CHAPTER 11

Respiration in coastal benthic communities

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Outline

This chapter reviews coastal benthic communities with the aim of deriving a global estimate for respiration in these ecosystems. Reefs, mangroves, salt marshes, macroalgae, sea grasses, and unvegetated sediments dominate respiration in the coastal ocean. Estimates of coastal benthic respiration are not well constrained but converge on about 620 Tmol C a⁻¹. In coastal benthic ecosystems autotrophs and multicellular heterotrophs contribute significantly, and in some systems even dominate respiration unlike most other oceanic ecosystems in which bacteria dominate respiration.

11.1 Introduction

The coastal zone is characterized by the presence of an active benthic compartment in close contact and interaction with the pelagic one (Soetaert et al. 2000). Benthic coastal communities are highly diverse and include systems in which biological entities are a structuring factor (e.g. coral reefs, mangroves, sea grass beds) as well as those in which physical features and processes determine the landscape (e.g. rocky shores, rippled sandy sediments). Benthic communities differ greatly in structure and their role in ecosystem metabolism depending on whether or not they extend within or below the euphotic zone. Benthic communities receiving sufficient irradiance as to support photosynthesis typically comprise photoautotrophs. These include microalgae, which form highly productive communities on the sediment surface (Cahoon 1999), and macrophytes, including macroalgae and angiosperms (Hemminga and Duarte 2000), which form extensive, highly productive beds and meadows. Similarly, a number of invertebrates (e.g. corals and giant clams), particularly those in tropical waters, contain photosynthetic symbionts (zooxanthellae), which confer them a significant photosynthetic capacity (Kühl et al. 1995). In addition, all structuring macroorganisms present in the illuminated benthic layer support epiphytic microalgae, which add substantially to the primary production of these ecosystems. In contrast, the benthic communities in the aphotic zone rely on organic matter produced elsewhere or by chemoautotrophs to support their metabolic demands.

Benthic communities often dominate ecosystem processes and metabolism, particularly in shallow coastal waters, such as reef lagoons, and are important sites for carbon cycling and bacterial activity, and are all potentially important contributors to ecosystem respiration. Whereas the metabolic balance of the coastal ocean has been subject of much debate (Smith and Hollibaugh 1993; Heip et al. 1995; Duarte and Agusti 1998; Gattuso et al. 1998), there is, at present, no comprehensive evaluation of the respiration rate of benthic coastal ecosystems, so that their...
Table 11.1 Global and specific respiration rate per benthic ecosystem

<table>
<thead>
<tr>
<th>Benthic ecosystem</th>
<th>Surface area (10^6 km^2)</th>
<th>Respiration (mmol C m^-2 d^-1)</th>
<th>Global (Tmol C a^-1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coral Reefs^a</td>
<td>0.6</td>
<td>359</td>
<td>79</td>
</tr>
<tr>
<td>Mangroves^b</td>
<td>0.2</td>
<td>426</td>
<td>28</td>
</tr>
<tr>
<td>Salt</td>
<td>0.4</td>
<td>459</td>
<td>67</td>
</tr>
<tr>
<td>Marshes^b</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sea Grasses^a</td>
<td>0.6</td>
<td>158</td>
<td>34</td>
</tr>
<tr>
<td>Macroalgae^b</td>
<td>1.4</td>
<td>483</td>
<td>247</td>
</tr>
<tr>
<td>Sediments (sublittoral)^a</td>
<td>24</td>
<td>—</td>
<td>166</td>
</tr>
<tr>
<td>Sum</td>
<td></td>
<td></td>
<td>621</td>
</tr>
</tbody>
</table>

^a This study, ^bGattuso et al. (1998). ^c Benthic respiration (R, mmol m^-2 d^-1) in marine sediments is assumed to depend on water depth (metres) as R = 32.1 e^-0.007z.

The objective of this chapter is to derive a global estimate for respiration in coastal benthic communities. We will first introduce the methodological approaches used to derive respiration rates in coastal ecosystems before discussing the rates measured in individual coastal benthic communities. The approach to derive a global system-specific respiration estimate differs per habitat because of differences in available data, research traditions, and inherent differences in ecosystem functioning. The respiration rates from the individual components of coastal ecosystems will then be combined to derive a global estimate by bottom-up scaling procedures (Table 11.1). The resulting estimate will be compared with alternative estimates, based on primary producer budgets (Duarte and Cebrian 1996) and coastal ocean carbon budgets (e.g. Smith and Hollibaugh 1993; Wollast 1998). Units of mmol C m^-2 and per day are used throughout this chapter though some of the data are better expressed per hour (incubation based estimates) or per year (mass balance based estimates) or have been converted from oxygen units using a respiratory quotient (RQ) of 1. Global respiration estimates are given in Tmol C a^-1 (1 Teramol = 10^{12} mol).

11.2 Approaches and methods

Respiration rates can be defined on the basis of (i) the consumption of organic matter, (ii) the use of oxidants, or (iii) the production of inorganic carbon. Quantification of respiration through consumption of organic matter is usually not feasible because changes in stocks are very small (during incubations) compared to natural variability and measurement precision. Moreover, any decrease in organic matter is the result of gross consumption and subsequent resynthesis by secondary producers.

The most straightforward method to measure respiration is the oxygen consumption method. It is a simple method because oxygen is readily measured using Winkler titration, colorimetry, and electrodes or opt(r)odes. Moreover, the solubility of oxygen in water is rather limited and even low rates of consumption result in detectable changes of the stock. However, oxygen consumption cannot be directly equated with aerobic respiration, because oxygen consumption also results from nitrification and reoxidation of reduced mineralization products (see below). In many coastal environments respiratory activities are so high that oxygen demand exceeds the ambient stock and supply rate of oxygen, and alternative oxidants are used through anoxic metabolic pathways. This is particularly prevalent within sediments, where the limited diffusion rates further constrain the capacity to resupply oxygen from the overlying waters (Soetaert et al. 1996, 2000; Glud et al. 2003). In coastal sediments, the major alternative electron acceptors are nitrate, nitrite, manganese oxides, iron oxides, and sulfate. These alternative oxidants are utilized not simultaneously but sequentially (Table 11.2), though there is often considerable overlap between the various respiration pathways. Coastal sediments often exhibit a vertical redox zonation of oxidant depletion in the order oxygen > nitrate > manganese oxide > ferric oxides > sulfate (Thamdrup and Canfield 2000 and see King, Chapter 2).

The electron acceptors are not only consumed in organic matter oxidation, but also in the reoxidation of the reduced components produced during anaerobic mineralization. These reduced components include ferrous iron, sulfide, methane, reduced
Table 11.2 Respiration pathways in coastal benthic communities

<table>
<thead>
<tr>
<th>Pathway</th>
<th>Reaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aerobic respiration</td>
<td>$[\text{CH}_2\text{O}]^* + \text{O}_2 \rightarrow \text{CO}_2 + \text{H}_2\text{O}$</td>
</tr>
<tr>
<td>Denitrification</td>
<td>$5[\text{CH}_2\text{O}] + 4\text{NO}_3^- \rightarrow 4\text{HCO}_3^- + 2\text{N}_2 + \text{CO}_2 + 3\text{H}_2\text{O}$</td>
</tr>
<tr>
<td>Manganese reduction</td>
<td>$[\text{CH}_2\text{O}] + 2\text{MnO}_2 + \text{H}_2\text{O} \rightarrow \text{HCO}_3^- + 2\text{Mn}^{2+} + 3\text{OH}^-$</td>
</tr>
<tr>
<td>Iron reduction</td>
<td>$[\text{CH}_2\text{O}] + 4\text{Fe(OH)}_3 \rightarrow \text{HCO}_3^- + 4\text{Fe}^{2+} + 7\text{OH}^- + \text{3H}_2\text{O}$</td>
</tr>
<tr>
<td>Sulfate reduction</td>
<td>$2[\text{CH}_2\text{O}] + \text{SO}_4^{2-} \rightarrow 2\text{HCO}_3^- + \text{H}_2\text{S}$</td>
</tr>
</tbody>
</table>

*Note: $[\text{CH}_2\text{O}]$ is used as a notation for organic material.

manganese, and ammonia. Each of these can be oxidized with an electron acceptor higher in the redox sequence and this occurs chemically as well as mediated by microbial activity (chemolithotrophy). Chemolithotrophs thus play a key role in elemental cycles and are essential to fully utilize the energy in organic matter. The widespread distribution of these chemolithotrophs adds considerable complexity to the system and complicates the relation between respiration and electron acceptor use (Jørgensen 2000). For instance, in deep-sea sediments, oxygen consumption is due to aerobic respiration, while the majority of oxygen use in coastal sediments derives from the reoxidation of sulfide, iron, and ammonium and other reduced components (Soetaert et al. 1996; Jørgensen 2000; Thamdrup and Canfield 2000). Thus, although oxygen consumption cannot be equated directly with aerobic respiration, it does provide a reliable estimate of total respiration because of the almost complete reoxidation of anaerobic respiration products. However, during incubations the production of reduced species may be decoupled from measured oxygen production. Despite this potential bias, estimates of respiration derived from rates of oxygen consumption encompass both aerobic and anaerobic pathways. The uncertainty related to reoxidation processes could be avoided if the production of dissolved inorganic carbon (\(\Sigma\text{CO}_2 \equiv \text{CO}_2 + \text{HCO}_3^- + \text{CO}_3^{2-}\)) is measured, because inorganic carbon is the final product of all respiration pathways (Table 11.2).

However, ambient concentrations of dissolved inorganic carbon are usually high ($\approx 2$ mM; that is, about 10 times that of dissolved oxygen), relative to the changes in dissolved inorganic carbon from respiration, so that highly accurate measurements of dissolved inorganic carbon are required to resolve the rates. Moreover, processes other than respiration (e.g. precipitation and dissolution of calcium carbonate, sulfate reduction, carbon dioxide assimilation by chemolithotrophs, and nitrification through its effect on pH) induce changes in dissolved inorganic carbon concentrations. The most appropriate method to quantify respiration consequently depends on the community and ecosystem.

The use of oxygen (and other oxidants) and production of dissolved inorganic carbon are related via the respiration ratio or RQ (Williams and del Giorgio, Chapter 1). For pure sucrose (CH\(_2\)O as in Table 11.2) or the carbohydrate end-member of marine organic matter (C\(_6\)H\(_{10}\)O\(_5\); Hedges et al. 2002) there is a 1:1 molar relationship between oxygen and dissolved inorganic carbon. However, respiration quotients for marine plankton are sometimes higher than 1 because additional oxygen is required for oxidation of hydrogen-rich, nitrogen-, and sulfur-containing material. For instance, use of model Redfield organic matter C\(_{106}\)H\(_{266}\)O\(_{106}\)N\(_{16}\)P\(_1\) and average marine plankton C\(_{106}\)H\(_{177}\)O\(_{37}\)N\(_{17}\)S\(_{0.4}\)P\(_1\) yield respiration coefficients (for complete oxidation) of 1.3 and 1.45, respectively (Hedges et al. 2002). The application of conventional Redfield C:N:P (106:16:1) ratios in coastal benthic ecosystems is not always justified, because riverine organic matter (119:8.9:1; Meybeck 1982) and marine benthic plants (550:30:1; Atkinson and Smith 1983) have stoichiometry ratios significantly differing from that of plankton.

Respiration measurements, whether based on oxygen consumption or inorganic carbon generation, can be based on direct (i.e. rate measurements during incubations) or indirect methods (i.e. chemical gradients combined with transport or mass-balance consideration) and hybrids or combined approaches. The most direct, integrative approach is based on mass-balance budgets for oxygen, carbon dioxide, and nutrients. Nutrient regeneration is linked to respiration and mineralization via Redfield.
stoichiometry of organic matter (see above), and increases in nutrient concentrations can thus be used to estimate net respiration. However, this approach may fail in systems with nutrient-poor organic matter since heterotrophic bacteria may assimilate inorganic nutrients there to gain enough nutrients for growth (Zehr and Ward 2002), and because many coastal systems are open to allochthonous nutrient inputs (e.g. riverine or atmospheric inputs), so that the use of nutrient budgets to infer respiration rates becomes very uncertain. Moreover, respiration rates for marine macrophytes based on Redfield stoichiometry will likely be too low because of low nutrient to carbon ratios of marine benthic plants (Atkinson and Smith 1983). Mass budgets usually attempt to balance the oxygen, carbon dioxide, or nutrient content of inflowing and outflowing water with that of gas exchange across the air–water interface, or they are based on concentration changes in chambers enclosing an area of sediment. The former method is also sometimes referred to as the upstream–downstream method (as it has been developed for unidirectional flowing waters) and it has been applied to riverine, estuarine, reef, and other coastal systems (e.g. Odum and Hoskins 1958). The second, flux-chamber method, is the methodology used most frequently to study non-vegetated, non-reef sediments.

Most respiration measurements are carried out in the dark to exclude oxygen production and carbon dioxide consumption by photosynthesis. However, respiration rates in the light may be higher than those in the dark, both at the level of individual organisms (physiological) as well as the entire community (heterotrophs consuming substrates produced in the light). Light enhanced respiration is widely recognized (see Raven and Beardmore, Chapter 3) and has been reported for benthic microalgal (Epping and Jorgensen 1996) and coral reef communities (Kühl et al. 1995; Langdon et al. 2003). The significance of this for coastal benthic respiration rates is yet to be evaluated.

11.3 Respiration in coastal benthic ecosystems

In this section we discuss the respiration rates of specific types of benthic systems, and roughly follow the communities described in Gattuso et al. (1998): we have somewhat arbitrarily divided coastal benthic communities (Table 11.1) into those dominated by emergent macrophytes (saltmarshes and mangroves), submerged macrophytes (sea grasses and macroalgae), coral reefs, and unvegetated sediments (though in the photic zone this may be covered by benthic algae).

11.3.1 Coastal sediments

In the context of sediment biogeochemistry and sediment community respiration, coastal sediments can be classified into the following typologies (partly based on Aller 1998): (i) steadily accreting silty and muddy sediment, (ii) highly mobile, silty, and muddy sediments (fluidized bed reactors), (iii) non-accumulating or eroding sediments (bypass zones), and (iv) sandy, permeable sediments. A further subdivision can be made between sediments within and below the euphotic zone, although in most sediment respiration studies irradiation conditions are not reported. The relative importance of these sediment typologies depends on the coastal system.

The majority of studies on sediment community respiration have been conducted on steadily accreting sediments below the euphotic zone (e.g. see compilations in Heip et al. 1995; Aller 1998, Thamdrup and Canfield 2000). This bias toward accreting silty sediments limits our understanding of sediment processes in general, and hampers any upscaling endeavors. Respiration in silty coastal sediments is mainly bacterial and occurs via anaerobic pathways because oxygen resupply by diffusion and/or irrigation of animal tubes cannot compensate for oxygen consumption through respiration and reoxidation of reduced products. The contribution of meiofauna to total sediment respiration is rather small (less than a few percent), but macrofauna typically contributes 10–30% of total respiration (Herman et al. 1999). The contribution of fauna to total respiration can be partitioned into direct contributions due to faunal respiration and indirect contributions due to faunal stimulated bacterial activities (Aller and Aller 1998; Glud et al. 2003), but the available data are too limited to allow quantification at the global scale.
Mobile muds are most prominent in deltaic sediments from major rivers such as the Amazon, Orinoco, and Fly rivers (Aller 1998), but do occur in other high-energy coastal systems, provided there is a supply of fine materials (e.g., fluidized muds in the high turbidity zones of tidal estuaries, Abril et al. 2000). These mobile beds are thought to function as suboxic, fluidized bed reactors: due to repetitive cycles of erosion and deposition there is an efficient incorporation of fresh organic matter and oxidants from the overlying water column, a steady removal of inhibitory metabolites, and a repetitive recycling among dissolved and particulate phases and among aerobic and anaerobic pathways, which together promote efficient degradation and respiration of organic materials (Aller 1998). These mobile muds are nevertheless the prime sites for oceanic carbon burial because they account for about 40–50% of all marine organic carbon burial at present (Hedges and Keil 1995). Bacteria dominate respiration in these mobile muds because the biomass of macro and meiofauna is limited (relative to accreting muddy sediments), due to high levels of physical stress that the animals encounter in these sites.

Sandy sediments, which cover about 70% of global continental shelves and most beaches, have conventionally been considered as biogeochemical deserts harboring little life. This misconception is based on the idea that significant reactions, fluxes, and respiration rates require large standing stocks

![Figure 11.1](image-url)  
**Figure 11.1** Respiration versus measures for sediment grain size. (a) Respiration (mmol m$^{-2}$ d$^{-1}$) versus median grain size in intertidal flat sediments (Middelburg et al. 1996). (b) Respiration (mol m$^{-2}$ a$^{-1}$) versus percentage silt (i.e., fraction <63 μm) in North Sea sediments (Dauwe et al. 2001).
of organic matter (Boudreau et al. 2001). Concentrations of organic matter (when expressed on weight basis) are low because of the well-established negative correlation between organic carbon content and (median) grain size (Middelburg et al. 1996). However, when organic matter concentrations are expressed on an area or volume basis (i.e., quantity per m² or m³), then organic carbon concentrations in sandy and silty/muddy sediments are much more similar (Middelburg et al. 1996). Moreover, the overall degradability of organic carbon in sandy sediments appears to be somewhat higher than that in muddy/silty sediments (Boudreau et al. 2001), mainly because accumulating aged, more refractory organic material does not dilute organic carbon in sands. As a consequence, respiration rates in organic-poor sandy sediments may be substantial. Figure 11.1 shows that there are no systematic relationships between sediment community respiration and grain size either expressed as median grain size (Fig. 11.1(a)) or as fraction of silt (less than 63 µm) (Fig. 11.1(b)).

Non-accumulating or bypass zones occur in most coastal environments when physical conditions are not favorable for settling or when deposited material is rapidly resuspended due to current and/or wave activity. Non-accumulating sediments may nevertheless have significant respiration activity. Animals, suspension and interface feeders in particular, may even use eroding sediments as a substrate to settle and live while exploiting the particulate organic carbon in the water column as their main food resource. While high current velocities or turbulence levels may not be favorable for organisms relying on passive settling of organic matter, it may be advantageous for suspension feeders, though too high current velocities may again lower filtration efficiency of suspension feeders (Herman et al. 1999). Sediments that show no accumulation or even erosion on the longer term, may nevertheless receive deposition during certain periods; for example, during spring bloom or during slack tides. Organisms can exploit this temporarily deposited material and these sediments can thus support an active community.

Although these sediment typologies differ in community structure and biogeochemical functioning, it appears that sediment oxygen uptake largely depends on water depth. Figure 11.2 shows a compilation of sediment oxygen uptake data for marine sediments shallower than 300 m (Andersson, unpublished results). There is a

![Figure 11.2](image-url)
highly significant decrease with depth, consistent with observations in the open ocean (Jørgensen 1983, see also Aristegui et al., Chapter 10) and estuaries (Heip et al. 1995 and see Hopkinson and Smith, Chapter 8). These data can be fitted with an exponential equation for sediment respiration versus depth:

\[ \text{Respiration} = 32e^{-0.0077z} \]

where \( z \) is water depth (m). Combining this equation with the surface area of the ocean shallower than 200 m (23.9 \( \times \) 10^6 km^2) results in a total sedimentary respiration of 166 Tmol C a\(^{-1}\) (See Table 11.1).

### 11.3.2 Coral reefs

Estimates of the global surface cover of coral reefs vary quite considerably (reviewed by Spalding and Grenfell 1997) due to the various definitions of coral reefs that have been used. The consensus opinion is that coral reefs cover approximately 0.6 \( \times \) 10^6 km^2. Data on community metabolism are numerous in coral reefs relative to other coastal ecosystems. The reason is that reefs are often subject to a unidirectional current from the ocean to the back reef area. Consequently, it is relatively easy to estimate ecosystem metabolism in transects, for example, 1 m wide and several hundreds of meters long, using Lagrangian techniques that measure changes in the water chemistry as the water mass crosses the reef system (Gattuso et al. 1999). Some measurements have also been carried out on smaller areas during standing water periods. Another approach, based on ecological stoichiometry and mass balance of carbon and phosphorus (Smith 1991) has provided estimates of community metabolism of entire reef systems, mostly atolls. One limitation of these techniques is that they do not adequately include the portion of the reef that faces the open water (outer reef slope) that is one of the most active zones. Finally, although reef mesocosms do not qualify as exact proxies of coral reefs, they are increasingly being used to address the metabolic response of corals to environmental forcing (e.g. Leclercq et al. 1999; Langdon et al. 2003).

Although the term “coral reef” is often used generically, this term encompasses various categories, defined according to the community structure or the geomorphology, and these different types of systems exhibit distinct metabolic performances. It is therefore useful to examine each of these categories separately. We use in the present contribution the categories defined by Kinsey (1985): “complete” reef systems, outer reef slope, high activity areas of near total cover by hard substratum (excluding pavement), algal pavement zone, reef-flat coral/algal zones, shallow lagoon environments, algal turfs and algal/sand flats, algal-dominated flats, “sand” areas, and uncertain designation.

The rate of community respiration spans more than one order of magnitude (1.3–910 mol C m\(^{-2}\)a\(^{-1}\)) and exhibits a rather high variability even within a single category (Fig. 11.3). It is lowest in sandy areas (39 \( \pm \) 23 mol C m\(^{-2}\)a\(^{-1}\)) and, as expected, highest in the high activity areas (413 \( \pm \) 187 mol C m\(^{-2}\)a\(^{-1}\)). Complete reef systems generally comprise lagoons with large areas covered by sediments. For instance, the southwest of New Caledonia reef complex comprises 95% sediment and 5% of hard-bottoms, covered by coral substratum (Clavier, personal communication). It is therefore not surprising that community respiration of complete reef systems (131 \( \pm \) 46 mol C m\(^{-2}\)a\(^{-1}\); \( N = 7 \)) is much closer to the value of sandy areas than to the value of high activities areas.

Like in other ecosystems, the rates of reef community respiration have exclusively been measured during the night time and the 24 h values are estimated assuming that respiration is similar in the light and dark. However, it is well established that respiration in the light often exceeds dark respiration in numerous aquatic autotrophs. For example, Kühl et al. (1995) estimated that respiration of one coral species investigated in laboratory conditions is more than 6 times higher at a saturating irradiance than in the dark. Despite the strong evidence that the assumption upon which community respiration is based is probably flawed, there is presently no direct estimate of the changes in respiration in any natural reef system. However, a recent breakthrough has been made by Langdon et al. (2003) in the Biosphere 2 coral reef mesocosm. They measured gross respiration (light plus dark) with a new 14C isotope dilution method and discovered that light
respiration is about twice the dark rate, with the result that the conventional daily respiration rate is underestimated by 40%. Biosphere 2 cannot be considered to represent an “average” reef because it mimics a high latitude, low energy, and algal-dominated system. The results of Langdon et al. cannot therefore be extended to all natural reefs but their data do provide, for the first time, a rough estimate of what the difference between light and dark respiration could be in a reef system.

One of the goals of the present book is to provide global estimates of respiration of aquatic organisms and ecosystems. However, estimating the global rate of respiration in coral reefs is extremely difficult for several reasons. First, the fact that community respiration during the day exceeds respiration at night now seems unquestionable. Second, there are only data for seven “complete” reef systems (that do not include the outer reef slope), which makes upsampling to the global scale very uncertain. Third, although there are many estimates for subsections of coral reefs (the categories described above), it is not yet possible to exploit these data to derive an estimate for an “average” reef. Considering both the overall objectives of this book and these three limitations, and without even attempting to provide an error estimate, we suggest the best current estimate of the global respiration of coral reefs at 79 Tmol C a⁻¹ (i.e. 131 mol m⁻² a⁻¹ × 6 × 10¹¹ m²).

11.3.3 Emergent macrophytes: mangroves and salt marshes

Mangroves and salt marshes are distinct ecosystems in which primary producers are structuring factors that emerge above the water. Mangroves are intertidal forests that grow above mean sea level. They cover about 0.18 × 10⁶ km² along sheltered tropical and subtropical shores (31°N to 39°S). Salt marshes are rooted-macrophyte dominated ecosystems in temperate zones that occur within the intertidal zone and are characterized by a zonation of plant species depending on elevation. They cover an area of 0.4 × 10⁶ km², that is, about twice that of mangroves (Gattuso et al. 1998). Although mangroves and salt marsh plants are the dominant producers in their respective ecosystems, there are also significant contributions from other producers (macroalgae, epiphytes, phytoplankton, and benthic microalgae) and from adjacent ecosystems (Middelburg et al. 1997). Moreover, a significant part of tree and salt marsh plant production is allocated to below-ground organs and usually not included in community metabolism studies.

Respiration measurements in mangroves and salt marsh systems are difficult to make and even more complex to be analyzed. First, these trees and some macrophytes are so large that compartment and chamber type of measurements for respiration and production are complicated. Moreover, production
is normally reported as net primary production based on biomass accumulation derived from allometric approaches. Second, a significant proportion of the respiration occurs in the parts of the tree and plant that are above the water. Third, measurements of respiration in the sediment compartment are complicated by the alternation between emergent and submerged conditions. This complicates not only the measurements, but also respiration rates and respiration pathways may vary with tidal stage. Fourth, sediment respiration in mangrove and salt marsh systems includes respiration from the tree/plant roots and rhizomes as well as that from heterotrophic organisms living on plant litter and allochthonous carbon inputs. Core incubation techniques (the usual technique for assessment of respiration rates in coastal sediments) can not be used because root respiration is excluded, while respiration fueled by root exudates is likely overestimated due to damage to (hair) roots during sampling (Gribsholt and Kristensen 2002). There is definitely a need for novel approaches to quantify respiration in situ in mangrove and salt marshes and to partition this respiration between plants and heterotrophs. Perhaps it is possible to apply Keeling-plot type analysis (Flanagan and Ehleringer 1998) to exploit the difference in carbon isotope composition between salt marsh plants and mangroves on the one hand and sedimentary organic matter on the other. In coastal systems with high rates of respiration or large contributions of salt marshes and/or mangroves to coastal (water column) respiration, it may be possible to obtain integrative measures from oxygen and carbon dioxide mass balances (Cai et al. 1999).

Given the large uncertainties and the limited amount of new data available since the compilation of Gattuso et al. (1998), we have adopted their values in Table 11.1: 426 and 439 mmol m$^{-2}$ d$^{-1}$ and 28 and 67 Tmol a$^{-1}$ for mangroves and salt marshes, respectively.

### 11.3.4 Submerged macrophytes: sea grasses and macroalgae

Sea grasses and macroalgae are important components of coastal ecosystems. Sea grasses encompass a group of about 50-60 species, which grow on the illuminated (>11% of surface irradiance) sandy and muddy shores of all continents except Antarctica (Hemminga and Duarte 2000; Duarte et al. 2002). Sea grass communities form highly productive meadows, which cover an estimated area of about 0.6 x 10$^6$ km$^2$ (Chapra-Roubaud and Sournia 1990) developing a global biomass of about 9.2 Tmol C (460 g dry wt m$^{-2}$ on average, Duarte and Chiscano 1999), which results in a net primary production of about 20 Tmol C a$^{-1}$ (92 mmol C m$^{-2}$ d$^{-1}$ on average, Duarte and Chiscano 1999). Macroalgae comprise about 8000 species (Dring 1992), which are the dominant benthic primary producers in rocky shores and also form dense communities in sandy sediments, particularly in subtropical waters, where species of green macroalgae are often important primary producers (Loeb and Harrison 1997). Macroalgae extend over an estimated area of 1.4 x 10$^6$ km$^2$ (Gattuso et al. 1998), contributing a net primary production of 212 Tmol C a$^{-1}$ (Chapra-Roubaud and Sournia 1990). Macroalgae develop the lushest plant communities in the sea, which are particularly well represented by the kelp forests growing on the rocky shores of cold, nutrient-rich waters (Loeb and Harrison 1997). Although these communities may develop very high biomasses, the average biomass of macroalgal communities (40 g dry weight m$^{-2}$, in Cebrían and Duarte 1994) is much lower than that of sea grass meadows, which develop an important below-ground biomass. The global macroalgal biomass is about 1.9 Tmol C. Macroalgae are also important components of coral reef communities, but the contribution of coral reefs to the metabolism of the coastal ocean are discussed in Section 11.3.2 above.

In addition to the important macrophyte biomass in sea grass and macroalgal stands, macrophyte-dominated ecosystems support an important biomass of epiphytic microalgae, which are believed to contribute about 20–50% of the total production of macrophyte-dominated benthic systems (Hid et al. 1995; Alongi 1998; Hemminga and Duarte 2000). Macrophyte-dominated marine ecosystems are, therefore, highly productive components of the coastal ocean, and are responsible for an important
share of the organic carbon production available for export (Duarte and Cebrián 1996).

Marine macrophytes respire, on average, about 51–57% of their gross primary production (Duarte and Cebrián 1996). Accordingly, the direct respiration by the macrophytes themselves can be estimated, using the estimates of their net primary production discussed above, as 220 and 19.7 Tmol C a\(^{-1}\) for macroalgae and sea grasses, respectively, yielding a total direct respiration of about 240 Tmol C a\(^{-1}\). Alternatively, the respiration rate of marine macrophytes can be estimated from the specific respiration rate of their tissues, which has been extensively measured in connection to estimates of photosynthetic activity (Enríquez et al. 1995, 1996; Vermaat et al. 1997). The respiration rate of marine macrophytes tends to decline, as that of land plants, with increasing tissue thickness (Enríquez et al. 1995, 1996), and this decline is associated to the decline in growth rate with increasing tissue thickness of autotrophs (Nielsen et al. 1996). The specific respiration rates of the photosynthetic tissues of marine macrophytes averages about 40 mmol C mol C\(^{-1}\) d\(^{-1}\) (Enríquez et al. 1995, 1996; Vermaat et al. 1997; Touchette and Burkholder 2000), and this average can be used to derive an independent estimate of the respiration rate of marine macrophytes from their global photosynthetic biomass as 28 and 65 Tmol C a\(^{-1}\) for macroalgae and sea grasses, respectively, yielding a total respiration of marine macrophytes of about 93 Tmol C a\(^{-1}\). This combined estimate is lower than that derived from the percent respiration of macrophyte gross primary production (240 Tmol C a\(^{-1}\)), probably because it does not account for the respiration contributed by the roots and rhizomes of sea grasses, which is about 15–57% of the total sea grass respiration (Hemminga and Duarte 2000), and because the specific respiration of tropical and subtropical macrophytes is likely to be above the mean value used. The respiration by marine macrophytes has been shown to be highly dependent on temperature (Touchette and Burkholder 2000), with a \(Q_{10}\) of about 2.5 (e.g. Marsh et al. 1986), so that tropical and subtropical communities are expected to show higher respiration rates than temperate and polar macrophyte communities of comparable biomass. This also suggests that global warming is likely to increase significantly the contribution of macrophyte respiration to the respiration of coastal ecosystems.

The metabolism of sea grass communities, including the plants and heterotrophic organisms, was studied since the early introduction of metabolic studies in aquatic ecology by Odum and Hoskins (1958). Since then, the respiration rate of a number of sea grass ecosystems has been studied in a number of sea grass meadows (Table 11.3), largely through the use of benthic chambers, although most of the studies refer to single estimates and annual estimates are still few. The estimates so far available yield a mean respiration rate of 159 ± 19 mmol C m\(^{-2}\) d\(^{-1}\), ranging from 14.1 to 596 mmol C m\(^{-2}\) d\(^{-1}\), with a log-normal distribution (Fig. 11.4). The mean respiration derived corresponds, when scaled to the surface area covered by sea grasses, to a global respiration of 34.6 Tmol C a\(^{-1}\), so that the estimated direct contribution of sea grasses that we derived in the previous paragraph (19.7 Tmol C a\(^{-1}\)) would represent about 57% of the community respiration. Indeed, the total respiration of macrophyte-dominated benthic systems is higher than that of the macrophytes alone, because macrophyte-dominated systems are habitats for a rich heterotrophic community (Loepp and Harrison 1997; Hemminga and Duarte 2000; Mann 2000), which also contribute significantly to total system metabolism. This must be particularly important for sea grass marshes, where, in addition to the rich heterotrophic epiphytic community they support, the underlying sediments are an active site for bacterial decomposition of organic matter. Bacterial metabolism is enhanced in sea grass sediments due to the increased inputs of organic matter under the plant canopies, and the direct stimulation of bacterial metabolism by release of organic matter together with oxygen from sea grass roots (Hemminga and Duarte 2000).

In contrast to sea grasses, the total respiration of macroalgae-dominated communities has been examined in only a limited number of studies (Table 11.4). A few additional estimates can be derived from carbon flow analyses (e.g. Newell and Field 1983). The available estimates indicate an average respiration rate of macroalgal beds
Table 11.3 Estimates of respiration rate in sea grass-dominated coastal benthic communities

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>$R$ (mmol C m$^{-2}$ d$^{-1}$)</th>
<th>Author</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mixed sea grass meadow</td>
<td>The Philippines</td>
<td>213</td>
<td>Barrón (unpublished data)</td>
</tr>
<tr>
<td>Enhalus acoroides</td>
<td>The Philippines</td>
<td>45</td>
<td>Barrón (unpublished data)</td>
</tr>
<tr>
<td>Cymodocea nodosa</td>
<td>Spanish Mediterranean</td>
<td>48</td>
<td>Barrón (unpublished data)</td>
</tr>
<tr>
<td>Posidonia oceanica</td>
<td>Spanish Mediterranean</td>
<td>68</td>
<td>Barrón (unpublished data)</td>
</tr>
<tr>
<td>Zostera noltii</td>
<td>South Portugal</td>
<td>182</td>
<td>Barrón (unpublished data)</td>
</tr>
<tr>
<td>Cymodocea nodosa</td>
<td>South Portugal</td>
<td>105</td>
<td>Barrón (unpublished data)</td>
</tr>
<tr>
<td>Zostera marina</td>
<td>Norway</td>
<td>65</td>
<td>Duarte et al. (2000)</td>
</tr>
<tr>
<td>Mixed community</td>
<td>Indonesia</td>
<td>238</td>
<td>Erftemeijer et al. (1993)</td>
</tr>
<tr>
<td>Mixed community</td>
<td>Sri Lanka</td>
<td>72</td>
<td>Johnson and Johnstone (1995)</td>
</tr>
<tr>
<td>Halodule uninervis</td>
<td>Indonesia</td>
<td>250</td>
<td>Lindboom and Sandee (1989)</td>
</tr>
<tr>
<td>Thalassia hemprichii</td>
<td>Indonesia</td>
<td>267</td>
<td>Lindboom and Sandee (1989)</td>
</tr>
<tr>
<td>Thalassia/Enhalus</td>
<td>Indonesia</td>
<td>250</td>
<td>Lindboom and Sandee (1989)</td>
</tr>
<tr>
<td>Zostera marina</td>
<td>Netherlands</td>
<td>94</td>
<td>Lindeboom and deBree (1982)</td>
</tr>
<tr>
<td>Zostera marina</td>
<td>Northeast USA</td>
<td>225</td>
<td>Murray and Wetzel (1987)</td>
</tr>
<tr>
<td>Zostera marina</td>
<td>Northeast USA</td>
<td>191</td>
<td>Nixon and Oviatt (1972)</td>
</tr>
<tr>
<td>Thalassia testudinum</td>
<td>Texas</td>
<td>531</td>
<td>Odum and Hoskins (1958)</td>
</tr>
<tr>
<td>Mixed</td>
<td>Texas</td>
<td>56</td>
<td>Odum and Hoskins (1958)</td>
</tr>
<tr>
<td>Mixed</td>
<td>Texas</td>
<td>447</td>
<td>Odum and Wilson (1962)</td>
</tr>
<tr>
<td>Thalassia testudinum</td>
<td>Texas</td>
<td>322</td>
<td>Odum (1963)</td>
</tr>
<tr>
<td>Thalassia testudinum</td>
<td>Puerto Rico</td>
<td>488</td>
<td>Odum et al. (1959)</td>
</tr>
<tr>
<td>Halodule wrightii</td>
<td>Mexico</td>
<td>597</td>
<td>Reyes and Merino (1991)</td>
</tr>
<tr>
<td>Thalassia + Halodule</td>
<td>Mexico</td>
<td>541</td>
<td>Reyes and Merino (1991)</td>
</tr>
<tr>
<td>Thalassia testudinum</td>
<td>Mexico</td>
<td>478</td>
<td>Reyes and Merino (1991)</td>
</tr>
<tr>
<td>Thalassia testudinum</td>
<td>Texas</td>
<td>131</td>
<td>Ziegler and Benner (1998)</td>
</tr>
</tbody>
</table>

Note: Overall mean = 159, median = 94, standard error = 19, $N = 64$.

Figure 11.4 Frequency distribution of respiration rate in macrophyte-dominated coastal benthic communities. Note logarithmic x-axis.
Table 11.4  Estimates of respiration rate in macroalgae-dominated coastal benthic communities

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>$R$ (mmol C m$^{-2}$ d$^{-1}$)</th>
<th>Author</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mixed community</td>
<td>Caribbean</td>
<td>1271</td>
<td>Adey and Steneck (1985)</td>
</tr>
<tr>
<td>Caulerpa spp.</td>
<td>The Philippines</td>
<td>103</td>
<td>Barrón (unpublished data)</td>
</tr>
<tr>
<td>Halimeda spp.</td>
<td>The Philippines</td>
<td>111</td>
<td>Barrón (unpublished data)</td>
</tr>
<tr>
<td>Brown algae</td>
<td>Australia</td>
<td>200</td>
<td>Cheshire et al. (1996)</td>
</tr>
<tr>
<td>Mixed community</td>
<td>Caribbean</td>
<td>975</td>
<td>Connor and Adey (1977)</td>
</tr>
<tr>
<td>Mixed community</td>
<td>French Polynesia</td>
<td>241</td>
<td>Gattuso et al. (1997)</td>
</tr>
<tr>
<td>Mixed community</td>
<td>Caribbean</td>
<td>833</td>
<td>Griffith et al. (1987)</td>
</tr>
<tr>
<td>Mixed community</td>
<td>Caribbean</td>
<td>16</td>
<td>Hawkins and Lewis (1982)</td>
</tr>
<tr>
<td>Mixed community</td>
<td>Hawaii</td>
<td>288</td>
<td>Kinsey (1979)</td>
</tr>
<tr>
<td>Kelp community</td>
<td>South Africa</td>
<td>341</td>
<td>Newell and Field (1983)</td>
</tr>
<tr>
<td>Fucus-dominated</td>
<td>Norway</td>
<td>96</td>
<td>Pedersen (1987)</td>
</tr>
<tr>
<td>Mixed community</td>
<td>Mexico</td>
<td>384</td>
<td>Reyes and Merino (1991)</td>
</tr>
<tr>
<td>Mixed community</td>
<td>Caribbean</td>
<td>255</td>
<td>Rogers and Salesky (1981)</td>
</tr>
<tr>
<td>Mixed community</td>
<td>Pacific</td>
<td>501</td>
<td>Smith and Marsh (1973)</td>
</tr>
<tr>
<td>Mixed community</td>
<td>Pacific</td>
<td>501</td>
<td>Smith (1973)</td>
</tr>
<tr>
<td>Mixed community</td>
<td>Caribbean</td>
<td>58</td>
<td>Vooren (1981)</td>
</tr>
</tbody>
</table>

Note: Overall mean = 483, median = 338, standard error = 29; $N = 21$.

of 483 mmol C m$^{-2}$ d$^{-1}$, with a log–normal distribution (Fig. 11.4). This average respiration rate yields, when upscaled to the global area covered by macroalgae, a global rate of 247 Tmol C a$^{-1}$, which implies that the direct contribution of macroalgae (220 Tmol C a$^{-1}$) accounts for about 90% of community respiration. This high contribution of macroalgae to community respiration might reflect a bias in the available community respiration data, or it is due to an overestimation of macroalgae respiration based on a fixed fraction of gross primary production.

From the calculations presented above, the total respiration of macrophyte-dominated benthic systems can be conservatively estimated at about 281 Tmol C a$^{-1}$, of which about 12% corresponds to sea grass ecosystems and the remaining corresponding to macroalgal beds. The total respiration in macrophyte-dominated benthic systems could well exceed the local primary production, in particular in sea grasses because they receive an important input of sestonic organic matter. Sea grass canopies have been shown to be enriched in particles (Duarte et al. 1999) and be capable of effectively trapping sestonic particles (Agawin and Duarte 2002), which represent an important input of organic matter. For example, for a Posidonia oceanica meadow where these processes were quantified, the input of seston was comparable to the local production of the sea grass and associated epiphytes (Gacia et al. 2002). The majority (70%) of the reports on the metabolism of macrophyte-dominated benthic systems (Tables 11.3 and 11.4) correspond to autotrophic systems in which production is higher than respiration, particularly for macroalgae, for which 95% of the communities studied (Table 11.4) were reported to be autotrophic. Although sea grass-dominated systems can be heterotrophic during certain periods of their seasonal development, all of the systems so far studied have been shown to be autotrophic at an annual basis (Hemminga and Duarte 2000). This is consistent with (i) the significant carbon burial in sea grass meadows (e.g. Mateo et al. 1997; Pedersen et al. 1997; Gacia et al. 2002), which is estimated to average 16% of the net production of the sea grasses (Duarte and Cebrián 1996), and (ii) the important export of sea grass detritus, which averages about 24% of their net primary production (Duarte and Cebrián 1996). Hence, sea grass meadows appear to be autotrophic systems (Gattuso et al. 1998; Hemminga and Duarte 2000) despite often large inputs of organic matter they receive. Similarly,
seaweed-dominated systems have also been shown to export significant amounts of organic matter (Barrón et al. 2003). Although those growing on rocky shores cannot store organic carbon in the sediments, they export substantial amounts of organic matter both as DOC released and detached fragments (Loeb and Harrison 1997; Mann 2000; Barrón et al. 2003), which must fuel respiration elsewhere. The export from macroalgal beds has been estimated to average 43% of their net primary production (Duarte and Cebrián 1996), thereby representing an important loss of materials which cannot be, therefore, respired within the system but that will fuel respiration rates in adjacent ecosystems or compartments (e.g. the pelagic compartment).

11.4 Global rate of respiration in coastal benthic communities

The estimation of the global rate of respiration in coastal benthic communities poses a major challenge because of the diversity of systems in question and the overall sparsity of data on certain components and their geographical distribution. Here we will follow the traditional approach based on upscaling from the rates of the contributing components, but we will in addition constrain the global respiration rate from above, that is, by deriving it from global estimates of organic carbon fixation (and inputs) and from coastal carbon budgets. Each of these approaches has severe limitations and requires further study before confidence limits can be established on the global estimates.

11.4.1 Scaling problems

Upscaling refers to the aggregation of information collected at a small scale to a larger scale. The traditional way of upscaling involves the multiplication of habitat area with habitat respiration activity followed by summation over the habitat involved: that is, the so-called bottom–up procedure (Table 11.1). Areal–up or bottom–up scaling is relatively straightforward provided the rates are truly additive, that is, the entities for upscaling can be considered closed systems and homogeneous, and that there are sufficient data. However, these conditions are very seldom met. First, the diversity of benthic ecosystems in the coastal ocean is very high and it is still unclear how best to partition these habitats into representative elementary units. Each of these ecosystems comprises many biological communities and shows heterogeneity at a variety of spatial and temporal scales. There is a fundamental lack of knowledge on the level of aggregation required to allow effective bottom–up scaling. In this chapter we have adopted a rather coarse resolution of benthic communities: emergent macrophytes (saltmarshes, mangroves), submerged macrophytes (sea grasses, macroalgae), coral reefs and nonvegetated sediments (though in the photic zone the latter may be covered by benthic algae). Second, even at this high level of aggregation there is large uncertainty in the respective surface areas because detailed geo-referenced biological datasets are scarce. Third, pelagic and benthic ecosystems in the coastal zone are intimately coupled and it is therefore difficult to partition benthic systems from their surroundings. There is also significant transfer of organic matter and energy among ecosystems, for example, the external subsidies to sustain metabolic imbalances. This open nature of coastal communities implies that conventional additive scaling procedures introduce uncertainties. Fourth, for some of these benthic habitats there are only a few data available (e.g. macroalgae) and most available datasets are incomplete in terms of temporal and spatial coverage. Fifth, each of these coastal benthic ecosystems shows a range of respiration rates as a consequence of variability in light and nutrient availability, carbon input, water depth, climate, community structure patterns, and other factors. Sixth, human perturbations of natural coastal communities may have affected and are still changing coastal ecosystem functioning, hence likely respiration, over decadal timescales (Rabouille et al. 2001). It is clear that these complications preclude the derivation of an accurate estimate of coastal benthic respiration, yet the data compiled can be used to derive a first-order approximation of the magnitude of respiration in the benthic compartment of the global coastal ocean, which can help assess the
relevance of this compartment in the context of total ocean respiration.

11.4.2 Bottom-up estimate

In the preceding sections we have evaluated and summarized the available data on respiration in the individual benthic communities and have derived ecosystem-specific global respiration rates (Table 11.1). These ecosystem-specific global respiration estimates amount to about 621 Tmol C a$^{-1}$ with coral reefs, submerged macrophytes, emergent macrophytes, and open sediments accounting for 13%, 45%, 15%, and 26%, respectively. Submerged macrophytes, and particularly macroalgae, appear to be the dominant contributors to benthic respiration in the coastal ocean, despite the fact that they cover only about 7% of the surface of the coastal ocean. The large contribution of sediments is due to their large surface area, while the significance of coral reefs, macroalgae, and salt marshes is primarily due to their high area specific rates of respiration. A significant, but unknown, part of mangrove and salt marsh respiration occurs in the air, above the water, and does not contribute to respiration in aquatic ecosystems, the subject of this book.

It appears that autotrophs and multicellular heterotrophs are responsible for a major part of the respiration in coastal benthic systems. Macrofauna in coastal sediments accounts for about 10–30% of total sediment community respiration. Autotrophs and multicellular organisms dominate total reef community respiration, in particular in hard-bottom communities. The high above- and below-ground biomasses of sea grasses, mangroves, and salt marsh plants and high production of macroalgae imply major contributions of these autotrophs to total community respiration. This would suggest that in coastal benthic ecosystems, microbes contribute relatively little to total community respiration and that coastal benthic ecosystems diverge from the majority of other aquatic ecosystems where microbes are the most important group in terms of their contribution to respiration.

Our estimate of global benthic respiration in the coastal zone (621 Tmol C a$^{-1}$) is larger than that reported by biogeochemists studying sediment oxygen uptake (e.g. 160 Tmol C a$^{-1}$, Jørgensen 1983). Those estimates are usually based on a combination of ocean hypsometry and sediment oxygen demand versus depth relationships, and usually exclude macrophyte-covered sediments and coral reef systems that have high area-specific respiration rates.

Gattuso et al. (1998) provided a synthesis of data on carbon metabolism in coastal aquatic ecosystems. They reported a global coastal ocean respiration of 518 Tmol C a$^{-1}$ based on the sum of global respiration rates of corals (80 Tmol C a$^{-1}$), saltmarshes (67 Tmol C a$^{-1}$), mangroves (28 Tmol C a$^{-1}$), submerged macrophytes (137 Tmol C a$^{-1}$), and shelf systems (206 Tmol C a$^{-1}$). Some of these numbers are very similar to those in Table 11.1 because we have either used their data (for salt marshes and mangrove respiration), or because there is significant overlap in the database used (e.g. coral reefs), but the present estimates—based on a larger dataset—significantly increase the respiration of submerged macrophytes (sea grasses and macroalgae). The estimate of Gattuso et al. (1998) for shelf respiration included the pelagic and benthic compartments. We can use our estimate for unvegetated sediment respiration (166 Tmol C a$^{-1}$) or Jørgensen’s (1983) estimate of 160 Tmol C a$^{-1}$ to derive the pelagic (40–46 Tmol C a$^{-1}$) contribution to the total shelf respiration estimate of 206 Tmol C a$^{-1}$ (Gattuso et al. 1998). The estimate of global coastal respiration from these author’s data (518 Tmol C a$^{-1}$) can then be corrected for pelagic shelf respiration and we obtain 472–478 Tmol C a$^{-1}$ which is still somewhat lower than the estimate we propose here (621 Tmol C a$^{-1}$).

11.4.3 Coastal carbon budget constraints

A number of geochemists have constructed carbon budgets for the entire coastal ocean and have reported a global rate of respiration for the coastal zone that includes the pelagic as well as the benthic. Smith and Hollibaugh (1993) made a cross-system analysis based on 22 coastal and estuarine systems and they derived a global coastal ocean respiration rate of 507 Tmol C a$^{-1}$, with about 30% (150 Tmol C a$^{-1}$) occurring on the bottom. Their estimate did not include coral reefs.
or mangroves. Wollast (1998) reported a global coastal ocean respiration rate of 300 Tmol C a\(^{-1}\) (range 95–548 Tmol C a\(^{-1}\)) based on a small dataset (\(N = 10\)) comprising temperate and boreal shelf systems from the Northern Hemisphere. This author also provided a separate estimate for coastal oceanic sediments of 150 Tmol C a\(^{-1}\) (range 65–333 Tmol C a\(^{-1}\)). Although coastal ocean benthic respiration estimates by Smith and Hollibaugh (1993) and Wollast (1998) are very similar to each other (150 Tmol C a\(^{-1}\)), and similar to the estimate for sediment respiration proposed by Jørgensen (1983), they likely do not include macrophyte-covered systems and coral reefs. Hence, these geochemical studies have significantly underestimated global coastal benthic respiration.

Rabouille et al. (2001) also investigated the carbon budget of the global coastal ocean but partitioned it into a proximal and a distal zone. The proximal zone includes large bays, estuaries, deltas, inland seas, and salt marshes, has a mean water depth of 20 m and a surface area of 1.8 \(\times\) 10\(^6\) km\(^2\). The distal zone includes the open continental shelves down to 200 m depth with a surface area of 27 \(\times\) 10\(^6\) km\(^2\) and a mean depth of 130 m. They reported a total coastal respiration rate of 348 Tmol C a\(^{-1}\), with 56.4 and 291.6 Tmol C a\(^{-1}\) in the proximal and distal coastal zones, respectively. Rabouille et al. (2001) reported benthic respiration rates of 30.4 and 93 Tmol C a\(^{-1}\) for the global proximal and distal zones, respectively. While their benthic respiration estimate for the distal zone is slightly lower than our estimate for sublittoral sediments (166 Tmol C a\(^{-1}\)), and those of Jørgensen (1983; 160 Tmol C a\(^{-1}\)) and Wollast (1998; 150 Tmol C a\(^{-1}\)), there is a large discrepancy for the proximal zone. The Rabouille et al. (2001) estimate (30.4 Tmol C a\(^{-1}\)) is about one order of magnitude smaller than the one fromGattuso et al. (1998; 312 Tmol C a\(^{-1}\)) and our estimate (455 Tmol C a\(^{-1}\)) for the proximal zone: that is the sum of coral, mangrove, salt marsh, sea grass, and macroalgal respiration.

### 11.4.4 Coastal primary production constraints

The carbon budgets constructed by geochemists can be complemented by a community ecology approach that explicitly takes into account differences among communities. In this regard, Duarte and Cebrían (1996) compiled extensive datasets on coastal net primary production and the fate of autotrophic production. They reported a total net primary production of the coastal ocean of 836 Tmol C a\(^{-1}\), with phytoplankton, microphytobenthos, coral reef algae, macroalgae, sea grasses, marsh plants, and mangroves contributing 375, 28, 50, 41, 37, and 92 Tmol C a\(^{-1}\), respectively. If microphytobenthos, coral reef, macroalgae, sea grass, marsh plant, and mangrove production (461 Tmol C a\(^{-1}\)), and riverine organic carbon inputs (34 Tmol C a\(^{-1}\)) are balanced by organic matter burial in sediments (about 13 Tmol C a\(^{-1}\); Hedges and Keil 1995) and respiration of heterotrophs, then coastal benthic respiration should be at least 482 Tmol C a\(^{-1}\). This is a minimum estimate since part of the respiration of autotrophs is not included, and part of the production of coastal plankton is also respired in benthic systems. The latter quantity can be estimated from the difference in sediment respiration rates (166 Tmol C a\(^{-1}\), Table 1) and sediment primary, that is, microphytobenthos, production (28 Tmol C a\(^{-1}\); Duarte and Cebrían 1996): that is, 138 Tmol C a\(^{-1}\). This implies that the total coastal benthic respiration due to heterotrophs should be about 620 Tmol C a\(^{-1}\), identical to that derived from the bottom–up approach (621 Tmol C a\(^{-1}\)). The excellent agreement of the bottom–up and community-production top–down approaches is pleasing, but it might give an impression of false accuracy and precision. The community-production based estimate represents a minimum for coastal respiration because it does not include the respiration of autotrophs, and we have shown before that respiration by autotrophs contributes significantly to, and sometimes even dominates, total ecosystem respiration. For instance, the contribution of submerged macrophytes to coastal benthic respiration alone is 240 Tmol C a\(^{-1}\) (See Table 11.1).

As an alternative, we can balance total net primary production (836 Tmol C a\(^{-1}\); Duarte and Cebrían 1996) or gross primary production (789 Tmol C a\(^{-1}\); Gattuso et al. 1998), and riverine carbon input (34 Tmol C a\(^{-1}\)) with burial (about 13 Tmol C a\(^{-1}\))
and respiration and export of organic matter from the coastal to open ocean. However, estimates of carbon transfer from the coastal to the open ocean show a large range: 40 Tmol C a$^{-1}$ (Rabouille et al. 2001), 183 Tmol C a$^{-1}$ (Wollast 1998), 225 Tmol C a$^{-1}$ (Gattuso et al. 1998) and 500 Tmol C a$^{-1}$ (del Giorgio and Duarte 2002) precluding the derivation of respiration rates by difference.

11.5 Conclusions

Respiration in benthic coastal ecosystems constitutes a major part of total coastal ocean respiration. Our estimate based on the sum of individual ecosystem contributions (621 Tmol C a$^{-1}$) is well above that based on published global coastal carbon budgets ($\sim$150 Tmol C a$^{-1}$), but similar to estimates of coastal respiration by heterotrophs based on the balance between net primary production and river inputs on the one hand, and sediment burial on the other ($\sim$620 Tmol C a$^{-1}$). Our estimate of global benthic respiration is highly uncertain because of the diversity of benthic communities, aggregation problems necessary to upscaling, limited availability of data, and large variability within and among ecosystems. We anticipate that improvement of georeferenced datasets on coastal habitats (typology) and other products of the Land–Ocean Interaction in the Coastal Zone program will ultimately result in more accurate estimates on this significant and changing term in the global oceanic respiration budget.

Human activities have already impacted and are increasingly influencing coastal benthic communities. The effects of human impacts on coastal benthic respiration are multiple and involve changes in the magnitude of respiration of existing communities as well as changes in the community composition and ecosystem functioning. Accelerated sea level rise will result in changing distribution patterns of littoral and shallow benthic communities such as salt marshes, mangroves, sea grasses, and coral reefs. Eutrophication of coastal systems due to excess nutrient inputs may not only result in changes in the magnitude of primary production, hence benthic respiration, but it may also induce alterations in the community composition of dominant primary producers. For instance, sea grass communities may be replaced by macroalgae or phytoplankton. Eutrophication also affects macrobenthos community composition and biomass with consequences for respiration pathways. Land use change and related alterations in riverine organic matter delivery to the coastal zone will have a direct impact on respiration by heterotrophs and indirectly as well on autotrophs. Rising temperatures will result in enhanced rates of respiration by autotrophs, in particular marine macrophytes, and their contribution to respiration in the coastal ocean will likely increase. Rising temperature will, at least temporarily, result in enhanced rates of respiration by heterotrophs, but the effect on the longer term is difficult to predict because respiration by heterotrophs is ultimately governed by organic matter supply (i.e. net production). The combined effect of altered community specific respiration rates and changes in benthic community distribution patterns is difficult to predict. Before we can assess these changes, let alone predict the effects of human impact, we need more knowledge on the factors governing respiration at the community level.

Acknowledgments

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References


RESPIRATION IN AQUATIC ECOSYSTEMS


