M \delta^{13}\text{C}_M) + \text{Sal}_F \text{DOC}_M \delta^{13}\text{C}_M - \text{Sal}_M \text{DOC}_F \delta^{13}\text{C}_F}{\text{Sal}(\text{DOC}_F - \text{DOC}_M) + \text{Sal}_F \text{DOC}_M - \text{Sal}_M \text{DOC}_F}$$

whereby: Sal = the sample salinity, $\text{DOC}_F \delta^{13}\text{C}_F$ = the DOC concentration and stable isotope composition at the freshwater or least saline end-member, $\text{DOC}_M \delta^{13}\text{C}_M$ = the DOC concentration and stable isotope composition at the marine end-member.

Examples of such non-conservative behavior are shown in Fig. 3.2, where DOC and $\delta^{13}\text{C}_{\text{DOC}}$ profiles are shown for two contrasting estuaries. The DOC profile for Mtoni Estuary (Tanzania) shows clear net inputs of DOC along the estuarine gradient, i.e., with DOC data points above the conservative mixing line (Fig. 3.2a). The corresponding $\delta^{13}\text{C}_{\text{DOC}}$ profile (Fig. 3.2b) indicates that the inputs of DOC in this estuary have a ^{13}C -depleted signature, consistent with the expected DOC inputs from mangroves, which occur along the length of the salinity profile measured (see also Machiwa 1999). The DOC profile from the Tien River estuary (Mekong Delta, Vietnam), where no mangrove vegetation is present, shows a contrasting pattern, with net losses of DOC along the salinity gradient, i.e., most DOC data points below the conservative mixing line (Fig. 3.2c). The $\delta^{13}\text{C}_{\text{DOC}}$ profile for this site (Fig. 3.2d) is similar in shape to the one from Mtoni and indicates that this loss of DOC coincides with a depletion in ^{13}C of the remaining DOC pool, most likely suggesting selective degradation of a more ^{13}C -enriched fraction of DOC.

The behavior of DOC in estuaries may also change seasonally: Dittmar and Lara (2001a), for example, reported DOC profiles for the Caeté Estuary (Brazil) which show both conservative characteristics and non-conservative behavior during different parts of the year. Similarly, Young et al. (2005) report DOC profiles from a tropical seagrass-covered and mangrove-fringed lagoon which suggest both net losses of DOC or net inputs during the mixing process, depending on the season.

River flows are often highly seasonal in tropical regions (e.g., Vance et al. 1998), with the exception of systems with large catchment areas along the equator such as the Congo River basin (see Coynel et al. 2005), and the composition and degradation status of organic matter can thus be distinctly seasonal (e.g., Ford et al. 2005,

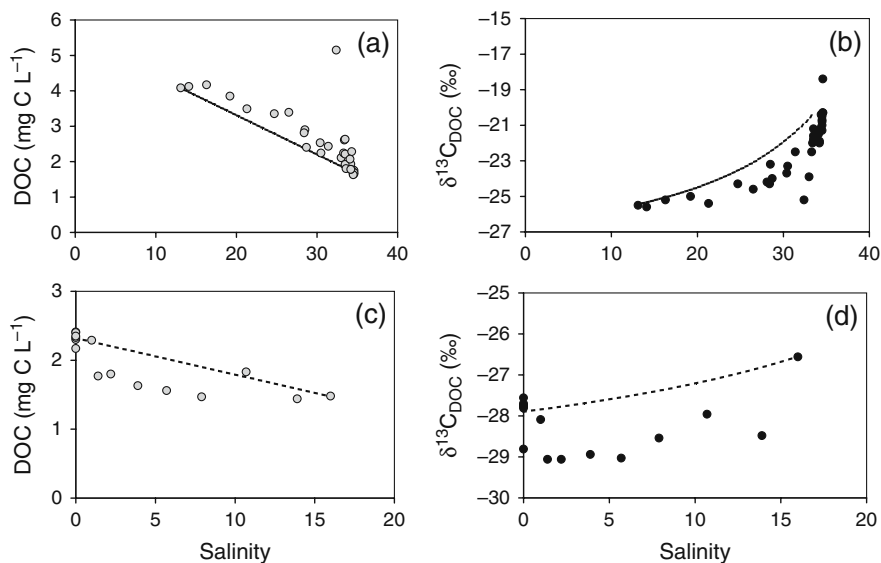


Fig. 3.2 Examples of non-conservative behavior of dissolved organic carbon (DOC) in tropical estuaries showing profiles of DOC (**a**) and $\delta^{13}\text{C}_{\text{DOC}}$ (**b**) from Mtoni Estuary (Tanzania) and from Tien Estuary (Mekong Delta, Vietnam) (**c**, **d**). Source: S Bouillon and AV Borges, unpubl. data. Dotted lines show the patterns expected for conservative mixing between the least saline and most saline end-members

Dai and Sun 2007). During low flow periods, estuaries have much longer residence times, with consequently much higher potential for biogeochemical processes to modify the quantity and composition of organic matter and nutrients (Eyre 1998). Conversely, during periods of high flow, large estuarine plumes may develop which allow for riverine material to be transported further offshore and with less processing of organic carbon within the estuary (e.g., Ford et al. 2005). In coastal bays, in contrast, the relative contribution of terrestrial material to the overall organic carbon pool may be more substantial during the dry season. Xu and Jaffé (2007) reported such a pattern for Florida Bay, which was ascribed to reduced primary production within the bay during the dry season. The fate of riverine organic matter is thus likely to differ substantially during high and low flow periods, although few studies have actually documented such patterns.

The delivery of terrestrial organic matter to offshore waters is important in at least some circumstances. Extensive offshore delivery has been demonstrated for a number of large river systems such as the Congo River (e.g., Schefuß et al. 2004), the Fly River in Papua New Guinea (Goñi et al. 2006) and the Ganges–Brahmaputra River system (Galy et al. 2007), and from tidal wetlands such as the extensive mangroves along the coast of Brazil (Dittmar et al. 2006). Carbon delivery from smaller rivers discharging to open coasts is probably less important. In Australia, for example, where small estuarine plumes punctuate long stretches of sandy coastline, a conservative tracer showed that estuarine particulates were distributed over only a small

area at the estuarine mouth, and terrestrial carbon contributions had little impact on background coastal sources (Gaston et al. 2006).

The contribution of terrestrial carbon to estuarine metabolism and local food-webs has received relatively little attention so far, in part due to the difficulty of detecting its incorporation. Stable isotope signatures of terrestrial C3 plants overlap with those of often-present local lateral inputs (e.g., mangroves) and may also overlap with those of *in situ* aquatic producers. In systems where organic matter derived from catchment C4 vegetation contributes significantly to the riverine carbon load, however, it becomes much more feasible to calculate terrestrial carbon contribution. Surprisingly, data from such systems suggest that terrestrial organic matter can be a major source of carbon even in intertidal mangrove sediments, and contributes equally to sedimentary bacterial communities (up to 40–50%; see Bouillon et al. 2007b, Ralison et al. 2008). The extent to which communities of higher organisms such as invertebrates and fish rely on terrestrial organic matter has recently become a topic of study in temperate waters (e.g., Darnaude et al. 2004), but in tropical systems this has to our knowledge not been studied in detail, although this may be a promising line of future work.

3.2.2 *Effects of Human Perturbations*

3.2.2.1 **Changing River Flows and Catchment Land-uses**

Freshwater flows from rivers into estuaries and ultimately into coastal waters are fundamentally important to carbon transfer. Dissolved and particulate carbon is transported directly in these waters. Freshwater flows also affect carbon movement indirectly, through their effects on salinity in estuaries that alter distributions of coastal plants and the migratory movements of aquatic animals. Freshwater surface and groundwater flow is an important factor, for example, in the distribution of mangrove (Hutchings and Saenger 1987) and saltmarsh plants (Pennings and Bertness 2001). Anthropogenic changes to freshwater flows from rivers therefore alter carbon transfer within and among systems via several different mechanisms. Freshwater is now in such short supply that a global shortage is looming (Postel 2000) and increased harvesting is a certainty. There is thus a need for strong, science-based decisions about water releases from dams to maintain ecosystem health (environmental flows) under pressing political realities (Arthington et al. 2006).

River flows discharging to the sea generally stimulate productivity (Gillanders and Kingsford 2002). In tropical systems, very clear correlations have been found between river flow and fisheries harvests. Flow in two different river systems on the east coast of Australia, for example, match annual fisheries catches, either with or without a time lag. Flows in the Fitzroy River are correlated with increased survival and growth of cohorts of barramundi (*Lates calcarifer*), and catches of this species are higher several years later (Staunton-Smith et al. 2004). Summer flows in the Logan River are positively correlated with catches of fish, crabs and prawns (Loneragan and Bunn 1999). This effect is detected in the same year, and might simply be a result of increased harvesting of recruits into fishing zones, as is probably

the case for banana prawns in the Gulf of Carpentaria, Australia (Vance et al. 1998). Another mechanism which has been suggested is that increased terrestrial organic matter loads to coastal waters increases the abundance of meiofauna and macrofauna, the main prey of the fisheries species (Loneragan and Bunn 1999).

Changing land-use in coastal catchments also affects the amount and nature of organic matter arriving in estuaries and coastal waters. In China, carbon loads from urban and agricultural areas are so now so prevalent that inputs from local mangrove forests have become unimportant in food webs (Lee 2000). The change from forest to agriculture over the last 200 years in catchments adjacent to the Great Barrier Reef, for example, is thought to have increased sediment delivery to the reef about four-fold (see Furnas 2003, cited in Ford et al. 2005), and presumably organic loads along with it.

3.2.2.2 Effects of Climate Change on Carbon Exchange

Patterns in carbon exchange among tropical systems sit within an overarching position of global carbon cycles (Cloern 2001). Carbon is central to the topical issue of climate change. Although the effects of climate change on marine systems has been considered (Poloczanska et al. 2007), we have been unable to find any studies of how climate change might affect carbon exchanges at the land–sea interface. The most certain effect of recent and predicted acceleration in changes to climate on carbon exchange will be through altered rainfall patterns and therefore river flows (Table 3.1). Where rainfall is reduced, the overall delivery of organic matter to estuaries and the coast will be lower. Conversely, where increased rainfall is predicted, we can also predict a greater contribution of terrestrial organic matter to the coastal zone. Overlaying those effects will be the increased variability in rainfall (Poloczanska et al. 2007), with more severe weather events leading to rainfall peaks of greater magnitude and frequency than currently occur. Extreme flow events will likely lead to large pulses of input of terrestrial matter, and as discussed above, probably to an increased importance of C4 material from agriculture.

The ramifications of climate change will, however, be much broader than this. The extent and type of land-use in coastal catchments will presumably be altered, through changes in agricultural activities and urbanization (Cloern 2001). Ultimately this will alter carbon inputs to estuaries and coastal waters (as discussed above).

3.3 Exchange of Carbon Between Vegetated Tropical Systems and Adjacent Systems

3.3.1 Transfer of Carbon from Intertidal to Subtidal — Outwelling

Concepts about carbon transfer among nearshore systems are dominated by the theory of net transfer of carbon from shallow, estuarine habitats to deeper, adjacent

waters. This 'outwelling hypothesis' is based on observations, from saltmarsh systems on the Atlantic coast of North America, that secondary production in adjacent waters could only be sustained if the marsh exports energy (Odum 1968). For tropical systems, this translates as a potential dependency on mangrove-derived organic matter for secondary production in adjacent systems. The export of particulate and dissolved organic carbon from mangroves has received considerable attention, even though the number of quantitative studies is still rather limited to allow for an accurate assessment of organic carbon export on a global scale (e.g., Bouillon et al. 2008b), and the assessment of export rates is hampered by methodological difficulties (e.g., Ayukai et al. 1998, see also Section 12.4 in Chapter 12). Some stable isotope studies show that invertebrates and fish in habitats within hundreds of meters of mangroves obtain carbon from the mangrove forest (Harrigan et al. 1989, Lugendo et al. 2007), although others have not found this (e.g., Connolly et al. 2005, see also Section 3.3.1.5). Lack of influence has been definitively demonstrated at sites further away (Lee 1995). Mangroves may serve both as exporters of organic and inorganic carbon, but also import organic matter during tidal inundation, and assessing the net balance of these processes is not straightforward.

Organic matter from vegetated, intertidal habitats such as mangroves in tropical waters might be exported via three main avenues (Fig. 3.3): (1) dissolved or particulate matter, (2) through migration of animals from intertidal to subtidal waters, and (3) through a series of predator-prey interactions known as trophic relay (Kneib 1997). Each of these pathways is discussed in more detail below. Pathways of DOC, POC, and macro-litter export are likely to differ substantially. For DOC, a number of studies have stressed the importance of sediment-water exchange and pore water flow as vectors for DOC exchange with estuarine or tidal creek waters (e.g., Ovalle et al. 1990, Dittmar and Lara 2001b, Schwendenmann et al. 2006, Bouillon et al. 2007c). Particulate organic carbon, in contrast, appears to be influenced more by water current velocities and runoff (e.g., Twilley 1985). The importance of tidal dynamics was also suggested by Twilley (1985) who compared organic carbon export in different types of mangrove forests and found that the cumulative tidal amplitude is a main driver of the magnitude of total organic carbon export.

3.3.1.1 Exchange of DOC and POC

Our understanding of organic carbon exchange in mangroves comes from a relatively small number of studies: a recent review documents only six and seven estimates for DOC and POC export, respectively, and 11 estimates for total organic carbon export (Bouillon et al. 2008b). It should also be kept in mind that these estimates have been derived using a variety of approaches, including tidal measurements of organic carbon combined with water current measurements, and flux estimates using flow-through flumes (see also Chapter 12). Global estimates of organic carbon export (POC+DOC) from mangroves are in the order of about $250 \text{ g C m}^{-2}\text{y}^{-1}$, with DOC and POC each representing about half of this flux. Together, this would amount to approximately 20% of the net primary production by mangroves, although it must be stressed that our current understanding of carbon cycling in

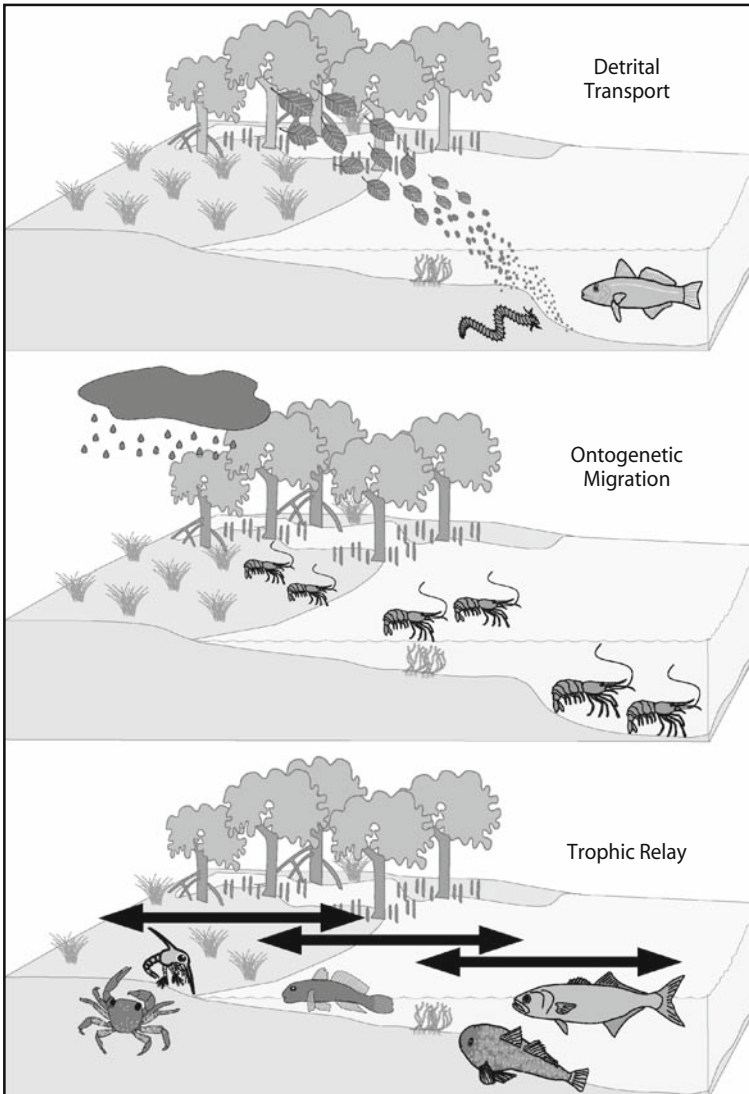


Fig. 3.3 Three mechanisms of transfer of organic matter from mangroves to food webs in deeper water (from Connolly and Lee 2007). Detrital transport includes movement of particulate and dissolved organic matter. Ontogenetic migration is movement in migrating animals such as banana prawns (*Fenneropenaeus merguensis*). Trophic relay (Kneib 1997) involves a series of predator-prey interactions; in Australia, for example, crabs and their larvae which are high on the shore are eaten by fish such as glassfish (Ambassidae), gobies (Gobiidae) and juvenile mullet (Mugilidae), which in turn are preyed upon by fish such as flathead (Platycephalidae) and tailor (Pomatomidae)

mangroves leaves a large uncertainty in assessing an overall C budget for these systems (see Bouillon et al. 2008b). One major shortcoming of most current flux estimates (apart from the limited number of data used to extrapolate to a global level) is the fact that they rarely include a source characterization, and thus do not differentiate between organic carbon fluxes of mangrove origin and those of other potential carbon sources. In that respect, current flux data could be inherently biased and provide an overestimate of actual organic carbon fluxes from mangroves. Source characterization could be particularly important to integrated POC flux measurements, since it is known that mangroves (and other intertidal systems) can trap significant amounts of particulate material, including organic carbon often of non-mangrove origin, during tidal inundation (e.g., Middelburg et al. 1996, Bouillon et al. 2003). Moreover, import and export fluxes of POC (of different origin) can be closely balanced (e.g., Ayukai et al. 1998), leaving only a small residual net flux. For dissolved organic carbon, there are indeed studies which report a net influx, rather than efflux of organic carbon in certain mangrove systems. The flume experiments by Davis et al. (2001) in fringing mangroves along the Taylor River, for example, show that despite seasonal variations, DOC was generally imported from the water column, while TOC showed only small net fluxes, which ranged from import to export. Boto and Wellington (1988) also noted net DOC uptake in mangrove sediments in Coral Creek in northern Australia. One aspect of the study by Davis et al. (2001) is that their flumes were in continuously submerged mangroves, along the flow-path of a channel, in a non-tidal system, and any influence of the tidal pumping phenomenon cannot be ascertained. Since tidal pumping is likely an important mechanism for solute export (e.g., Dittmar and Lara 2001a, Schwendenmann et al. 2006, Bouillon et al. 2007c), DOC export in non-tidal systems may be significantly lower than in most other mangrove settings. In general, tidal hydrology and cumulative tidal amplitude would appear to be important determinants of the degree of organic carbon export. Subsequently, carbon export has been suggested to be higher in riverine forests than in fringe and basin forests (see Twilley 1985), and higher during periods of higher freshwater runoff in estuarine systems (Sutula et al. 2003). Similarly, Romigh et al. (2006) reported a seasonal pattern in DOC fluxes (i.e., periods with net export as well as periods with net import of DOC) consistent with a strong influence of freshwater discharge and tidal amplitude on DOC fluxes.

3.3.1.2 Exchange of Dissolved Inorganic Carbon

The focus on carbon exchange in tropical coastal ecosystems has so far been directed to organic carbon species, but to our knowledge no studies have attempted to directly quantify exchange of dissolved inorganic carbon (DIC). Nevertheless, tropical coastal ecosystems are sites with intense cycling of inorganic carbon, in particular the classical mangrove-seagrass-coral reef sequence. Mangroves are known for their intense mineralization and high CO₂ exchange (e.g., Borges et al. 2003). Tropical seagrass beds can attain very high primary production rates (e.g., Hemminga et al. 1994) resulting in significant lowering of pCO₂ levels in the water column (Bouillon et al. 2007a). Coral reefs, on the other hand, are a major contributor to

overall oceanic CaCO_3 production (Gattuso et al. 1998). A recent comparison of DIC and DOC profiles from a number of tidal mangrove creeks and estuaries indicated that the lateral inputs of DIC from the mangroves was on average about eight times higher than for DOC (Bouillon et al. 2008b). If this is confirmed in other systems and/or through direct quantitative estimates of DIC exchange, this would imply that the mineralization of mangrove carbon and its subsequent export as DIC is substantially higher than the export of mangrove-derived material as organic carbon.

3.3.1.3 Migration and Trophic Relay

The transfer of energy from nearshore to offshore waters in migrating animals is an often overlooked but potentially important mechanism (Kneib 2000). Many important fisheries species, including crustaceans such as crabs and prawns, arrive in estuarine waters as larvae or post-larvae, then grow in the upper estuary, before migrating as larger animals (with their carbon) to the sea. In tropical waters, migration of key species such as banana prawns (*Fenneropenaeus merguensis*) is often strongly seasonal. In the Gulf of Carpentaria, northern Australia, this results from strong freshwater flows through estuaries (Vance et al. 1998). In peninsular Malaysia, where the seasonality of migration for this same species is less pronounced because of more evenly distributed rainfall, the transfer of carbon in the body of animals is still important, because there is the same pronounced net migration out of estuaries (Ahmad Adnan et al. 2002). In southern USA, carbon transfer has been inferred from stable isotopes studies showing the movement of substantial numbers of pink shrimp (*Farfantepenaeus duorarum*) from seagrass meadows to unvegetated fisheries areas (Fry et al. 1999). The total carbon load transferred in this way has not been estimated, and it might ultimately prove to be small relative to particulate and dissolved transfer. This energy source is, however, probably important in coastal food webs because the animals that migrate are highly likely to be predated, and the link with food webs is therefore much more direct than for DOC and POC exported from estuaries.

The phenomenon of trophic relay was first described from temperate saltmarshes, which have small, resident fish and crustacean species that are preyed upon by somewhat larger fish visiting the marsh as transients at high tide. These predators are themselves potentially preyed upon by larger piscivorous fish, thus producing the effect of a relay system that transfers energy from shallow to deeper waters (Kneib 1997). There is preliminary evidence that this concept also applies in tropical systems. For example, glassfish (*Ambassis jacksoniensis*) have been shown to feed on huge quantities of shore crab larvae on a subtropical marsh in Queensland (Hollingsworth and Connolly 2006). Such marshes are inundated only on spring tides, and inundation has an extraordinary effect on the pattern of feeding by fish. Glassfish visiting the marsh on the first night of a tidal cycle feed only lightly, eating a small number of a range of prey types. This inundation apparently acts as a cue for shore crabs to release larvae, and on subsequent nights, glassfish eat an average of 100–200 crab larvae per fish (Fig. 3.4). Glassfish are a small, extremely abundant

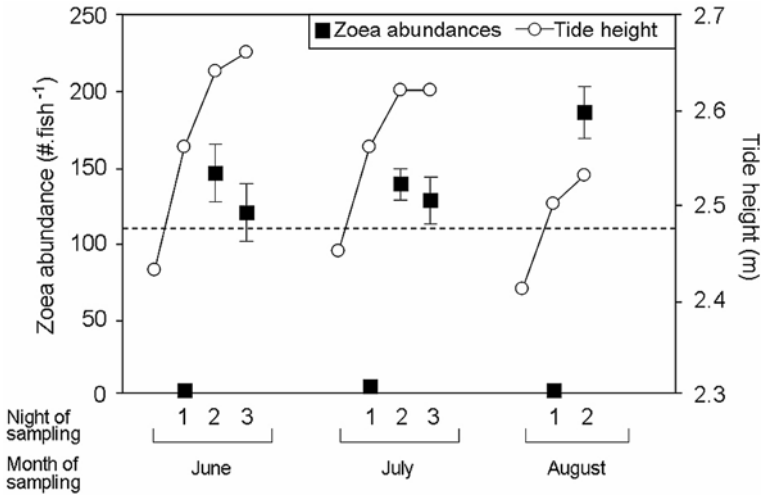


Fig. 3.4 Crab zoea abundances (mean \pm SE) in glassfish (*Ambassis jacksoniensis*) stomachs after feeding on subtropical saltmarsh (data from Hollingsworth and Connolly 2006). In each monthly cycle, fish do not feed on zoea on the first night a marsh is flooded but do so on subsequent nights. Tidal height is shown for each night of sampling and the night before sampling. Tidal height at which marsh is inundated (2.48 m) is shown by dotted line

schooling species, and would be preyed upon by many of the larger fish in channels adjacent to these subtropical marshes (Baker and Sheaves 2005). Substantial effort has recently been aimed at understanding the trophic structure of fish communities in tropical systems (Nagelkerken and van der Velde 2004). Although the extent of piscivory generally remains to be demonstrated (Sheaves and Molony 2000), the first studies combining food web and movement analysis show that trophic relay is potentially very important (Kruitwagen et al. 2007, Lugendo et al. 2007).

3.3.1.4 Effects on Organic Matter Transfer on Food Webs and Ecological Structure

The transport and accumulation of macro-litter in adjacent systems has a number of impacts on the sedimentary environment and faunal communities, but few studies have documented such effects. Daniel and Robertson (1990) suggested that the presence and abundance of exported mangrove detritus had a positive influence on certain groups of macrobenthos such as penaeid shrimps, e.g., by serving as a shelter from predation. For benthic microfauna, in contrast, Alongi (1990) did not find convincing evidence that exported mangrove detritus enhanced the densities of flagellates, ciliates or protozoa. In a long-term experiment in which mangrove litter was added to a microcosm with a sandy substrate, Lee (1999) found no marked influence of litter addition to macrofaunal biomass, but species richness and diversity decreased with increasing litter inputs. The latter could be due to the negative

effects of tannins leaching from litter (Alongi 1987, Lee 1999). Organic carbon in sediments can obviously serve as an important food source for organisms, but the oxygen depletion and accumulation of toxic by-products occurring when high loads of organic matter are delivered to sediments has been shown to result in potential decreases in the abundance and diversity of benthic fauna (Hyland et al. 2005). Although initial reports suggested an important direct trophic role for mangrove organic matter in adjacent aquatic foodwebs (Odum 1968), most later studies found little or no unambiguous evidence for such a role and suggest that the contribution of mangrove-derived carbon to nearshore foodwebs is minimal (see Bouillon et al. 2008a, and Section 3.3.1.5). Considering the importance of dissolved organic matter exchange, the lack of data on the fate of DOC and DON (dissolved organic nitrogen) is striking, and presents an important area for future work. The experiments by Dittmar et al. (2006) indicated that DOC from mangrove pore waters is partly photo-degraded and chemically modified, but that a major part remains after several weeks of incubation in the presence of a natural bacterial community. This suggests that part of the mangrove-derived DOC pool is sufficiently refractory to be dispersed over large areas when hydrodynamic conditions allow.

The quality of organic matter is also important as a determinant of consequences of carbon transport for fauna. For example, excessive labile organic matter (e.g., from shrimp farming) can lead to extensive hypoxia zones (Chua 1992), whereas more refractory organic matter can accumulate in marine sediments (POC) or can be transported in dissolved form (DOC) offshore (Alongi and Christoffersen 1992).

3.3.1.5 Detecting ‘False Positives’ in Outwelling Studies—Avoiding Pitfalls in Stable Isotope Gradient Analysis

A large number of studies have used stable isotope ratios to infer the relative contribution of carbon from intertidal vegetation, particularly mangroves, and other potential sources to the sedimentary or suspended organic matter pool (e.g., Machiwa 2000, Kuramoto and Minagawa 2001, Thimdee et al. 2003). A common strategy has been to relate variations in $\delta^{13}\text{C}$ values of POC to the admixture of mangrove-derived carbon and ‘marine’ phytoplankton, where the latter is characterized by typical $\delta^{13}\text{C}$ values of about -20 to -18‰ (e.g., Rezende et al. 1990, Chong et al. 2001). This oversimplified approach has a major shortcoming because it is based on an assumption that phytoplankton within estuaries or mangrove creeks has a $\delta^{13}\text{C}$ signature similar to that of marine phytoplankton, which is unlikely since mangrove creeks and estuaries typically have $\delta^{13}\text{C}$ signatures for DIC which are distinctly depleted in ^{13}C by $6\text{--}8\text{‰}$ (Bouillon et al. 2008a). Primary producers in the water column are therefore expected to show a similar depletion relative to producers from open marine systems, and the same holds for benthic microalgae (Guest et al. 2004).

The depleted $\delta^{13}\text{C}$ values of DIC near mangroves also affects values of benthic macrophytes such as seagrasses. Seagrass $\delta^{13}\text{C}$ values usually range between -16 and -12‰ (Hemminga and Mateo 1996), but $\delta^{13}\text{C}$ values of seagrasses adjacent to mangrove forests typically show a gradient of more depleted values close to the mangroves, becoming more enriched with increasing distance towards the

sea (e.g., a range of almost 10‰ over <4 km distance found by Hemminga et al. (1994) and Marguillier et al. (1997)). Studies that overlook the DIC isotope gradient with increasing distance offshore from mangroves therefore also overlook a probable gradient in isotope ratios of primary producers with distance offshore. Any gradient in isotope ratios of particulate carbon or even in animal tissues described in such studies might therefore provide ‘false positives’ in their test of the importance of mangrove carbon.

The isotopic depletion of the DIC pool near mangroves, and its effect on other local autotrophs, means that reliance on any autotroph will look like a mangrove contribution to food webs adjacent to mangroves in isotope gradient studies. It is important, therefore, to adopt specialized strategies to overcome this challenge in studies of potential outwelling. First, isotope values of potential alternative sources should be measured intensively and at a fine spatial scale. If plankton cannot be properly collected, spatially intensive DIC sampling provides a realistic alternative. Second, because carbon isotope measurements alone often cannot resolve the contribution of various sources to the POC pool, a combination of isotopes with other tracers should be considered (such as POC/PN ratios, e.g., Gonnee et al. 2004; POC/Chl. *a* ratios, e.g., Cifuentes et al. 1996; or other biochemical tracers such as lignin-derived phenols, Dittmar et al. 2001, see also Chapter 12).

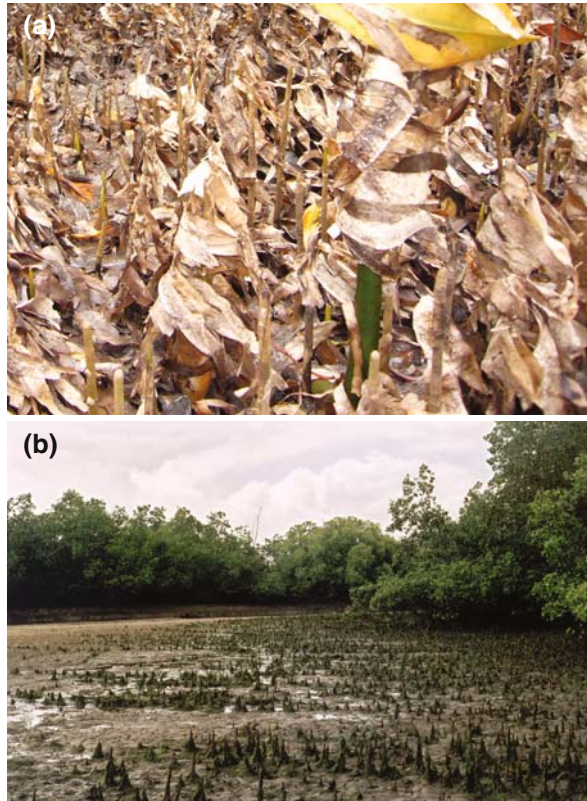
3.3.2 *Transfer of Carbon to Intertidal Habitats—Inwelling*

3.3.2.1 *Seagrass to Mangroves*

The role of macrolitter in material exchange has been poorly studied in tropical coastal systems, and represents an important gap in our knowledge, since the few available studies suggest that the quantities of floating or suspended macrolitter can be high in comparison to the normal POC or DOC concentrations.

Slim et al. (1996) documented tidal transport of seagrass, mangrove, and macroalgal litter in a Kenyan bay. They found clear evidence for bidirectional transport of macrolitter, with a dominance of seagrass litter during both ebb and flood periods, but mangrove litter being more important during ebb than during flood periods. The accumulation of mangrove-derived material in this system has also been demonstrated based on organic carbon and stable isotope evidence (Hemminga et al. 1994, Bouillon et al. 2004). The deposition of litter in intertidal mangroves can be highly conspicuous in sites close to seagrass beds or where macroalgae are abundant (Fig. 3.5), and is also evident based on stable isotope data in bulk sediments which are often distinctly different from that of the dominant local vegetation (Middelburg et al. 1996, Bouillon et al. 2004; Fig. 3.6) and in the distribution pattern of n-alkanes in mangrove sediments close to the seagrass beds (P.V. Khoi and S. Bouillon, unpubl. data). Wooller et al. (2003) found the sediment organic matter in *Laguncularia* mangroves in Twin Cays (Belize) often to be dominated by non-mangrove sources, including seagrass material, as evidenced by some sites having high $\delta^{13}\text{C}$ signatures combined with high C/N ratios, consistent with those of

Fig. 3.5 Deposition of seagrass litter in intertidal *Avicennia marina* forests in Gazi Bay (Kenya) (a), deposition of the macroalgae *Ulva* spp. in *Sonneratia alba* mangroves in Mtoni Estuary, Dar es Salaam (Tanzania) (b)



Thalassia sp. from adjacent seagrass systems. Massive deposits of seagrass material have also been reported on tropical sandy beaches (Hemminga and Nieuwenhuize 1991) and in intertidal flats (de Boer 2000), but little is known on the fate of this material and its potential trophic importance in these unvegetated systems.

3.3.2.2 Seagrass to Mudflats

For shallow sand and mud flats, recent experimental work in temperate waters has resulted in a new conceptualization of food webs. Deliberate ^{13}C tracer experiments on the intertidal flats of northern Europe clearly show that benthic microalgae in the sediment are a major contributor to food webs (Middelburg et al. 2000). This has formed part of the more general realization that benthic microalgae are highly productive and easily assimilated in a food web context (MacIntyre et al. 1996).

In tropical Australian systems, there is evidence from fatty acid studies that benthic microalgae make at least some contribution to the nutrition of invertebrates (Meziane et al. 2006). On the other hand, carbon isotope evidence from the same mudflats shows a strong reliance on allochthonous carbon from adjacent

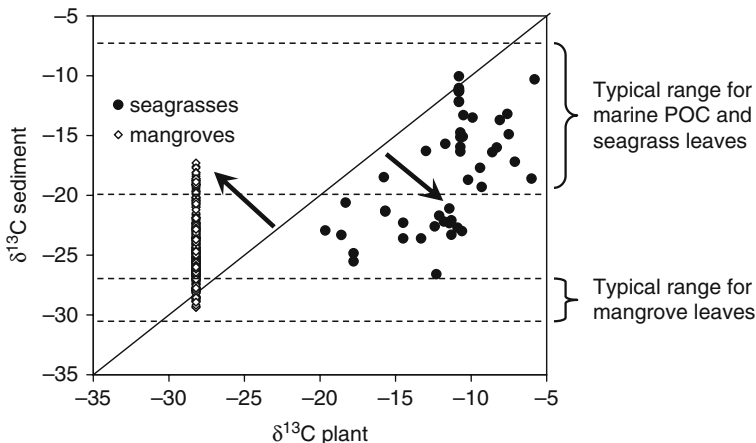


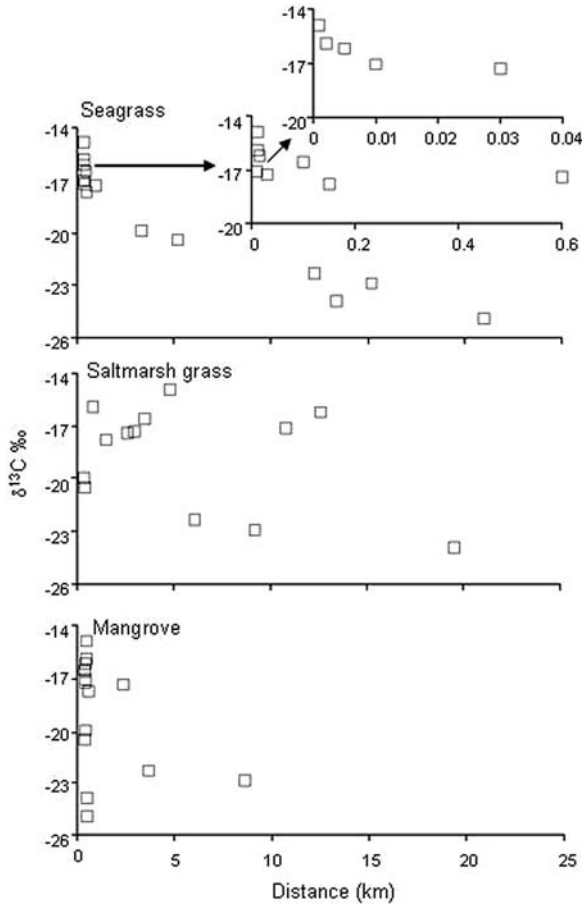
Fig. 3.6 Comparison of sediment organic carbon $\delta^{13}\text{C}$ signatures with those of the dominant seagrass species (data for tropical and subtropical systems only) or mangroves. For mangroves, we used a global average $\delta^{13}\text{C}$ value for plant material of -28.2‰ (see Bouillon et al. 2008a). For data sources for seagrass systems, see Bouillon et al. (2004); data for mangrove systems are also presented in Kristensen et al. (2008). Sediment $\delta^{13}\text{C}$ signatures in mangroves are often distinctly more ^{13}C -enriched to those of mangrove litter inputs, and conversely, sediment $\delta^{13}\text{C}$ data from seagrass beds are consistently ^{13}C -depleted relative to the dominant seagrass vegetation. POC = particulate organic matter

seagrass meadows (Melville and Connolly 2005). This transfer of organic material from seagrass meadows to mud flats is further supported by recent results for the commercially-important portunid mud crab, *Scylla serrata*. Mud crabs generally have relatively enriched carbon isotope ratios, showing reliance on organic matter from either seagrass meadows or saltmarsh grass. Mud crab ratios, however, show very strong spatial variation. A survey of mud crabs at different distances from key habitats found that distance to seagrass, and not distance to saltmarsh (or mangroves), explained much of the variation (Fig. 3.7). This isotope evidence suggests that, where seagrass is present in shallow tropical waters, carbon from the meadows will have a disproportionately high contribution to animal nutrition, whereas further from meadows and where no seagrass exists, animals rely on a generalized carbon pool from a variety of sources.

3.3.3 Scales of Carbon Transfer Among Systems

The source of energy to consumers and its movement among habitats has been a key focus in ecology. Carbon is expected to move more in aquatic than terrestrial systems because water acts as an efficient transport medium (Polis et al. 1997). In practice, however, the degree to which carbon is transported and utilized in food webs varies among systems.

Fig. 3.7 Relationships between carbon stable isotope ratios ($\delta^{13}\text{C}$) of mud crabs *Scylla serrata* and the distance crabs were caught from the nearest patch of three habitats (seagrass, saltmarsh, mangroves). The strongest relationship is with seagrass distance, and for this habitat exploded views of small distances show the tight relationship. No relationship exists for saltmarsh or mangroves. Data from Waltham and Connolly (unpubl.)



First, the extent of carbon dispersal from river plumes to coastal ecosystems depends on flow rates. Major rivers such as the Amazon River affect pelagic and benthic processes over tens of kilometers (Smith and Demaster 1996). The discharge from smaller rivers, however, can be retained in small, distinct plumes that remain close to the coastline, over an area less than 1 km^2 (e.g., Gaston et al. 2006).

Within estuaries themselves, carbon is potentially moved on tidal currents. The amount of carbon available to move has been difficult to quantify, because of high rates of allochthonous input from riverine sources and autochthonous production from often extensive fringing vegetation, and high secondary productivity and, therefore, consumption of carbon. Depending on season and location, mangrove carbon has been detected as detritus in sediment at between 2 and 4 km from mangrove forests, using both stable isotope (Rodelli et al. 1984) and fatty acid (Meziane et al. 2006) techniques. For some estuaries, however, the large scale movement of carbon expected from the outwelling theory has not been substantiated (e.g.,

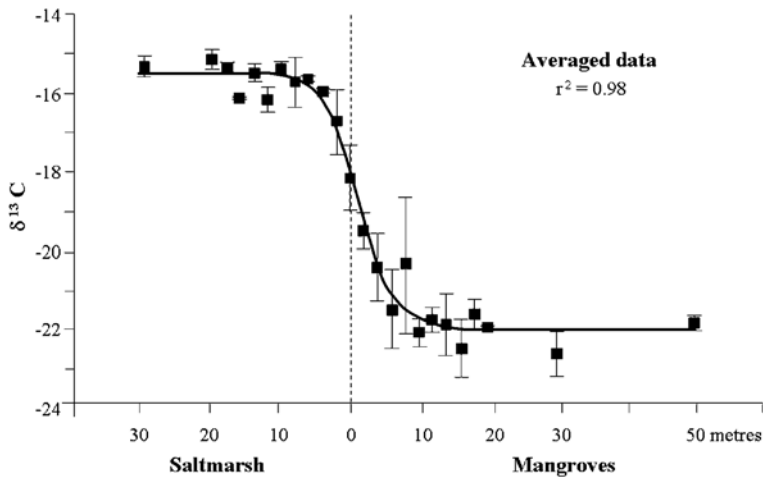


Fig. 3.8 Carbon stable isotope values of the grapsid crab *Parasesarma erythroductyla* across the mangrove/saltmarsh interface (mean \pm SE) from three sites; after Guest and Connolly 2004). The rapid change at the interface indicates that crabs utilize different carbon (energy) sources in the two habitats

Loneragan et al. 1997). More recent evidence suggests that the movement of carbon in estuarine habitats can occur at a finer scale than has previously been considered. For example, in a tropical study examining the carbon isotopes of shore crabs at sites separated by hundreds of meters, Hsieh et al. (2002) found that the crabs derive their carbon from the sites in which they reside rather than from further afield. A subsequent study of the movement and assimilation of carbon by shore crabs in a subtropical estuary showed that crabs obtain their nutrition from sources within the surrounding few meters (Fig. 3.8). Detailed measurements of crab and POM movement suggests that the short distance carbon is transported occurs through movement of POM rather than crabs, which have a very small foraging area (Guest et al. 2004, 2006).

3.3.4 Carbon Exchange in Coral Reefs

Compared to other tropical coastal ecosystems, very few studies have addressed the exchange of carbon between coral reefs and adjacent waters (Gattuso et al. 1998).

Delesalle et al. (1998) estimated for a French Polynesian coral reef system that 47% of organic matter production and 21% of carbonate production was exported, the latter being in agreement with previous estimates by Smith et al. (1978; 25%). These numbers were considered minimum estimates, since they did not consider DOC exchange, exchange of macro-debris, and since their measurements were carried out during relatively calm weather conditions and only considered export towards the ocean on the outer part of this fringing reef. The extensive sampling setup by Delesalle et al. (1998) also revealed that horizontal and downslope

advection of particles was the dominant pathway of export, rather than vertical transport offshore. The latter is also supported by the data in Hata et al. (1998, 2002), who estimated that only about 20–35% of the POC exported from reef flats was recovered in sediment traps at 40–50 m depth at some distance outside the reefs.

Hata et al. (1998) estimated that the net export rate of organic carbon from a coral reef in Palau represented about 4% of the gross primary production, but this study considered only export of particulate organic carbon and not DOC. Furthermore, since the majority of gross primary production is generally respired in such systems (up to 94%, estimated by Hata et al. 2002), this may still represent a significant part of the (relatively small) net organic carbon production. Hata et al. (2002), for example, estimated that the majority of net community production (80–100%) was exported as DOC or POC, with DOC fluxes being 5–6 times higher than POC fluxes. Considering the open character of coral reefs, such a high degree of export, in particular of the DOC produced within these systems, is not entirely surprising. Coral cays can act, however, to trap and store carbon. Pile (2005) showed on the Great Barrier Reef, for example, that almost all of the ultra-nanoplankton in ambient water is removed by filter feeding organisms on the coral reefs in one pass of the water over the reef. This powerful filtering role suggests net uptake of carbon on reefs, at least over short periods, once the activities of all sessile organisms are taken into account. Similarly, de Goeij and van Duyl (2008) found that the surface of coral reef cavities (including the associated biota) can act as net sinks of DOC.

Export of the excess organic carbon production in the form of living biomass (e.g., juvenile fish migrating to other environments to complete their life cycle) has been proposed to be a major component of the organic matter export in coral reefs (50–75%, see Gattuso et al. 1998), as well as export of drifting algae in systems where algae are an important component of the reef (Kilar and Norris 1988, see also Hata et al. 1998).

3.4 Conclusions and Future Research Directions

Tropical and subtropical coastal ecosystems are characterized by intense primary production and a high degree of carbon exchange on various spatial scales, which can be abiotically driven (flux of particulate and dissolved material) as well as biologically driven (animal movement and trophic relay). The past few decades have seen an increased awareness of the role of the tropical coastal zone in global carbon budgets. We are still far from being able to constrain this role in quantitative terms, however, because of: (1) the complexity of assessing material fluxes and combining this with information on the origin of the material considered, and (2) the diversity of ecosystems in the tropical coastal zone (estuaries, lagoons, mangroves, mudflats, seagrass beds, and coral reefs). These factors necessitate a range of approaches and analytical techniques to adequately address their biogeochemical functioning. Moreover, assessing the importance of biologically mediated carbon exchange is complex and has only rarely been attempted in quantitative terms.

Even carbon budgeting efforts for individual ecosystems are hampered by a striking scarcity of data on basic processes such as primary production (e.g., Bouillon et al. 2008b), water-atmosphere CO₂ fluxes (e.g., Borges et al. 2005), or carbon burial rates (Duarte et al. 2005). The collection of baseline data from a range of tropical coastal ecosystems thus remains important as a complement to state-of-the-art analytical techniques to trace and quantify carbon exchange (see Section 12.4 in Chapter 12).

One area in which carbon pathways are yet to be used but should prove effective is as indicators of ecosystem health. The goal of conservation should be about more than species conservation, and should also conserve ecological processes. There is very little guidance in the aquatic conservation literature on what processes might really be important (or measurable). Carbon transfer and utilization is probably central; for example, the source of an animal's food is one of the central organizing themes in ecology (Polis et al. 1997), and a range of tracer tools are available to elucidate carbon pathways (see Chapter 12). As carbon pathways are better understood, it will be possible to detect changes in these pathways due to disturbances such as eutrophication, land-use change in catchments (C4 agriculture), clearing of coastal habitats such as mangroves, and accidental destruction of seagrass through dredging and land claims.

Carbon isotopes are already being used to study ecosystem health in tropical inland waters. In the headwaters of pristine rivers, food webs are supported predominantly by allochthonous input of riparian vegetation (the original river continuum concept by Vannote et al. 1980). In tropical streams, once riparian vegetation is removed, the fundamental pathways are altered, from the original reliance on allochthonous inputs of macrophytes to autochthonous in-stream production, usually of microalgae which rapidly increase production because of greater light availability (Douglas et al. 2005).

Degraded estuarine habitats are beginning to be restored in tropical areas, for example in the Florida Everglades restoration project. Such efforts usually incorporate monitoring of flora and fauna assemblages, but these can be poor indicators of ecological processes. The degree to which restored habitat mimics ecological processes in natural habitat is best measured directly. Again, carbon pathways are an obvious candidate, since they are relatively easily measured using chemical tracers and can be predicted from models based on data from other, less perturbed systems (Twilley et al. 1999).

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