
Estuarine respiration: an overview of benthic, pelagic, and whole system respiration

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Outline

This chapter reviews rates of benthic, pelagic, and whole system respiration in estuaries. We define estuaries as semi-enclosed coastal bodies of water with some degree of mixing between fresh and salt water. Rates of respiration in these locations are high, reflecting high rates of organic loading from both autochthonous and allochthonous sources. Areal rates of pelagic respiration (58–114 mmol C m⁻² d⁻¹) are 2–4 times higher than benthic respiration rates (34 mmol C m⁻² d⁻¹), consistent with estimates that only about 24% of total organic inputs to estuaries are respired by the benthos. Estimates of whole system respiration derived from open-water techniques (294 mmol C m⁻² d⁻¹) are substantially higher than those obtained by summing component rates (92–148 mmol C m⁻² d⁻¹), most likely due to the different spatial scales sampled by the two different approaches. The fundamental limit on benthic, pelagic, and whole system respiration appears to be the supply of organic matter, and in many locations allochthonous inputs fuel a major portion of estuarine respiration. Nonetheless, information on the factors that affect benthic respiration is far greater than it is for pelagic respiration, and knowledge of whole system respiration is particularly lacking. This prevents a full understanding of the fate of the vast amount of organic carbon that is imported and produced in estuarine ecosystems.

8.1 Introduction

Estuaries are those regions at the interface of the terrestrial and oceanic realms where seawater is measurably diluted by freshwater runoff from land. Whether they be drowned river valleys, sandbar-built lagoons, or fjords, estuaries have one thing in common, they are the loci through which all products eroded or washed from land pass on their way to the ocean. On average, 0.08–0.17 mol organic C m⁻² of land per year are exported from the terrestrial biosphere (Schlesinger and Melack 1981; Meybeck 1982; Mulholland and Watts 1982) and transported by the world's rivers to estuaries. Some

estuaries receive further sources of organic carbon, including wastewater effluents and adjacent oceanic upwelling (Smith and Hollibaugh 1997). For such a small region to be the recipient of such a mass of allochthonous organic matter is equivalent to local production on the order of 8 mol C m⁻² year⁻¹. This is half the average areal rate of gross primary production for the entire biosphere (Odum 1971). Estuaries are also sites of tremendous inorganic nutrient loading, however, rivaling that of intensively fertilized agroecosystems (Howarth *et al.* 2000). High rates of nutrient loading in combination with a tidal-energy subsidy (Odum 1971) and a diversity of functional groups of primary producers,

including macrophytes, benthic macrophytes, and phytoplankton, contribute to rates of organic production in estuaries that are among the highest in the entire biosphere, including tropical rain forests and agroecosystems (Kelly and Levin 1986). Indeed, nutrient-enhanced eutrophication is arguably the most severe, present-day threat to the integrity of estuaries with extensive consequences including anoxic and hypoxic waters, reduced fishery harvests, toxic algal blooms, and loss of biotic diversity (Howarth *et al.* 2000).

The fate of allochthonous and autochthonous inputs of organic matter to estuaries reflects the balance between the inputs and consumption by heterotrophs (measured as both heterotroph respiration and heterotroph biomass growth), harvest of fish and shellfish, burial in sediments and export to the ocean. Net ecosystem production ($NEP = P - R$) is the balance between all forms of production (P) and respiration (R) by all organisms. NEP is a measure of ecosystem trophic state and represents the extent to which an ecosystem is a net source or sink of atmospheric carbon dioxide.

Estuaries are complex, open systems that experience large inputs of both organic matter and inorganic nutrients from land. Thus they have the potential to be either autotrophic or heterotrophic systems (i.e. $P > R$ or $P < R$). During primary production inorganic nutrients are taken up from the environment and during respiration they are released. In autotrophic systems there is net assimilation of inorganic nutrients and net production of organic matter: such systems must receive external sources of nutrients. Heterotrophic systems are net remineralizers of organic matter and thus are net exporters of inorganic nutrients but also net importers of organic matter. Estuaries are sites of high secondary production and much research has focused on mechanisms that control the production of commercially important fisheries (Houde and Rutherford 1993) and the efficiency of trophic transfer (Nixon 1988). For estuaries to sustain high levels of commercial fisheries harvest, we expect NEP to be positive, that is, $P - R > 0$ or for there to be allochthonous organic matter inputs to subsidize the harvest. Thus this autotrophic characteristic could be supported by net assimilation of inorganic

nutrients from watershed drainage, or it could also be supported by the excess organic matter inputs from land. A key to quantifying the overall fate of allochthonous organic matter inputs to estuaries and estuarine primary production is to directly measure the rate of ecosystem respiration.

In this chapter we review rates of estuarine respiration for aquatic portions of estuaries. We consider benthic and pelagic components of overall system respiration. Due to the lack of standardized approaches, we do not consider portions of estuaries dominated by macrophytes, such as sea grass beds and intertidal marshes as there are few measures of respiration in these habitats, relative to open-water habitats. We have also opted not to focus on respiration "hotspots," such as oyster and mussel reefs, as information necessary to integrate these regions into the larger estuary (e.g. areal extent) is often lacking. This is not to say these areas are unimportant. In many estuaries, benthic filter feeders such as clams, oysters, or mussels control overall levels of water column productivity (e.g. Peterson 1975; Dame and Patten 1981; Kautsky 1981). Focusing on estuarine open-water habitats where a great number of studies have been conducted in a wide variety of locations facilitates comparisons across systems.

8.2 Measuring estuarine respiration

There are a variety of ways to estimate estuarine respiration. The most common approach is to isolate various *components* of the system, such as the benthos or the water column, in containers and to measure concentration changes in metabolic reactants (e.g. oxygen) or products (e.g. carbon dioxide) over time. A second approach is to measure diel changes in concentrations of metabolic reactants or products in the entire water column. This *open-water whole system* approach typically involves following a specific water mass, identified either by its unique salinity signature or by an added tracer, such as rhodamine dye. This approach is not frequently employed in estuaries, as advective and dispersive transport can be large in estuaries and mask signals resulting from primary production and respiration (Kemp and Boynton 1980). A rarely used third approach relies on calculating respiration indirectly

as the difference between independent measures of P and $P - R$. Water, salt, and biogeochemical models have been used successfully to calculate $P - R$ directly (e.g. Nixon and Pilson 1984; Smith and Hollibaugh 1997). The modeling approach for measuring $P - R$ can be superior to methods involving the summation of each component of gross primary production (GPP) and R , because measures of GPP and R often have variances as large as or greater than the difference between P and R (Smith and Hollibaugh 1997).

8.2.1 Benthic respiration

The most direct approach to measure benthic respiration is to place an opaque chamber over the sediment so as to isolate a small volume of water over a known bottom area. Benthic respiration is calculated as the rate of change of dissolved gas (CO_2 , oxygen) or inorganic nutrient concentrations measured over time, accounting for sediment surface area and enclosed water volume considerations. The rate of respiration in the water above the sediment (measured in separate bottles) is subtracted from the chamber rate to estimate the sediment contribution alone. Water is stirred in the chambers by a variety of methods, including battery-powered propellers. Benthic chambers usually have a wide flange that rests on the sediment surface and a skirt that penetrates the sediment. The flange and skirt insure constancy of internal volume, prevent erosion from water currents and help isolate the chamber water mass. Benthic chambers result in minimal sediment disturbance, but the logistics of deployment and sampling prevent their common usage.

More commonly benthic respiration is measured in cores collected from the field and incubated in the laboratory under controlled conditions. As with benthic chambers, respiration is calculated from the rate of change of metabolic products over time, accounting for surface area to volume relations and correcting for water column respiration. The duration of incubation depends on sediment activity rates, the surface area to volume ratio, and analysis detection limits. Solute changes are typically linear for well in excess of 24 h, indicating the presence of large, relatively labile organic matter

stores. Water overlying cores is usually exchanged with fresh estuarine water prior to incubation, as the coring and transporting process usually result in some disturbance of the sediment surface and the overlying water. The advantage of core incubations is that conditions can be experimentally manipulated, easily enabling controls of benthic respiration to be evaluated (e.g. temperature or organic matter amendments).

Benthic respiration is most easily measured as the consumption of dissolved oxygen in water overlying the sediment. To convert oxygen-based measures of respiration to C-based units however, requires knowledge of the respiratory coefficient ($\text{RQ} = \Delta\text{CO}_2 / -\Delta\text{O}_2$),¹ which is generally not known but typically assumed to be 1.0. In situations where there is considerable anaerobic respiration, oxygen will underestimate organic carbon mineralization to the extent that reduced end-products of anaerobic metabolism are not reoxidized. Even when end-products are reoxidized, there is often a considerable time lag before oxygen is consumed. The direct method for measuring organic carbon respiration is to measure inorganic carbon concentration (dissolved inorganic carbon—DIC) over time. DIC, which we will hereafter simply label carbon dioxide, can be measured directly as the sum of all inorganic carbon species dissolved in estuarine water. It can also be calculated from measures of pH and alkalinity, after correcting for alkalinity changes associated with nutrients and organic acids. Unfortunately, even carbon dioxide flux is not without problems, as carbon dioxide change can also be associated with carbonate dissolution and precipitation and chemoautotrophic growth.

A final consideration in benthic respiration measurements is the effect of water movement on solute fluxes (including oxygen and carbon dioxide). In an attempt to mimic *in situ* water current fields in chambers or cores, investigators typically generate circular flow fields (Boynton *et al.* 1981). It has been shown however that solute fluxes can be artificially enhanced by circular flow fields, especially in permeable sediments (Glud *et al.* 1996).

¹ See Chapter 1 for a discussion of the basis of the value of the RQ.

8.2.2 Pelagic respiration

Respiration in the water column is far simpler to measure than benthic respiration, but not without its challenges. Typically, a water sample is enclosed in a bottle or a nonpermeable bag (to translate natural turbulence) and incubated under controlled conditions until there is sufficient change in solute concentrations. Chamber size generally ranges from 60 cm³ BOD bottles to 20 dm³ carboys. The advantage of large chambers is the ability to capture a larger percentage of the plankton community. The statistical probability of capturing macrozooplankton increases with sample size (Sheldon *et al.* 1972). Often, 200- μ m screening is used to screen out the large zooplankton from small incubation vessels, so as to decrease variability. For most of the twentieth century, oxygen was the solute measured to estimate organic carbon degradation. As there is seldom anaerobic metabolism occurring in the water column, the carbon equivalent of oxygen consumption can be determined if nitrification is measured simultaneously (or the change in NH₄⁺ and NO₃⁻ concentrations).

Plankton respiration is generally much lower than benthic respiration and incubation intervals are typically much longer (benthic respiration can be amplified by maximizing the sediment surface area to overlying water volume ratio). The primary reason why the oxygen technique for measuring primary production was dropped during the 1950s and 1960s in favor of the ¹⁴C technique was greatly increased sensitivity. As a result, measures of plankton respiration, which are a component of the oxygen technique, were seldom made thereafter. Only in the past decade or two has the precision and sensitivity of instrumentation for measuring carbon dioxide and oxygen concentrations increased sufficiently to enable relatively short incubations. The precision (as measured by the standard error of the mean of replicates) of modern, computer-controlled instrumentation for measuring carbon dioxide and oxygen concentration is currently on the order of 0.5 μ M DIC and 0.02 μ M O₂.

Minimum planktonic incubation times must reflect not only the precision of instrumental analysis, but also variation between bottles. With increased precision of oxygen and carbon dioxide

measurements, planktonic incubations can be quite short. Based on a standard error for initial and final dissolved oxygen replicates of about 0.05 μ M and an average rate of pelagic respiration of 10 mmol O₂ m⁻³ d⁻¹, the minimum incubation time required for the standard error of the rate calculation (slope of Δ O₂/ Δ time) to be 10% or better is less than 2 h. This is a best case scenario, however, and based on oligotrophic systems that seem to have little bottle to bottle variation. In eutrophic estuarine systems, we find that bottle to bottle variation for the second time point is substantially higher than it is for oligotrophic systems. Incubation times are likely to increase as a result. For carbon dioxide, incubation time is considerably longer. Recently there has been an interest in using membrane inlet mass spectrometry to measure dissolved oxygen. In addition to greatly shortened analysis times (<1 min), simultaneous measures of oxygen and O₂/Ar ratios show the potential to increase the measurement precision, thereby affording reduced incubation times.

What is an acceptable duration of incubation? There is strong evidence that heterotrophic plankton respiration is closely coupled to the production of fresh photosynthate and incubations in the dark that require more time than it takes for the depletion of fresh photosynthate are likely to lead to underestimated rates of respiration. High temporal resolution analyses of plankton respiration often show a non-linear trajectory developing within hours or even minutes of incubation initiation (Sampou and Kemp 1994; Hopkinson *et al.* 2002). On the other hand, the average night has 12 h of darkness when photosynthate production is halted. So while planktonic respiration might be underestimated during daylight periods, when there is a close coupling between photosynthate production and heterotrophic respiration, there should be no such bias during night. Thus there will be on some scale a rundown in respiration in the dark, but if we try to avoid this and measure instantaneous rates then we might end up overestimating respiration in natural systems.

8.2.3 Open-water whole system respiration

Open-water approaches are another option for measuring respiration (Odum and Hoskin 1958;

Odum and Wilson 1962; Balsis *et al.* 1995). In this approach the total mass of oxygen or carbon dioxide in the water column is measured over time. Without being contained however, changes in these constituents are also due to exchange with the atmosphere and mixing with adjacent water masses. Problems are exacerbated in stratified systems because advection and mixing with additional water masses must be quantified. To address these problems in stratified systems, Swaney *et al.* (1999) used statistical regressions of oxygen with salinity, temperature, and time to calculate diel changes in oxygen attributable to biological activity. Atmospheric exchange is difficult to quantify accurately. Exchange is controlled by the saturation deficit or excess and the exchange coefficient (piston velocity). Factors controlling piston velocity include wind speed and current velocity. Time course changes in the mass of sulfur hexafluoride (SF_6) gas added to estuarine waters has proven to be an effective means of integrating wind, rainfall, and current velocity effects on gas exchange (Carini *et al.* 1996). Recently a new technique was developed to measure exchange coefficients that is based on the rate of dissipation of heat applied to micropatches on the water surface (Zappa *et al.* 2003).

While the open-water, whole-system diel change approach is not without its own significant methodological problems, it does avoid problems associated with container approaches that may underestimate respiration for a variety of reasons, including reduced turbulence and altered

heterotrophic communities. Unfortunately, it is difficult to apply in large estuarine systems and is not often employed. Further it is not clear how to extrapolate rates of respiration measured during night to rates on a daily basis. While it is often assumed that respiration rates at night are time invariant, there is evidence to suggest they are not (e.g. rates that vary even at night). Isotopic approaches that involve the analysis of isotopes of carbon dioxide, water, and oxygen could help resolve some of these scaling issues.

8.3 Benthic respiration

There have been a great number of studies on estuarine benthic respiration over the past 50 years. We have compiled data from approximately 50 locations, primarily in temperate regions, where there was information for an annual cycle on benthic respiration as well as ancillary information on other system attributes such as system productivity, water temperature, and depth. We did not include studies with less than annual coverage.

8.3.1 The data

The mean annual respiration of all the studies we compiled is $34 \text{ mmol C m}^{-2} \text{ d}^{-1}$ and ranges from a low of $3 \text{ mmol C m}^{-2} \text{ d}^{-1}$ to a high of $115 \text{ mmol C m}^{-2} \text{ d}^{-1}$ (Fig. 8.1). The highest rate is from Corpus Christi estuary, Texas, which

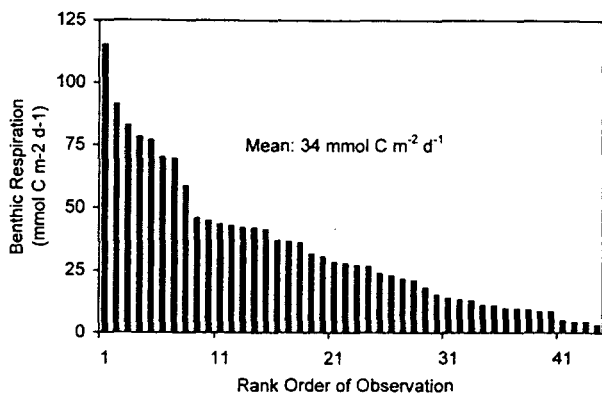


Figure 8.1 Average annual rate of benthic respiration from 48 sites around the world. The data are presented in rank order. While rates are presented in terms of $\text{mmol C m}^{-2} \text{ d}^{-1}$, data may have been measured as oxygen consumption. These rates were converted to carbon equivalents either by the original author(s) or by us assuming an RQ of 1. See text for problems associated with this conversion approach. Many of these values represent averages of multiple stations within single regions.

has allochthonous organic matter inputs from sea grasses as well as fringing salt marshes. We have not included data from estuarine reefs habitats, which can have substantially higher rates of respiration. For instance, average annual respiration of oyster reefs in the Duplin River estuary in the southeastern United States is $780 \text{ mmol C m}^{-2} \text{ d}^{-1}$, over an order of magnitude higher than the mean estuarine rate (Bahr 1976). There are less than two orders of magnitude that range in the rates we have compiled. This is less than the actual range because we averaged rates within study areas, thus removing the highs and lows that occur over an annual cycle. Ranges of rates even within single study areas can be as large as that reported across all our study areas. For instance, along the salinity gradient in the Plum Island Sound estuary, mean respiration over a 12 month period ranges from $21 \text{ mmol C m}^{-2} \text{ d}^{-1}$ at a sandy, euryhaline site, to $171 \text{ mmol C m}^{-2} \text{ d}^{-1}$ at a muddy, mesohaline site with abundant clams (Hopkinson *et al.* 1999). In Boston Harbor benthic respiration ranges from 24 to 111 from site to site (Giblin *et al.* 1997). On first glance, it appears that sediment respiration is lowest in sandy sediments and highest where there is an abundant benthic filter feeding community. However, not all sandy sites have low rates, witness the high rates of respiration ($65\text{--}83 \text{ mmol C m}^{-2} \text{ d}^{-1}$) in sandy Georgia coastal sediments (Smith 1973; Hopkinson 1985).

8.3.2 Carbon dioxide versus oxygen measures of respiration

Since respiration is typically measured as either oxygen consumption or carbon dioxide production, we might ask whether the two approaches measure the same processes and give similar results. Lacking simultaneous measures of oxygen and carbon dioxide, most investigators assume an RQ of 1 and Redfield C:N:P stoichiometry. The validity of this assumption is often incorrect however. It had been assumed that most benthic respiration was aerobic and that oxygen utilization by nitrification could be accounted for easily. It was also assumed that under anaerobic conditions when sulfate reduction was the dominant respiratory pathway, any reduced sulfur produced during respiration would

eventually be reoxidized and that carbon dioxide production associated with sulfate reduction would be balanced by oxygen consumption when reduced sulfur was reoxidized, that is, no net reduced sulfur storage.

The RQ of benthic systems ranges widely across studies and also across sites within study areas. Intensive, multiyear studies in Plum Island Sound, Boston Harbor, and Tomales Bay illustrate the extent to which oxygen and carbon dioxide fluxes differ (Fig. 8.2(a)). In Tomales Bay carbon dioxide flux is 2.2 times greater than oxygen flux (Dollar *et al.* 1991) on average (RQ = 2.15). In Plum Island estuary, average annual carbon dioxide flux for three sites is $1.35 \times \text{O}_2$ flux, ranging from 0.88 to 1.71 across sites. Carbon dioxide production was less than oxygen consumption only in the permanently freshwater site where porewater sulfate concentrations are low and methanogenesis is a major metabolic pathway (Hopkinson *et al.* 1999). In Boston Harbor, mean annual carbon dioxide flux is $1.21 \times \text{O}_2$ consumption, but ranges from 1.05 to 1.49 across sites (Giblin *et al.* 1997). For all these sites, with the exception of the freshwater site, oxygen flux substantially underestimates total organic carbon metabolism because of non- O_2 based anaerobic metabolism.

Dissolved inorganic carbon flux exceeds oxygen consumption when organic matter is degraded anaerobically, that is, without oxygen as the terminal electron acceptor. During anaerobic sulfate reduction 1 mole of SO_4^{2-} oxidizes 2 moles of organic carbon, leading to the production of 2 equivalents of alkalinity, 1 mole of reduced sulfur (HS^-) and no consumption of oxygen. The reduced sulfur can be stored in the sediment, typically as pyrite (FeS_2), or it can diffuse into oxidized regions and be reoxidized. When reoxidized, 2 moles of oxygen are reduced and 2 equivalents of alkalinity are consumed. The net rate of sulfate reduction can be estimated from the net alkalinity flux. In Tomales Bay, the difference between carbon dioxide flux and oxygen consumption was shown to be due to the net reduction of sulfur. There was a net production of alkalinity that was proportional to the imbalance between carbon dioxide and oxygen. With oxygen flux "corrected" for alkalinity flux, the carbon dioxide/"corrected" oxygen flux was reduced to

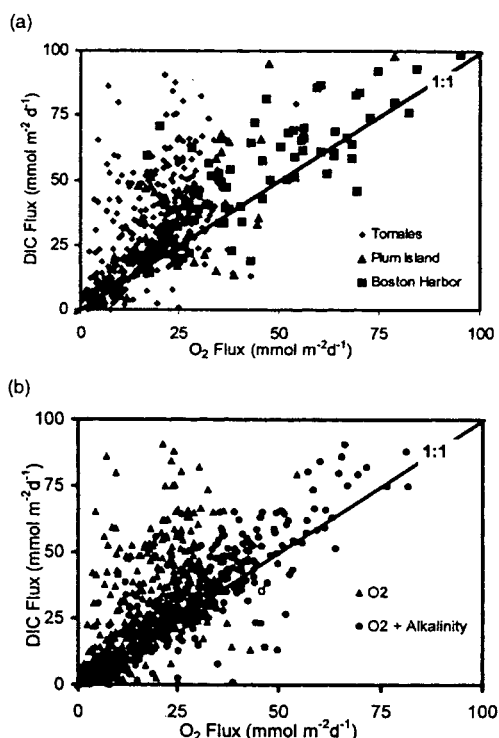


Figure 8.2 The relation between rates of benthic respiration measured as either oxygen consumption or carbon dioxide production. (a) The relations for several stations within three estuaries: Tomales Bay (Dollar *et al.* 1991), Boston Harbor (Giblin *et al.* 1997), and Plum Island Sound (Hopkinson *et al.* 1999). (b) The effect of "correcting" oxygen consumption for anaerobic metabolism that does not result in the consumption of oxygen but which produces alkalinity. Diamonds represent oxygen flux alone, while triangles represent the sum of oxygen and alkalinity flux (from Tomales Bay website and Dollar *et al.* 1991).

1.09 (from 2.15—Fig. 8.2(b)). Independent measures of net pyrite formation in Tomales Bay sediments were in balance with net alkalinity flux. Thus oxygen-based estimates of benthic respiration can underestimate total organic carbon mineralization substantially.

In estuarine systems benthic respiration is generally high (averaging $30 \text{ mmol C m}^{-2} \text{ d}^{-1}$ for the studies examined) and sulfate is in abundance. As a result, sulfate reduction is one of the dominant

metabolic pathways in sediments. In experimental mesocosms, Sampou and Oviatt (1991) showed the importance of sulfate reduction to increase with increased organic matter loading to sediments: the greater the loading the smaller the aerobic zone in sediments. In mesocosms with added sewage sludge, sediment carbon metabolism was dominated by sulfate reduction (75% of total). Total carbon dioxide flux from the sediments was in excess of sediment oxygen consumption but could be balanced by sedimentary sulfide storage.

One further consideration in measuring benthic respiration is that carbon dioxide flux is not exclusively due to respiration. Carbonate incorporation into shells of benthic macrofauna, and carbonate precipitation and dissolution can also contribute to measurable carbon dioxide fluxes. In Norsminde Fjord, Denmark, calcium carbonate deposition by mollusks was an important carbon dioxide flux during late summer, as revealed by positive relationships between carbon dioxide flux and mollusk density (Therkildsen and Lomstein 1993). In order to obtain a better understanding on the potential of carbonate precipitation or dissolution in sediments, pH and concentrations of carbonates and calcium in porewater should be measured.

8.3.3 Controls of benthic respiration

There is no single explanation for what controls the magnitude and seasonal pattern of benthic respiration that holds for all the systems we examined. However, there are some general patterns that emerged from our analysis. The magnitude of organic matter supply explains the largest percentage of the variance across systems when dealing with annual rates. Temperature explains a large percentage of the seasonal variance within systems. While these patterns hold in general, there are exceptions to each. In the section that follows, we will discuss the major controls and how they operate and interact.

Spatial patterns

There have been numerous attempts and approaches to determine the effect of the rate of supply organic matter on benthic metabolism

(e.g. Hargrave 1973; Nixon 1981). Unfortunately, it is extremely difficult and seldom possible to quantify input. Inputs can be based on primary production, primary production plus allochthonous organic matter inputs, or organic matter deposition rates onto benthic sediments. Estimates of organic matter deposition have been attempted in shallow coastal areas using sediment trap approaches, but resuspended bottom sediments can contribute more to the traps than deposition of fresh particles from the water column. Proxy measures of organic matter inputs have also been used, including sediment organic content and chlorophyll content. Bulk descriptors of sediments, such as organic content and grain size, generally explain little of the variation in benthic respiration rates, however, at neither local nor regional scales. Others have attempted to model inputs on the basis of overlying water primary production and loss of organic matter during settling. Ideally we would like to know the total rate of organic matter input to a system (primary production and allochthonous inputs), the percentage of inputs that settle to the bottom (and the controls on the percentage that settles), and the relation between inputs to the bottom and the magnitude and timing of benthic respiration.

We compiled data from 20 sites with information on both benthic respiration and water column net primary production and allochthonous organic matter inputs to the estuarine ecosystem (Fig. 8.3(a)). There is little relation between only autochthonous production and benthic respiration (data not shown). This is to be expected in estuarine systems where allochthonous inputs represent a substantial portion of total organic matter inputs. van Es (1982) considered the large intercept ($30 \text{ mmol C m}^{-2} \text{ d}^{-1}$) for a regression between net primary production and benthic respiration in the Ems-Dollard estuary to be a measure of the importance of allochthonous organic matter inputs to the benthic system. Our data show a strong relation between total organic matter inputs (allochthonous and autochthonous) and benthic respiration: the greater the organic input to an estuarine system, the greater the benthic respiration. The R^2 of the regression between total system production and benthic respiration indicates

that this parameter explains 44% of the variation in respiration. From the slope of the regression, we see that on average 24% of the total system production is respired in benthic sediments in estuarine systems. Experimental approaches have also been used to show the importance of organic matter inputs in controlling the magnitude of benthic respiration. In large mesocosms (supposedly mimicking Narragansett Bay), Kelly and Nixon (1984) showed that benthic respiration increased with increased organic matter deposition. Their studies also showed that the effects of fresh organic deposition could be short lived, however, as small inputs of very labile organic matter caused dramatic increases in benthic respiration that lasted only a few days.

We find little relation between the magnitude of total organic matter inputs to an estuary and the percentage respired by the benthos (Fig. 8.3(b)). While on average the benthos respire 24% of inputs, at low input rates the benthos respire anywhere from about 10% to nearly 100% of the production. With increasing inputs, there is less variability so that at the highest levels of production about 20–30% of inputs are respired. It is not clear whether this pattern is the result of inadequate sampling of higher production systems or whether benthic system efficiency (or vice versa pelagic efficiency) varies with input rates (see Hargrave 1973, 1985).

Water column depth and turbulence have also been used, independently, to explain spatial patterns in rates of benthic respiration. Depth can be expected to play a role, as the residence time of particles in the water column prior to settling should be proportional to depth. The greater the depth of the water, the longer the particle is in the water column, the greater the particle degradation while in the water column and hence less organic matter reaches the benthos. Turbulence can be expected to play a role if it delays the time for particle sedimentation. We find that depth is poorly correlated with benthic respiration, however (Fig. 8.4(a) and (b)). At depths shallower than 10 m there is absolutely no relationship between either benthic respiration and depth or the percentage of total system production that is respired by the benthos. It is only in the presumably rare estuarine systems, greater than 10 m deep,

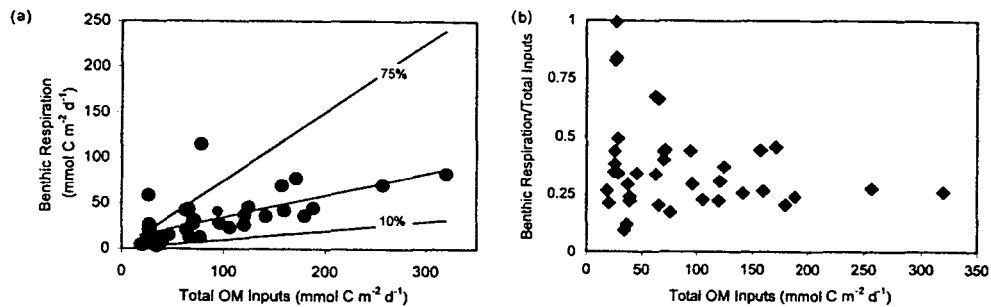


Figure 8.3 The relation between organic matter inputs to a system and benthic respiration. Organic matter inputs include both primary production within the system (e.g. planktonic primary production) and allochthonous inputs from outside the system (e.g. riverine input of organic matter to an estuary). (a) Relation between inputs and benthic respiration. Included are lines that describe the best fit relation as well as the amount of benthic respiration to be expected if either 10% or 75% of total organic inputs were respired by the benthos. (b) The relation between total system organic matter inputs and the portion that is respired by the benthos.

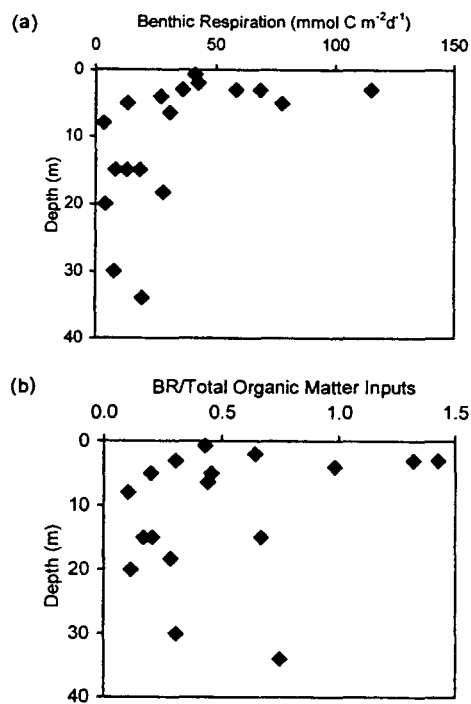


Figure 8.4 The relation between water column depth and benthic respiration. (a) The figure shows benthic respiration versus depth. (b) The figure shows how the relative portion of organic matter inputs respired by the benthos varies with depth.

where there is the tendency for absolute or relative rates of benthic respiration to decrease with increasing depth ($R^2 < 0.11$). The estuarine systems contrast with their deep-water oceanic cousins where there is a strong correlation between system depth and benthic respiration (see Middelburg, Chapter 11).

Hargrave (1973) showed that mixed layer depth was related to the relative importance of benthic respiration. In shallow estuarine systems and those that are stratified, turbulence from tidal currents and winds retards particle sedimentation thereby increasing residence time in the pelagic zone and the extent of organic matter degradation prior to settling. However we have insufficient data to examine rigorously the effect of turbulence. The general lack of a relationship between benthic respiration and depth might be expected, as there is tremendous variability in the amount of organic matter potentially available to the benthos. Given sufficient data, it would be interesting to evaluate the effect of depth and/or turbulence when corrected for total organic matter inputs.

Temporal patterns

The supply rate of organic matter to the benthos as estimated from measures of autochthonous and allochthonous inputs to the estuary are our best predictors of spatial patterns in benthic respiration.

What factors control variability over time? Factors often shown to be important include temperature (e.g. Nixon *et al.* 1980) and animal activity (e.g. Aller 1982).

At regional scales, average annual temperature explains none of the variability in annual average

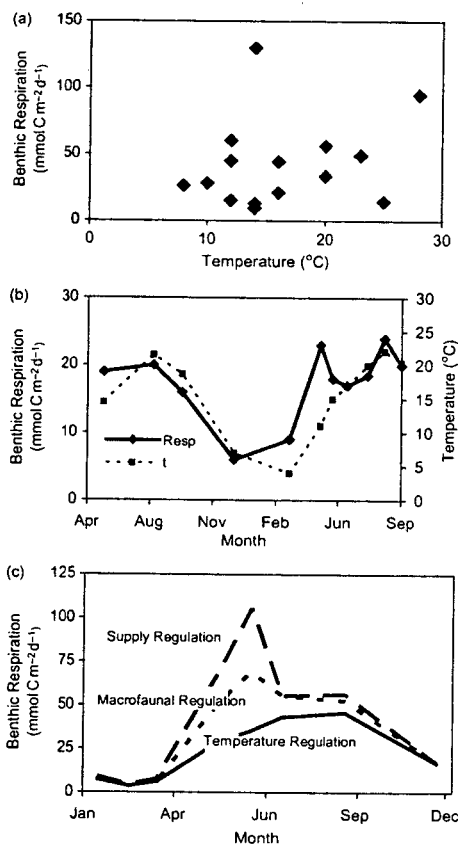


Figure 8.5 Factors controlling spatial and temporal variation in benthic respiration. (a) The relation between mean annual temperature and mean annual benthic respiration rate for a variety of temperate estuaries. There is no significant relationship. (b) The seasonal pattern of benthic respiration and temperature in Buzzards Bay. Note the strong rise in benthic respiration in late winter when temperature is still declining. Banta *et al.* (1995) showed this asynchrony was due to deposition of the spring bloom. (c) The seasonal pattern of benthic respiration in Chesapeake Bay as it relates to variations in temperature, macrofaunal biomass, and organic matter supply.

benthic respiration (Fig. 8.5(a)). Even within certain estuaries, temperature generally explains little of the difference in benthic respiration between sites (e.g. Fisher *et al.* 1982; Giblin *et al.* 1997; Hopkinson *et al.* 1999, 2001). At the site level, however, patterns of benthic respiration over an annual cycle are often strongly related to temperature, with respiration increasing with temperature. While Giblin *et al.* (1997) observed no correlation between temperature and benthic respiration across sites in Boston Harbor, up to 90% of the annual pattern in benthic respiration at individual sites could be explained by temperature.

Different responses to temperature are often seen across seasons and an asynchrony between an increase in benthic respiration and temperature in spring. Earlier we mentioned that benthic respiration in mesocosms can respond very quickly to fresh inputs of labile organic matter, such as would be expected following phytoplankton blooms. Banta *et al.* (1995) showed an overall strong relation between seasonal temperature and benthic respiration patterns, but a pronounced departure from this pattern in early spring. In fact, while temperatures were still dropping during late winter, benthic respiration reached its second highest level over the annual period (Fig. 8.5(b)). Banta *et al.* related the increased respiration to the deposition of the spring phytoplankton bloom. While temperature alone explained 42% of the annual pattern, 72% could be explained when sediment chlorophyll *a* content (indicator of fresh plankton inputs) and temperature were regressed against benthic respiration.

Other investigators have demonstrated the importance of fresh organic matter inputs in interpreting temporal dynamics as well (e.g. Fisher *et al.* 1982; Graf *et al.* 1982; van Es 1982; Grant 1986; Dollar *et al.* 1991). It is interesting that there are often differences in the timing of response to fresh organic matter inputs. Whereas Banta *et al.* showed a nearly simultaneous response, Hargrave (1978) showed a 1–2 month lag between deposition and respiration. To some extent the timing of the response can be attributed to benthic community composition. When benthic respiration is entirely microbial, temperature plays a larger role and lags are greater, whereas when benthic macrofauna are a

major component of the community, lags can be shorter.

Benthic animals, which change in abundance and activity over an annual cycle, also have been shown to exert an influence on seasonal patterns of benthic respiration. Kemp and Boynton (1981) showed that seasonal patterns of benthic respiration in Chesapeake Bay sediments could be attributed to temperature and macrofaunal biomass (see Fig. 8.5(c)) as well as substrate supply. On the basis of macrofaunal size-class distributions and temperatures, they were able to predict benthic respiration with close agreement to measured rates. Residuals as large as 40% could not be explained during spring, however. While at the time the unexplained residual was attributed to the non-linear effect of macrofaunal "microbial gardening," it is more likely the result of deposition of the spring bloom (Boynton and Kemp 1985).

Other controls on benthic respiration

While major spatial and temporal patterns in benthic respiration are largely explained by variations in organic loading rates, temperature, and macrofaunal activity, they do not explain other patterns such as organic matter preservation in sediments or respiration enhancement in shallow water systems with permeable sediments. Organic matter preservation in the sea is an active area of research (Hedges and Keil 1995). There is a critical interaction between organic and inorganic materials with a direct relationship between organic matter content in sediments and mineral surface area. More than 90% of total sediment organic matter can not be physically separated from its mineral matrix and is thus unavailable to benthic microbes and macrofauna (Mayer 1994a, b). This may partially explain the lack of correlation generally found between sediment organic content and benthic respiration. In fine grained sediments, which have the greatest surface area and hence high organic content, organic matter may be unavailable.

In contrast, coarse sediments in shallow water systems while typically having low organic content can have extremely high respiration rates. Investigations of this paradox are an active area of benthic research, which focuses on the role of advective

water movement and particle trapping in coarse, permeable sandy sediments. Here sedimentary organic content is low due to low mineral surface area, but because of strong advective flushing of bottom water through the coarse sediments, particulate organic matter from the water column can be efficiently filtered by the sediments and then decomposed by benthic organisms (Huettel and Rusch 2000).

8.4 Pelagic respiration

In contrast to that of the benthos, there have been far fewer studies of respiration in estuarine pelagic communities. We identified 22 estuarine locations for which direct measures of respiration in the water column are available. All but one of these locations is in the Northern Hemisphere. Most are in the temperate climatic region. All of the studies reported here focused on the open water portion of estuarine environments. Due to the paucity of data, we include all available data regardless of the extent to which they represent full annual coverage within a location.

8.4.1 The data

Mean pelagic respiration rates among locations range from 1.7 to 84 mmol C m⁻³ d⁻¹ over their study periods, although variability in rates within any one location can often far exceed this range. (Table 8.1). The lowest mean rate is observed in the Gulf of Finland, the northern-most estuary, and the highest mean rate is observed in the one tropical, Southern Hemisphere location. Other than these extremes, however, there is no apparent trend in respiration rates with location or latitude. Minimum respiration rates tend to be rather similar among most locations, whereas maximum rates are substantially more variable. Although it is typical to report arithmetic mean values, a convention we have followed here, frequency distributions of respiration rates tend to be highly skewed, rather than normally distributed, which can greatly bias calculated mean values. This pattern is readily seen in the combined dataset of surface respiration rates (some 700 observations) from all locations where

Table 8.1 Arithmetic mean and range of pelagic respiration rates (mmol C m⁻³ d⁻¹) reported for the open-water portion of estuaries

Location	Latitude	Longitude	Coverage	Mean	Min.	Max.	N	Reference
Gulf of Finland	59.83	-23.25	Jan.-Nov.	1.7	0.1	3.8	14	Kuparinen 1987
Loch Ewe	57.78	5.60	Not available	5.9	0.5	20.2	43	Williams 1984
Gulf of Riga	57.30	-23.85	May-Jul.	14.6	2.9	35.6	18	Olesen <i>et al.</i> 1999
Tweed estuary	55.77	2.00	Apr.-Aug.	11.5	0.7	31.9	8	Shaw <i>et al.</i> 1999
Roskilde Fjord	55.75	-12.08	May-Sep.	44.8	10.4	123.8	57	Jensen <i>et al.</i> 1990
Gulf of Gdansk	54.50	-19.25	Feb.-Nov.	7.4	0.4	32.2	149	Witek <i>et al.</i> 1999
Southampton estuary	50.90	1.40	Feb.-Sep.	9.3	0.1	24.6	49	de Souza Lima and Williams 1978
Urdaibai estuary	43.37	2.67	Aug.	59.0	4.8	214.3	38	Iriarte <i>et al.</i> 1996
Urdaibai estuary	43.37	2.67	Feb.-Nov.	41.3	5.9	227.3	36	Revilla <i>et al.</i> 2002
Ria de Vigo	42.24	8.76	Apr.-Nov.	15.1	1.9	47.2	31	Moncoiffe <i>et al.</i> 2000
Bay of Blanes	41.67	-2.80	Jan.-Dec.	5.1	0.1	45.0	25	Satta <i>et al.</i> , 1996
Ria de Aveiro	40.63	8.65	Oct.-Jan.	15.8	2.3	82.7	20	Cuhna <i>et al.</i> 1999
Chesapeake Bay	39.33	76.18	Feb.-Nov.	14.3	1.6	57.8	64	Smith and Kemp 1995
Tomales Bay	38.13	122.87	Jan.-Nov.	16.9	3.8	45.8	22	Fourqurean <i>et al.</i> , 1997
San Francisco Bay	37.84	122.67	Feb.-Dec.	5.8	0.4	25.5	32	Rudek and Cloern 1996
San Francisco Bay	37.58	122.20	Feb.-Apr.	10.7	2.5	25.2	23	Caffrey <i>et al.</i> 1998
Savannah River	32.03	80.85	Feb., Jul., Oct.	9.1	0.5	34.8	24	Pomeroy <i>et al.</i> 2000
Ogeechee River	31.92	81.18	Feb., Jul., Oct.	11.0	0.2	28.6	15	Pomeroy <i>et al.</i> 2000
Georgia estuary	31.90	80.98	Dec.-Jan.	13.8	0.1	17.0	149	Turner 1978
Altamaha River	31.38	81.33	Feb., Jul., Aug., Oct.	17.5	0.5	53.5	28	Pomeroy <i>et al.</i> 2000
Satilla River	30.96	81.68	Feb., Jul., Aug., Oct.	14.3	0.7	66.7	47	Pomeroy <i>et al.</i> 2000
St. Mary's River	30.71	81.40	Jul., Oct.	14.9	5.8	33.1	12	Pomeroy <i>et al.</i> 2000
Celestun Lagoon	20.75	90.25	Mar.-Mar.	26.5	8.9	74.5	13	Herrer-Silveira 1998
Fly River Delta	-8.75	-143.50	Feb.	84.0	23.4	150.2	14	Robertson <i>et al.</i> 1993

Note: Summarized are only those studies where plankton community respiration was measured directly and could be extracted from the original source. All rates were measured as *in vitro* changes in oxygen concentrations and converted to C equivalents either by the original author(s), or by us assuming an RQ of 1. *N* is the number of reported rate measurements of each study. Negative longitudes are degrees eastward from Greenwich.

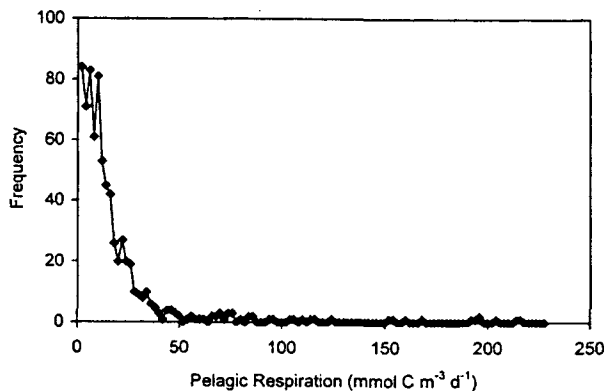


Figure 8.6 Frequency distribution of individual pelagic respiration rates measured in 21 estuarine sites from around the world. While rates are presented as $\text{mmol C m}^{-3} \text{d}^{-1}$, original data were measured as *in vitro* oxygen consumption and converted to carbon equivalents either by the original author(s) or by us assuming an RQ of 1. The data ($n = 707$) follow a highly lognormal distribution, such that the arithmetic mean is 17.8 while the geometric mean is only 9.1.

individual measurements could be extracted from the original literature (Fig. 8.6). Respiration rate, which ranges from 0.05 to $227 \text{ mmol C m}^{-3} \text{d}^{-1}$, is best described by the lognormal distribution (chi-square goodness of fit test, $p < 0.01$). As a result, while the arithmetic mean is 17.8, the geometric mean is only 9.1 and the mode is just $4.0 \text{ mmol C m}^{-3} \text{d}^{-1}$.

8.4.2 Variability in pelagic respiration—effects of temperature and substrate supply

Respiration rates of the pelagic community tend to be much more variable than those measured in the benthos (Kemp *et al.* 1992; Rudek and Cloern 1996; Pomeroy *et al.* 2000). In comparing studies of pelagic respiration, we conclude that there are few, if any, consistent patterns in the variability of respiration among estuaries. Large seasonal variations appear to be one prominent feature of water column respiration in most estuaries, although diel variability can be as much as 50% of seasonal variability (e.g. Sampou and Kemp 1994) and in many systems spatial variability is often larger than seasonal variability (e.g. Jensen *et al.* 1990; Smith and Kemp 1995; Iriarte *et al.* 1996). Attempts at explaining variability in pelagic respiration usually focus on the effects of temperature and substrate supply as regulatory mechanisms.

Temperature sensitivity of respiration rate should be expected due to the profound physiological

effects of temperature on cellular metabolism (e.g. Li and Dickie 1987). Sampou and Kemp (1994) investigated the effect of temperature on plankton respiration in the Chesapeake Bay by conducting a series of temperature-manipulation experiments (from 5–30°C) in both spring and summer. In these experiments, relationships between respiration and manipulated temperature were not significantly different between seasons, nor were they different from the relationship obtained from *in situ* measurements of respiration and temperature over the annual cycle. This supports the notion of a temperature sensitivity of pelagic respiration, but suggests an absence of significant physiological adaptation and/or selection for temperature optima in the plankton community over the annual cycle.

Can variations in ambient water temperatures explain differences in respiration rates among or within estuaries? When we combine the data from all locations, there is a significant, logarithmic relationship with temperature (Fig. 8.7). The R^2 of the regression, however, indicates that temperature can explain only 28% of the variability in pelagic respiration rates among estuaries. Within individual locations, attempts at correlating pelagic respiration and ambient water temperatures have produced mixed results. Strongly positive relationships between respiration and temperature have been observed in a number of locations, such as Tomales Bay (Forqurean *et al.* 1997), the Gulf of Gdansk (Witek *et al.* 1999), and all of the Georgia river

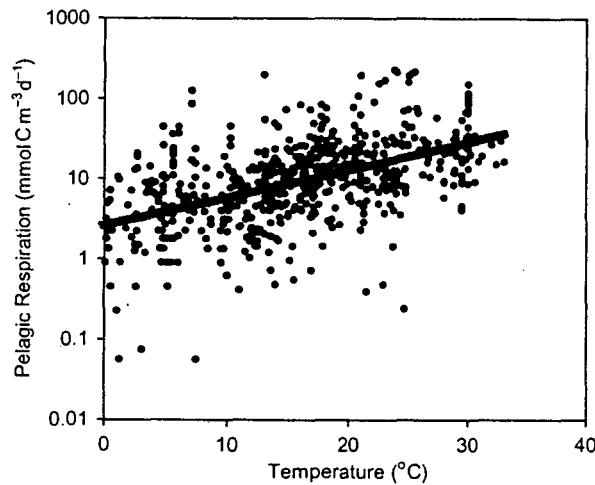


Figure 8.7 The relationship between pelagic respiration rate ($\text{mmol C m}^{-3} \text{d}^{-1}$) and water temperature ($^{\circ}\text{C}$) for the surface waters of estuaries. The fitted line is the ordinary least squares regression $\log R = 0.89 + 0.08 \times \text{Temp}$; $n = 648$, $R^2 = 0.28$, $p < 0.001$.

estuaries (Turner 1978; Pomeroy *et al.* 2000). In the Urdaibai estuary respiration was observed to be highly sensitive to the 5°C temperature changes that occurred on timescales of just a few days (Iriarte *et al.* 1996). One difficulty in inferring causality from these statistical correlations, however, is the fact that in temperate estuaries other factors (e.g. increased organic production by algae) often tend to co-vary with water temperature. Several estuaries, in fact, show no apparent relationship between temperature and respiration. Prominent among these locations are Roskilde Fjord (Jensen *et al.* 1990), San Francisco Bay (Rudek and Cloern 1996), and the Bay of Blanes (Satta *et al.* 1996). Iriarte *et al.* (1996) found that observed temporal relationships between respiration and temperature in the Urdaibai broke down in a region of the estuary that receives substantial inputs of organic matter from a sewage treatment plant. The utility of temperature as an explanation for variability in respiration within and among estuaries thus remains equivocal.

Several lines of evidence suggest that availability of organic substrates explains a large part of the variability in pelagic respiration rates. This is to be expected, as pelagic respiration must ultimately be dependent on the supply of organic matter, just as in the case of the benthos. Strong positive

relationships between respiration in the euphotic zone and phytoplankton biomass (as measured by chlorophyll *a* concentrations) or productivity have been observed at seasonal timescales in many estuaries. These include all those locations mentioned above where respiration and temperature showed no significant relationship. For example, in the eutrophic Roskilde Fjord, Jensen *et al.* (1990) found phytoplankton biomass to be the single best predictor of variations in respiration across both seasonal and spatial scales within the estuary. In both the Chesapeake Bay (Smith and Kemp 1995) and the Urdaibai estuary (Iriarte *et al.* 1996), seasonal relationships between pelagic respiration and phytoplankton production appear to vary along spatial trophic gradients, with the strongest relationships occurring in areas experiencing the lowest levels of primary production. Interestingly, the spatial patterns in the strength of production-respiration relationships are opposite each other in these estuaries. In Chesapeake Bay, lowest productivities and the tightest relationship occur in the upper reaches of the estuary. In the Urdaibai, this situation occurs at the seaward end of the estuary. Nonetheless, these results are consistent with the idea of a greater degree of autotrophic-heterotrophic coupling, and a higher degree of dependence on autotrophic production by heterotrophs, in less

productive areas, relative to higher productive areas.

On shorter timescales, Sampou and Kemp (1994) observed a diel periodicity in surface water respiration rates, for periods of both low (spring) and high (summer) respiratory activity, that exhibited a characteristic pattern of peak rates just after mid-day and decreasing to a night-time minimum. They attributed this pattern to a tight coupling between respiration and the daily pattern of primary production, where enhanced respiration during the day corresponded to peak rates of phytoplankton exudation of dissolved organic matter. In contrast to the tightly coupled diel cycles in the surface waters, these authors found no such cycles in respiration occurring in the deeper, aphotic, layers of the water column. This layer was separated from the euphotic layer by a strong pycnocline, which effectively broke this link between production and respiration over diel timescales.

While a strong relationship between plankton production and respiration appears to be a common feature of most estuarine ecosystems, it should be noted that such a close coupling does not immediately imply causality by either variable. The question of control in autotrophic-heterotrophic coupling may be largely circular. Indeed, it has been suggested that the high rates of primary production in estuaries may be attributable, in part, by the

high rates of nutrient regeneration associated with heterotrophic respiration (Smith and Hollibaugh 1993). Further, it may be that a strong relationship between production and respiration is indicative of regulation of both rates by a common variable. There is growing evidence that pelagic respiration in some estuaries can be strongly stimulated by nutrient enrichment. For example, in the Georgia rivers estuaries (Pomeroy *et al.* 2000), the most frequent positive response in respiration rate to enrichment was to glucose, but in a number of cases inorganic nitrogen, or occasionally inorganic phosphorus, stimulated a significant response. In the Chesapeake Bay (Smith and Kemp 2003), enrichment experiments showed organic carbon (as glucose) to be primarily limiting to respiration in the upper, oligohaline region of the Bay and inorganic nutrients (primarily phosphorus) to become limiting in the lower, polyhaline region. The interacting effects of carbon and nutrient substrates in controlling pelagic respiration, and its coupling to primary production, is an area of research that would greatly benefit from further study.

Most of the studies of planktonic respiration we compiled (Table 8.1) also include measures of phytoplankton biomass (as estimated by chlorophyll *a* concentration), allowing us to make comparisons across locations (Fig. 8.8). In the combined dataset, chlorophyll *a* does no better than temperature in

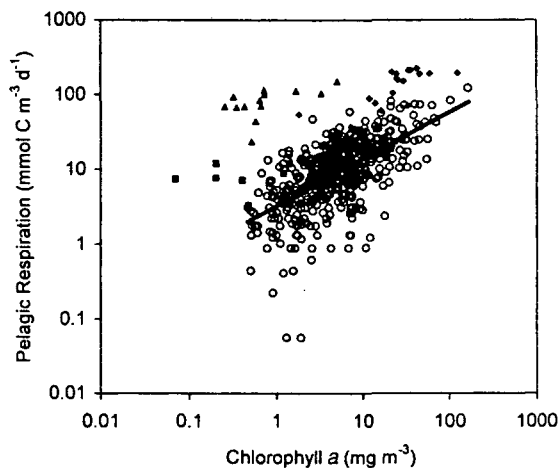


Figure 8.8 The relationship between pelagic respiration rate ($\text{mmol C m}^{-3} \text{d}^{-1}$) and chlorophyll *a* (mg m^{-3}) in the surface waters of estuaries. Closed symbols represent sites receiving substantial allochthonous organic input and excluded from the regression analysis. The closed squares are data from the Georgia rivers, the closed triangles are from the Fly River Delta, and the closed diamonds are from the Urdaibai Estuary in the vicinity of a sewage treatment plant. The open symbols are for the remainder of the data, for which allochthonous inputs are not so dominant. The fitted line is the ordinary least squares regression, using the open symbol data only, $\log R$ ($\text{mmol C m}^{-3} \text{d}^{-1}$) = $1.19 + 0.63 \times \log \text{chl}$ (mg m^{-3}); $n = 450$, $R^2 = 0.38$, $p < 0.001$. The regression for the entire dataset, line not shown, is $\log R$ ($\text{mmol C m}^{-3} \text{d}^{-1}$) = $1.45 + 0.54 \times \log \text{chl}$ (mg m^{-3}); $n = 531$, $R^2 = 0.25$, $p < 0.001$.

explaining variations in respiration rates among estuaries (R^2 of 0.25 versus 0.28, respectively). It is evident, however, that estuaries receiving substantial allochthonous inputs of organic matter, such as the Georgia rivers, the Fly River, and that portion of the Urdaibai estuary in the vicinity of a sewage treatment plant, all tend to separate out from the pattern displayed by the remainder of the data. In these locations, relationships between respiration and chlorophyll *a* tend to be rather flat. In contrast, the combined data for the remaining locations show a fairly reasonable relationship, of the form $\log R$ ($\text{mmol C m}^{-3} \text{ d}^{-1}$) = $1.19 + 0.63 \times \log \text{chl}$ (mg m^{-3}); $n = 450$, $R^2 = 0.38$, $p < 0.001$, and thus now explains close to 40% of the variability in respiration. It is interesting to note that the slope of this relationship is significantly less than one, with pelagic respiration rates increasing proportionately less than chlorophyll *a* concentrations for this subset of estuaries. Thus, at high algal biomass proportionately more of the primary production associated with this biomass will remain unrespired within the pelagic community.

The data points that fall below the predicted values at the low end of the relationship in Fig. 8.8 are primarily those from the Gulf of Finland (Kuparinen 1987). This is the northern-most location in the dataset and exhibits the lowest seasonal water temperatures. Based on this, we combined temperature and chlorophyll *a* in a multiple linear regression for all estuarine locations. The resulting regression equation is: $\log R$ ($\text{mmol C m}^{-3} \text{ d}^{-1}$) = $0.39 + 0.08 \times \text{temp}$ ($^{\circ}\text{C}$) + $0.45 \times \log \text{chl}$ (mg m^{-3}); $n = 502$, $R^2 = 0.49$, $p < 0.001$. Temperature and chlorophyll *a* are themselves poorly, though significantly, related ($\log \text{chl}$ (mg m^{-3}) = $1.08 + 0.03 \times \text{temp}$ ($^{\circ}\text{C}$); $n = 502$, $R^2 = 0.05$, $p < 0.001$), but together they explain 49% of the variability in respiration across all locations, with 80% of all observed values falling within 50% of predicted values. The even distribution of residual indicates this equation is an unbiased predictor of pelagic respiration rates. The 51% of the variability unexplained by temperature and chlorophyll is presumably due, in large part, to the influence of allochthonous inputs of organic matter in many of these estuaries. We have insufficient data, however, to include such a parameter in the predictive equation.

8.4.3 Contribution of various communities to pelagic respiration

The relative contribution of various metabolic groups to total respiration in estuarine waters remains an active research area. Iriarte *et al.* (1991) postulated that relationships between respiration and chlorophyll *a* should be strongest at high levels of phytoplankton biomass because the algae themselves would tend to dominate total respiration. At lower phytoplankton biomass levels the situation should be reversed due to a predominance of microheterotrophic respiration. Support for this was seen in San Francisco Bay (Rudek and Cloern 1996), but this pattern is not readily apparent from the data compiled here (Fig. 8.8). The importance of microheterotrophic communities to pelagic respiration has been inferred from significant positive relationships between respiration and bacterial abundance and/or substrate uptake rates in many estuaries (Jensen *et al.* 1990; Satta *et al.* 1996; Smith 1998, Smith and Kemp 2003; Witek *et al.* 1999, Revilla *et al.* 2002). Fourqurean *et al.* (1997), on the other hand, found no significant relationship between respiration and bacterial abundance or uptake rates in Tomales Bay, which also has very high phytoplankton to bacterioplankton biomass ratios. These authors thus concluded that phytoplankton were responsible for the bulk of total respiration rates in this estuary.

Several investigators have addressed the relative contributions of the various functional groups present in estuarine waters by quantifying the size distribution of respiration rates. This work has largely been confined to the contributions of the various microplankton groups. It is generally assumed that incubations conducted in 300 ml BOD bottles, largely considered the standard incubation vessel for pelagic respiration rate measurements, do not capture the contribution of macrozooplankton communities. Of course, a commonly assumed corollary to this is that respiration by macrozooplankton is relatively insignificant component of total pelagic community respiration rates, although this is not well tested in estuarine environments. Caution must be taken in the interpretation of microplankton respiration rates subject to filtration (Hopkinson *et al.* 1989), but results with

this approach may be useful in a comparative sense. In the eutrophic Roskilde Fjord, Sand-Jensen *et al.* (1990) found that microbial respiration (operationally defined as cells passing through a 1 μm pore-size filter) accounted for 45%, on average, of total pelagic respiration rates. Similarly, in the productive waters of the Chesapeake Bay, Smith and Kemp (2001) observed microbial respiration ($<3 \mu\text{m}$ cells) averaged 54% of total respiration rates. In contrast, contributions of microbial respiration in a turbid, moderate productivity estuary of the Georgia coast, Griffith *et al.* (1990) found microbial respiration ($<1 \mu\text{m}$ cells) to account for a higher proportion of total respiration, with a mean of 73%. Robinson and Williams (Chapter 9), on the other hand, find about 40% of planktonic respiration in oceanic waters appears to be associated with the bacterial ($<1 \mu\text{m}$) fraction. Although a trend of decreasing importance of microbial respiration along gradients of increasing productivity in estuaries is intuitively appealing, there are exceptions to this pattern. In the Gulf of Finland, a much less productive system than either the Roskilde or the Chesapeake, contributions of the $<3 \mu\text{m}$ size fraction amounted to only 36%, on average, of total pelagic respiration rates. In the Urdaibai estuary (Revilla *et al.* 2002), contributions of the $<5 \mu\text{m}$ size-fraction represented, on average, 99% of the total community respiration, although these numbers are biased by the fact that in most of the $<5 \mu\text{m}$ size-fractioned samples respiration actually exceeded that measured in the whole-water fraction, suggesting an enhancement of microbial activity upon filtration (Hopkinson *et al.* 1989).

8.5 Open-water whole system respiration

It has only been in the past 10 years or so that total system metabolism has been measured with the open-water technique in enough estuaries to warrant an analysis of metabolic patterns. New measurements are primarily from estuaries within the US NOAA National Estuarine Research Reserve program (Caffrey 2003). Data are available for North American estuaries in both tropical and temperate regions. Unfortunately, few ancillary data on estuarine conditions (e.g. temperature,

chlorophyll *a*, benthic respiration, pelagic respiration, depth) have been reported for most of these sites, which prevents a rigorous analysis of controls on whole system respiration.

8.5.1 The data

Whole system measures of respiration range from 69 $\text{mmol C m}^{-2} \text{d}^{-1}$ in the Newport River, NC, USA to 631 $\text{mmol C m}^{-2} \text{d}^{-1}$ in Bojorquez lagoon, Mexico and average 294 $\text{mmol C m}^{-2} \text{d}^{-1}$ (Fig. 8.9(a)). While the highest rate of respiration is from the southernmost, warmest site, the lowest rate is not from the northernmost, coldest site. Thus temperature and geographic latitude do not fully explain the variability in rates across sites.

8.5.2 Relation between whole system respiration and gross production

The methodology for measuring whole system respiration provides concurrent measures of system gross production (P_g). Estimates of P_g range from 60 to 870 $\text{mmol C m}^{-2} \text{d}^{-1}$ with the lowest and highest rates being from the same sites where the extremes in respiration rate were observed. Mean P_g is 262 $\text{mmol C m}^{-2} \text{d}^{-1}$.

There is a nonlinear, logarithmic relation between P_g and system respiration, with decreasing increases in respiration per unit increase in P_g (Fig. 8.9(b)). The R^2 for the logarithmic relationship indicates that P_g explains 77% of the variability in respiration across sites. The high R^2 also indicates very close coupling between primary production and system respiration across all systems in this compilation. This nonlinear relation further suggests that allochthonous organic matter inputs are most important at low rates of P_g and that as P_g increases the relative importance of allochthonous organic matter inputs to estuaries decreases. As such, there is a tendency for estuarine systems to be heterotrophic at lower rates of P_g ($<400 \text{ mmol C m}^{-2} \text{d}^{-1}$) and autotrophic at higher rates of P_g ($>500 \text{ mmol C m}^{-2} \text{d}^{-1}$)—Fig. 8.9(c).

The ratio between P_g and system respiration demonstrates the trophic status of an ecosystem. Systems with P_g in excess of respiration (positive net ecosystem production) are autotrophic systems: more organic carbon is produced than consumed

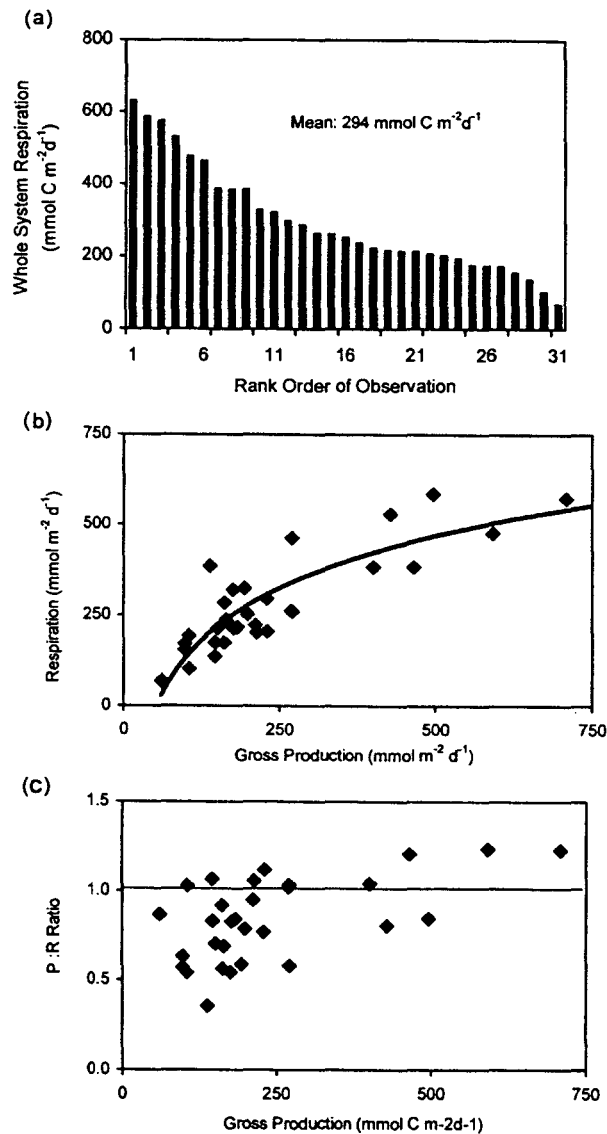


Figure 8.9 Open-water whole system measures of estuarine respiration. (a) The range of rates observed across a variety of temperate and tropical estuaries. (b) The relation between whole system respiration and whole system gross production. The curvilinear relation indicates that increases in Pg do not translate into equivalent increases in respiration and that therefore estuaries with very high levels of Pg have a tendency to become autotrophic. (c) The relation between estuarine $P:R$ ratio and whole system Pg. At lower levels of production estuaries tend to be heterotrophic ($P:R < 1$) = y-axis refers to $P = R$, rather than $P:R$. The data for these figures come from Odum and Hoskins (1958), Odum and Wilson (1962), Kenney *et al.* (1988), Carmouze *et al.* (1991), Reyes and Merino (1991), D'Avanzo *et al.* (1996), Ziegler and Benner (1998), and Caffery (2003).

in respiration. In heterotrophic systems (negative NEP), R exceeds P_g , indicating the importance of allochthonous organic carbon inputs to a system (assuming the system does not consume capital produced and stored in previous times). The $P:R$

ratio ranges from as low as 0.36:1 to as high as 1.38:1. The average $P:R$ ratio is 0.86:1, implying that these estuaries are generally net heterotrophic ecosystems. This suggests that, on average, the sum of total respiration plus organic matter export

from these estuaries must depend on an input of allochthonous organic material equivalent to at least 14% of P_g .

Many factors can influence the autotrophic-heterotrophic nature of estuaries, including water residence time, lability of allochthonous organic matter and the ratio of inorganic to organic nitrogen load (Hopkinson and Vallino 1995). Kemp *et al.* (1997) showed that estuarine NEP was largely controlled by the relative balance between inputs of inorganic nutrients and allochthonous organic carbon loading. Terrestrial organic matter sources are C-rich, relative to planktonic material, and therefore release proportionally lower quantities of inorganic nutrients than that from decomposing planktonic material. When these terrestrial inputs are respired in the estuary, the P_g resulting from this nutrient source will be substantially less than the R associated with the release of these nutrients. Hence, when organic matter loading is dominated by terrestrial sources, estuaries tend towards negative NEP as a direct result of the low C:N ratio of estuarine organic matter relative to that of terrestrial. It would appear that in the future we can expect estuaries to become increasingly autotrophic (Kemp *et al.* 1997) as the long-term trend in inputs is for organic loading to decrease (due to decreased wetlands and sewage treatment that removes BOD) and inorganic loading to increase (due to intensification of agricultural N fertilization and increasingly N-rich diet for an increasing global population).

8.5.3 Comparison of component-derived and open-water whole system-derived measures of respiration

Rates of whole system respiration are very high relative to measures of planktonic and benthic respiration. The average rate of pelagic respiration we observed in our synthesis is $17.8 \text{ mmol C m}^{-3} \text{ d}^{-1}$ (geometric mean is 9.1). Assuming an average depth for all pelagic sites of 6.4 m (the average depth reported for benthic studies in Fig. 8.4), average depth-integrated pelagic respiration is $114 \text{ mmol C m}^{-2} \text{ d}^{-1}$. This is 4 times higher than benthic respiration ($34 \text{ mmol C m}^{-2} \text{ d}^{-1}$).

This calculated relative dominance by the pelagic system seems reasonable and is consistent with our previous estimate that on average 24% of total system production (autochthonous and allochthonous) is respired by the benthos (Fig. 8.3). The sum of benthic and pelagic components of system respiration are not equivalent to directly measured rates of system-determined respiration, however ($148 \text{ mmol C m}^{-2} \text{ d}^{-1}$ benthic and pelagic versus $294 \text{ mmol C m}^{-2} \text{ d}^{-1}$ for system-determined respiration).

Few studies have attempted to explain the disparity between component-derived and whole system-derived measures of respiration (e.g. Odum and Hoskin 1958; Kemp and Boynton 1980; Ziegler and Benner 1998). The comparisons we make in this synthesis are not based on simultaneous measures of benthic, pelagic and whole system respiration. Thus our conclusions may be spurious because of sampling bias. Significantly higher estimates of respiration based on whole system measures, relative to those based on component measures, have, however, been reported in a few specific locations where concomitant measures of each component were made. These locations include Chesapeake Bay, USA (Kemp and Boynton 1980), Laguna Madra, USA (Ziegler and Benner 1998) and the Plum Island Sound estuary, USA (C. Hopkinson, unpublished data), and suggest this difference is real. Clearly, container and whole system approaches operate on different spatial, and sometimes temporal, scales. This may be a large part of the explanation for the disparity between the two estimates of respiration. For example, it is likely that whole system-derived measures are "seeing" the effect of respiration in adjacent ecosystems, such as intertidal marshes (e.g. Cai *et al.* 1999), or in components within the estuary that are not adequately sampled by containers, such as floating rafts of senescent vascular plant material (e.g. Ziegler and Benner 1998). Alternatively, the lack of agreement may also, in part, be explained by methodological uncertainties inherent in each of the two approaches. For example, respiration may be decreased in containers when the contained community is removed from fresh organic matter inputs (organic matter deposition in cores or fresh

phytoplankton photosynthate in dark bottles). In addition, respiration may be reduced in containers because of reduced turbulence. In fact, there have been many reports about the effect of stirring when measuring benthic respiration in cores (e.g. Boynton *et al.* 1981; Huettel and Gust 1992). As discussed in Section 8.2.3, however, the open-water approach to measuring total system respiration is not without its share of significant methodological problems as well. The application of the method suffers in estuaries in particular, where physical processes can often dominate open-water oxygen dynamics. This is particularly true for estuaries that are strongly stratified and experience pronounced short-term variability in tidal and wind-induced currents. Failure to account for the influence of physical processes on the open-water approach can result in unrealistically high estimates of biological rates (Kemp and Boynton 1980). There is currently no clear consensus on which approach is generally more appropriate for the estimation of total system respiration in estuaries, although we suspect that this will become an area of increased scientific interest as the disparity becomes more widely recognized.

8.6 Conclusion and synthesis

This review has shown rates of estuarine respiration are high, reflecting the high rates of organic matter loading to estuaries from both autochthonous and allochthonous sources. Direct field measurements of respiration suggest that the average rate of benthic respiration is $34 \text{ mmol C m}^{-2} \text{ d}^{-1}$ while the average rate of pelagic respiration is between 9.1 and $17.8 \text{ mmol C m}^{-3} \text{ d}^{-1}$, depending on whether a geometric or arithmetic mean for the data is used. Assuming an average depth for all pelagic sites of 6.4 m, the depth-integrated pelagic respiration is between $58\text{--}114 \text{ mmol C m}^{-2} \text{ d}^{-1}$. The areal rates of pelagic respiration are thus, on average, 2–4 times higher than benthic respiration rates in estuaries. This is consistent with estimates that only 24% of total organic inputs (allochthonous plus autochthonous) are respired by the benthos in these systems.

Combining the two direct measurements of respiration rate gives a range from 92 to $148 \text{ mmol C m}^{-2} \text{ d}^{-1}$, depending on whether one adopts the algebraic or geometric mean for pelagic respiration rate. In contrast, estimates of whole system respiration obtained by the open-water approach averaged $294 \text{ mmol C m}^{-2} \text{ d}^{-1}$ for the locations compiled in this review. While this disparity may be attributable to methodological uncertainties inherent in each of the two techniques, it is more likely due to the different spatial scales sampled by the two different approaches. For instance there is the inclusion of respiration by other estuarine communities in the open-water techniques that are excluded in container approaches, such as respiration in adjacent intertidal marshes.

From this review, it is clear that the fundamental limit on benthic, pelagic and whole system respiration is the supply of organic matter. While major differences in benthic respiration among locations are best explained by variation in organic loading rates (44% explained), temporal patterns at specific sites are controlled by a combination of factors, primarily temperature, organic matter supply, and macrofaunal biomass and activity. We have a better understanding of what controls temporal variation in benthic respiration at single sites than we do of what controls spatial variation in respiration. This probably reflects the difficulty of quantifying organic matter inputs to benthic systems. Variations in pelagic respiration, within and among sites, are largely controlled by differences in the supply of organic matter and temperature. Allochthonous supply, as estimated from phytoplankton biomass (chlorophyll *a*) and temperature each explain about 25% of the variation in rates among estuaries. The 50% or so of the variability unexplained by temperature and chlorophyll *a* is presumably due, in large part, to the influence of allochthonous organic matter inputs. We lack sufficient information to quantify this relation however. For estuaries, in general, both allochthonous and autochthonous sources of organic matter fuel estuarine pelagic and benthic metabolism, and in some locations allochthonous inputs appear to be a major source of organic matter fueling estuarine respiration. There is a tendency

for estuarine systems to be net heterotrophic at rates of primary production $< 400 \text{ mmol C m}^{-2} \text{ d}^{-1}$.

Given the estimates of respiration derived in this review and an estimated global area of estuaries of $1.4 \times 10^{12} \text{ m}^{-2}$ (Gattuso *et al.* 1998) we can make an initial estimation of total annual respiration in estuaries as $76\text{--}150 \times 10^{12} \text{ mol C a}^{-1}$ (i.e. $76\text{--}150 \text{ Tmol C a}^{-1}$). The wide range is due to the difference in component and whole system-derived estimates of respiration. Estuarine area does not include salt marshes or other wetlands. Woodwell *et al.* (1973) estimated that estimates of estuarine area are accurate to $\pm 50\%$. Global estuarine respiration is distinctly higher than the magnitude of estimated total carbon delivery from land to the ocean, 34 Tmol C a^{-1} , and total estuarine planktonic and benthic primary production, 35 Tmol C a^{-1} (Smith and Hollibaugh 1993), suggesting that most estuaries are generally net heterotrophic zones. We have not accounted for primary production or respiration of salt marshes or mangroves within estuaries, but acknowledge that whole water estimates of estuarine respiration probably reflect some salt marsh contribution (wetlands occupy approximately $0.4 \times 10^{12} \text{ m}^2$ Woodwell *et al.* 1973).

This global estimate of estuarine respiration is subject to a great deal of uncertainty. Our knowledge of benthic, pelagic, and whole system respiration in estuaries is confined largely to the temperate environments of North America and Europe, and generally biased towards river-dominated coastal plain estuaries. The magnitude and factors that regulate respiration in the many estuaries of Asia, Africa, Australia, and South America are essentially unknown. In addition, our knowledge about benthic respiration and the factors that affect its variability is far greater than it is for pelagic respiration. We think the reasons for this are twofold. First, benthic rate measurements are technologically easier, given the larger rates of oxygen decline that occur in benthic incubations, relative to those occurring in pelagic incubations. Second, in the field of estuarine ecology, there has been an emphasis on controlling eutrophication in estuaries and the importance of nutrient loading in causing eutrophication. Benthic nutrient regeneration is a major source of internally

regenerated nutrients and benthic denitrification is the primary nitrogen sink in estuaries. Measures of benthic respiration are thus typically made concomitant with measures of benthic nutrient fluxes. This is in contrast to measures of pelagic respiration, which are typically the objective of a study in and of themselves, and have only relatively recently been conducted on a routine basis as a result of methodological improvements in precision oxygen measurements. Finally, our current state of knowledge on whole system respiration in estuaries is particularly lacking. This paucity of information on whole system respiration prevents us from knowing the fate of the vast amount of organic carbon that is imported and produced in estuarine systems. Thus we lack information on the overall role of estuarine ecosystems in the overall global carbon budget. Increased research should be focused on quantifying estuarine respiration and in understanding differences in estimates of respiration derived from "container" and open-water techniques.

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