Latitudinal variation of the balance between plankton photosynthesis and respiration in the eastern Atlantic Ocean

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Abstract

A knowledge of the balance between plankton gross primary production (GPP) and community respiration (CR) in the open ocean is vital to an accurate determination of the global carbon cycle, yet the paucity of open ocean measurements severely limits our understanding. This study measured GPP, net community production, dark CR, and size-fractionated primary production in the upper 200 m of a 12,100 km longitudinal (32°-48°N) transect in the eastern Atlantic Ocean during May and June 1998. This comprehensive data set, which spans five contrasting plankton regimes, including two open ocean oligotrophic provinces, is used to derive a GPP:CR relationship, which suggests that net heterotrophy (GPP < CR) prevails in the eastern Atlantic when primary production falls below ~100 mmol O₂ m⁻² d⁻¹. The predictive capability of this relationship is compared with that of the only other published relationship based on similar methodologies and is found to give a more representative description of the autotrophic (GPP > CR) to heterotrophic seasonal cycle in the Bay of Biscay. This improved predictive power is attributed to the increased representativeness of the current data set. Specifically, the interpretation suggests that the influence of community structure on net ecosystem metabolism implies that prediction of GPP:CR balances in pelagic ecosystems can be best achieved by use of a data set that covers a wide range of community structure and not only a wide range in the magnitude of primary production.

The significant contribution of the marine biota to the global carbon cycle (e.g., Sarmiento and Siegenthaler 1992) ultimately results from the balance between gross primary production (GPP) (all photosynthesis independent of its fate) and community respiration (CR) (the oxidative consumption of organic matter by autotrophic and heterotrophic organisms). Quantification of such a balance (net community production, NCP = GPP − CR) in the open ocean is hampered by the poor marine CR database, the question as to what each analytical technique measures in terms of GPP or net primary production (NPP = GPP minus algal respiration) (Williams 1993), and the time-consuming methods available for directly measuring NCP. Existing global estimates therefore rely on empirical relationships between the magnitudes of GPP (Williams 1998) or NPP (del Giorgio et al. 1997) (derived from ΔO₂ or δ¹³C techniques), and bacterial (del Giorgio et al. 1997) or total CR (Duarte and Agusti 1998; Williams 1998; Duarte et al. 1999) to predict NCP where only primary production data are available. These studies disagree by about one order of magnitude on the predicted rate of GPP at which CR exceeds GPP (GPP ~ 1 mmol O₂ m⁻³ d⁻¹ vs. GPP = 16.7 mmol O₂ m⁻³ d⁻¹), which has generated an active debate on the net metabolism of open ocean unproductive ecosystems. The conflicting conclusions that (1) microbial respiration exceeds photosynthesis in unproductive aquatic systems (del Giorgio et al. 1997; Duarte and Agusti 1998) and (2) the open ocean is in metabolic balance (Williams 1998) have been questioned on the basis of the inadequacy of the data sets (Geider 1997; but see also del Giorgio and Cole 1997; Williams 1998; Duarte et al. 1999) and the form of data analysis (Duarte et al. 1999; Williams and Bowers 1999). However, the paucity of NCP measurements in the oligotrophic open ocean has prevented an independent test of either of these models.

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So far, GPP:CR relationships have been obtained by aggregating independent data from different times and locations, without explicit attention to the state or type of community studied. One implicit assumption is the prevalence of steady-state conditions during each sampling period—that is, that the connection between the processes of production and consumption of organic matter occurs locally in both space and time. Although Williams (1998) highlighted the importance of using depth-integrated data of GPP and CR to account for the compensation of imbalances over the water column, current published GPP:CR relationships do not explicitly incorporate an analysis of the horizontal or temporal scales involved. However, accumulation of dissolved organic matter (DOM) in the upper mixed layer (see Hansell and Carlson 1998) may give rise to the linkage of production and consumption of organic matter over large spatial or long temporal scales (e.g., Pomeroy and Wiebe 1993; Sherr and Sherr 1996), thus affecting the GPP:CR balance at local scales, as shown in seasonal temperate systems (e.g., Blight et al. 1995; Serret et al. 1999).

In addition, the relationship between GPP and CR may not only be different over different spatial and temporal scales, but, more important, it will probably differ between systems near equilibrium and those that are transient (Burke et al. 1997). In practice, given the imprecise nature of the concept of equilibrium in ecology, and especially in pelagic systems, and the extreme difficulty in addressing the large time- and space scales of trophic functioning, the critical point is to ensure that data are representative of the functional community—that is, that they characterize long-term averages (Hairson and Hairson 1993).

Even if the data used are representative, the simple use of GPP:CR relationships to estimate trophic status (i.e., the GPP:CR balance at ecologically significant scales; e.g., Smith and Hollibaugh 1997 and references therein) assumes that the degree of heterotrophy of pelagic ecosystems may be predicted from their total amount of GPP, which overlooks the influence of food web structure on net ecosystem metabolism. However, the net balance of an ecosystem must be dependent not only on the total amount of GPP but also on the type and activity of the community of heterotrophs that such production sustains (Hairson and Hairson 1993; McGrady-Steed et al. 1997; Petchey et al. 1999). If food web organization, and not only primary production, influences the degree of heterotrophy of the pelagic ecosystems, the variation of CR with GPP may be different when analyzed within or between different communities. Consequently, generalized GPP:CR relationships might be dependent on the range of different communities studied and not only on the range of GPP.

We present here data of GPP and CR in the euphotic zone of five biogeochemical provinces of the eastern Atlantic Ocean in the austral spring-to-summer transition period, providing new empirical evidence of the GPP:CR balance in two open ocean oligotrophic habitats. This data set allows us to explore the regional variability of net community production, but, more important, because it is representative of contrasting plankton regimes, it also enables us to investigate the influence of the type of plankton community on GPP:CR balances.

**Materials and Methods**

**Sampling**—A latitudinal (32°S–48°N) transect across the Eastern Atlantic Ocean (Atlantic Meridional Transect [AMT]–6 cruise; see Aiken et al. 2000) was conducted on board *RRS James Clark Ross* on passage between Cape Town, South Africa, and Grimsby, United Kingdom (15 May–16 June 1998) (Fig. 1): 24 stations were sampled daily (between 08:00 and 09:00 GMT) at ~320 km intervals. Vertical profiles of temperature and conductivity were performed by use of a Seabird 911+ conductivity-temperature-depth (CTD) rosette fitted to a rosette of 12 × 30 liter Niskin-type sampling bottles. Vertical profiles of photosynthetically active irradiance (400–700 nm) were calculated by integrating the measurements of downwelling irradiance at seven SeaWiFS wavelength bands derived from daily casts of an optical profiler (SeaOPS) and a free-fall optical profiler (SeaFALLS) (Aiken et al. 2000). Water was collected from 9–12 depths in the upper 200 m.

**Dissolved oxygen**—A 60-cm³ gravimetrically calibrated, borosilicate glass bottle was carefully filled from each Niskin bottle by use of silicon tubing. Measurements of dissolved oxygen were made with an automated Winkler titration system based on that described in Williams and Jenkinson (1982). Oxygen saturation was calculated by use of the equations for the solubility of oxygen in seawater of Benson and Krause (1984).

**Size-fractionated chlorophyll a concentration**—A total of 200–300 cm³ water samples were sequentially filtered through 20, 2, and 0.2 µm pore size polycarbonate filters. Chl a was extracted from the filters in 90% acetone at −20°C for 12–24 h and measured by use of a Turner 10-ÅU fluorometer calibrated against Chl a standards (Sigma).

**Size-fractionated and total particulate organic carbon production (PO44CP) rates**—At each station, samples were collected from each of seven depths corresponding to optical depths ranging from 97% to 1% of surface irradiance. Water from each depth was distributed into four 75-cm³ acid-cleaned polypropylene bottles (three transparent and one dark). Each bottle was inoculated with 185–370 KBq (5 to 10 µCi) NaH¹⁴CO₃ and then incubated for 6–7 h in an on-deck incubator that simulated the irradiance at the original sampling depths by use of various combinations of neutral density and blue plastic filters. A previous comparison of this on-deck incubation procedure and an in situ incubation technique found no statistical difference between the respective ¹⁴C derived estimates of primary production (Joint et al. 1993). After the incubation period, samples were filtered at very low vacuum (<50 mm Hg) through 0.2, 2, and 20 µm polycarbonate filters. Filters were then fumed with concentrated HCl for 12 h. Radioactivity was measured with a Beckman LS6000 SC scintillation counter. Quenching was corrected by use of an external standard. Total primary production was determined by summing the integrated size fractionated rates. Following the method of Marañón et al. (2000), the hourly production rates were converted to daily rates by taking into account the length of daylight and as-
assuming that dark respiratory losses represent 20% of light \( \text{PO}^{14} \text{CP} \) (see also review by Geider 1992).

**GPP, NCP, and dark CR**—GPP, NCP, and dark CR (DCR) were determined from in vitro changes in dissolved oxygen after 24-h light and dark bottle incubations. Water samples (25 \( \text{dm}^3 \)) were collected each day from the CTD rosette into acid-washed opaque polypropylene aspirators from depths equivalent to 97%, 33%, and 1% of surface irradiance. Water was siphoned from each 25 \( \text{dm}^3 \) opaque aspirator into 15 × 60 cm\(^3\) borosilicate glass bottles through silicon tubing. From each depth, five replicate bottles were fixed immediately, five bottles were kept in darkness, and five bottles were incubated under irradiance conditions that simulated those of the original sampling depth, as described above. Samples collected from depths at which in situ temperature was >5°C lower than surface water temperature were also incubated in the dark in temperature controlled water baths at near in situ temperature for 24 h. In these instances, reported DCR rates correspond to those measured at about in situ temperature, whereas most GPP were discarded. Only seven of these GPP data from ~40–75 m depth in the area of the Guinea Dome (between ~3°N and 13°N) are included after detailed comparison with Chl \( \alpha \) concentration and
PO\(^{14}\)CP rates. After the incubation period, dissolved oxygen concentration was determined following the method described above. Production and respiration rates were calculated from the difference between the means of the replicate light and dark incubated and zero time analyses: NCP = measured \(\Delta O_2\) in light bottles (mean of \([O_2]\) in 24-hr light − mean initial \([O_2]\)); DCR = measured \(\Delta O_2\) in dark bottles (mean initial \([O_2]\) − mean \([O_2]\) in 24-hr dark); GPP = NCP + DCR. Euphotic zone integrated values were obtained by trapezoidal integration of the volumetric data down to the depth of 1% surface incident irradiance. Following the method of Miller and Miller (1988), we calculated the standard deviation of integrated NCP through propagation of the random error in the volumetric measurements as 
\[
\sigma_{\text{integrated}} = \frac{1}{2} \sqrt{\frac{1}{\sum (z_{i+1} - z_i)^2 \left( \sigma_{z_{i+1}}^2 + \sigma_{z_i}^2 \right)}}
\]
where \(\sigma\) is the SD, \(z\) is the sampled depth, and \(i\) is the depth level. Euphotic depth ranged from ~30 m in the Benguela Current Coastal Province (BENG) to >100 m in the North Atlantic Subtropical Gyre.

Results

Individual data of temperature, salinity, dissolved oxygen, and Chl a concentrations, PO\(^{14}\)CP rates, percentage of PO\(^{14}\)CP by cells <2 µm, and GPP, DCR, and NCP rates at every sampled station are available in Web Appendix 1 on the L&O website at http://www.aslo.org/lo/toc/vol46/issue_7/1642a1.pdf.

Water column thermal structure—The spatial distribution of temperature (Fig. 2) reflects the hydrographic characteristics of the different provinces traversed during the cruise: BENG, Eastern Tropical Atlantic Province (ETRA), Eastern (Canary) Coastal Province (CNRY), North Atlantic Subtropical Gyral Province (NAST-E), and North Atlantic Drift Province (NADR) (Longhurst 1998), sampled during the spring-to-summer transition period.

In the southernmost part of the transect, the upwelling system in the BENG (~33°S–18°S) is shown by the tilting of the isotherms. Areas of intense upwelling, with surface temperature <15°C, were found close to areas of relaxed upwelling or convergence, which reflects the highly dynamic characteristics of this coastal regime (e.g., Luthjermans and Meeuwis 1987). A sharp hydrographic front, located at ~16°S–12°S, separated the mixed waters of the BENG from the strongly stratified waters of the ETRA. The Angola-Benguela Front (e.g., Shannon et al. 1987) is regarded as the convergence zone between the cold northward-flowing Benguela Current and the warm southward-flowing Angola Current. Several distinct hydrographic features can be seen in the ETRA (~10°S–11°N) (see Longhurst 1998; Stramma and Schott 1999; and references therein): in the tropical cyclonic Angola Gyre, centered ~8°S, a sharp and relatively shallow thermocline (~50 m) was observed. The depth of the middle thermocline (corresponding roughly to the 21°C isotherm) decreased from 50 to ~30 m at the equatorial divergence. North of the Equator (3°N), the northern tropical convergence lying between the South Equatorial Current and the North Equatorial Counter Current (Guinea Current) can be seen in the compression and deepening of the thermocline down to ~60 m depth. Further north, through the North Equatorial Counter Current, surface temperature and the depth of the thermocline progressively decreased, reaching the minimum at the Guinea Dome (at ~12°N). The relatively shallow thermocline throughout the ETRA (17°C isotherm above 65 m depth) is characteristic of this tropical area dur-
ing the southern autumn-winter, resulting from the intensification of the Trade Winds (Longhurst 1998 and references therein). To the north of the ETRA, the cruise track approached the northwestern African coast, entering the CNRY province (~15–23°N) (Longhurst 1998), where coastal upwelling was evident in both the tilting of the isotherms at 20°N and the spatial distribution of surface Chl a (see Fig. 1). Northward of ~23°N, as the track moved away from the African coast, the interface with the NAST-E province was identified by the spreading of the thermocline and the deepening of the upper mixed layer down to >100 m depth. A broad frontal zone north of ~37°N marked the transition from the NAST-E to the cooler and less saline waters of the NADR, where a shallower (<50 m) thermocline was observed. In the northernmost part of the transect (at ~48°N), the thermocline tilted at the European shelf break upwelling.

**Oxygen saturation and Chl a concentration**—Figure 3 shows the spatial variability of the percentage of oxygen saturation (%O₂ sat) and Chl a concentration along the AMT6 transect. The %O₂ sat in the upper ocean is a valuable tool for broadly summarizing the recent history of biological activity (e.g., Chapman and Shannon 1985; Najjar and Keeling 1997). High levels of O₂ sat (>105%) and Chl a (>1 mg m⁻²) were observed near the surface in both temperate waters and coastal upwelling systems (BENG and CNRY). The latter also exhibited low O₂ sat in subsurface waters, thereby causing the strong vertical oxygen gradients characteristic of these systems (Chapman and Shannon 1985). Some stations in the north BENG (e.g., ~25°S) and south of the CNRY presented subsurface Chl a maxima and very low levels of O₂ sat (<30%) in subsurface waters. The N BENG was the only region where O₂ sat <100% was found at the surface of strongly upwelled stations. The highest phytoplankton biomass was found at the northern end of this region, near the frontal zone between the BENG and ETRA. Both oligotrophic provinces (ETRA and NAST-E) exhibited low phytoplankton biomass, subsurface Chl a maxima (DCM), and %O₂ sat >100% through the surface mixed layer. The location of the DCM at the base of the euphotic layer and its Chl a concentration (~0.2–0.4 mg m⁻²) are characteristic of low latitudes in the Atlantic Ocean (e.g., Marañón et al. 2000 and references therein). Oxygen saturation did not show any relation to the DCM. Both the thermocline and the DCM were shallower in the ETRA, where strong vertical oxygen gradients were observed (<50% O₂ sat below the thermocline). The lowest deep oxygen content and highest Chl a concentration in this region were observed in the area of the Guinea Dome (Oudot 1989). North of ~25°N, a marked increase in deep oxygen content was observed.

**Total and size-fractionated particulate organic carbon production (PO¹⁴CP)**—The latitudinal distribution of total particulate primary production (Fig. 4) resembles that of Chl a, whereas the relative dominance of picoplankton (Fig. 5) tended to decrease with the productivity of the province. Higher values of PO¹⁴CP were measured in the Chl a-rich waters of the coastal upwelling regions of BENG and CNRY and in temperate waters. In the BENG and CNRY provinces, the highest PO¹⁴CP rates were always found near the surface at stations with low surface temperature and high surface Chl a concentration, whereas stations with relatively higher surface temperature and subsurface Chl a maxima (e.g., ~25°S) had low PO¹⁴CP rates throughout the water column. The contribution of picoplankton to total primary production was always very low in areas of high phytoplankton biomass, both at the surface productive and subsurface unproductive Chl a maxima. The ranges of both Chl a concentration (~55–150 mg m⁻²) and PO¹⁴CP rates (~0.3–3 g C m⁻² d⁻¹) measured in the BENG, as well as their distribution in relation to hydrographic conditions, are consistent with studies of the hydrodynamic control of phytoplankton patchiness and growth in this system (e.g., Shannon and Pillar 1986; Pitcher et al. 1992). Similarly, values measured at the CNRY stations (~0.4–2 mg Chl a m⁻³ in the surface; ~0.7–2.5 g C m⁻² d⁻¹) are representative of mesotrophic and eutrophic conditions, respectively, in this province (Morel et al. 1996).

Although in the northern ETRA, subsurface maxima of PO¹⁴CP were observed that corresponded to the vertical distribution of Chl a, south of the Equator, no increase in PO¹⁴CP rates was seen in relation to the DCM. In contrast
to upwelling provinces, in the ETRA, the relative contribution of picoplankton to total primary production increased with productivity and especially with phytoplankton biomass. In both the northern and southern part of the province, >60% of the primary production was attributable to cells <2 \( \mu \text{m} \) when Chl \( a \) concentration was >0.3 mg m\(^{-3}\). Throughout the ETRA, low levels of surface Chl \( a \) (~0.2 mg m\(^{-3}\)), relatively deep (~40 m) Chl \( a \) maxima, and low primary production (~40–350 mg C m\(^{-2}\) d\(^{-1}\)) suggest that our sampling occurred prior to the development of the characteristic summer pelagic bloom in this province (Longhurst 1998).

In the NAST-E, very low PO\(^{14}\)CP rates were measured, with values only exceeding 0.1 mg C m\(^{-2}\) h\(^{-1}\) near the surface and in deep waters (~60–110 m). The percentage of total primary production attributable to picoplankton increased with depth, reaching >70% in the DCM. Integrated values of PO\(^{14}\)CP of ~370 mg C m\(^{-2}\) d\(^{-1}\) were measured at stations near the boundaries of this province, whereas ~150 mg C m\(^{-2}\) d\(^{-1}\) characterized the stations with the deepest mixed layer and DCM. These values are within the range of those reported by Marañón et al. (2000) for this region and agree with those measured during the low production season at Bermuda (NAST-W) (Michaels and Knap 1996), being slightly lower than those reported by Morel et al. (1996) for the tropical northeast Atlantic at 20°N, 30°W.

PO\(^{14}\)CP rates increased in the NADR province, where, corresponding to the distribution of Chl \( a \), a subsurface production maximum was observed in the southernmost station, whereas higher surface rates were measured at the European shelf break. In this productive region, as in the BENG and CNRY upwellings, and contrary to the unproductive ETRA and NAST, the relative contribution of picoplankton to total primary production decreased with productivity.

**Plankton oxygen production and consumption**—The range of gross production of oxygen by phytoplankton (GPP) was
about four times that of DCR (Fig. 6A,B). GPP and DCR were not directly related, although both exhibited patterns related to the distribution of Chl a. High surface values of GPP were measured in surface Chl a-rich waters, but an increase of GPP at the DCM of oligotrophic provinces was only detected in the northern ETRA. A subsurface GPP maximum was also observed south of the CNRY upwelling region. On the contrary, the highest DCR rates were measured not in the most productive waters but in the low productive DCM observed at some stations of the BENG and CNRY upwellings. Throughout both oligotrophic provinces, and especially in the ETRA, relatively high DCR rates (>1 mmol O₂ m⁻³ d⁻¹) were measured in the unproductive, O₂-supersaturated waters of the upper mixed layer. In these provinces, no relationship was found between the vertical distribution of DCR rates and the DCM.

Figure 6C combines the balance between GPP and DCR (NCP) in the euphotic zone, together with DCR measurements below the 1% light level; i.e., under the assumption that GPP is negligible below the euphotic layer (hence NCP = -DCR), it depicts the spatial variability of NCP in the upper 200 m. Within the euphotic zone, NCP was only positive in the productive surface waters of the upwelling and frontal regions, which were rich in Chl a and supersaturated with respect to O₂, and where phytoplankton production was dominated by larger cells (>2 μm). As with GPP, the latitudinal variability of surface NCP was related to that of surface Chl a. In both oligotrophic provinces, NCP was consistently negative in the euphotic zone throughout the region. Higher negative values were found in the ETRA, where Chl a and PO₄CP were also higher (Figs. 1, 3B, and 4) and the thermocline shallower (Fig. 2). In the NAST-E province, positive NCP was only measured in the relatively productive surface waters of the stations sampled near its boundaries.

In productive provinces, higher NCP was usually found in areas of elevated %O₂ sat (see Figs. 3A and 6), despite the distributions of biomass and PO₄CP rates in these provinces being governed by the highly dynamic coastal upwellings and fronts (see above and, e.g., Pitcher et al. 1992). A similar trend exists in the spatial distribution of NCP and %O₂ sat in the upper 200 m. Such a correspondence suggests a tight and rapid recycling of the organic matter produced locally. This contrasts with the situation in oligotrophic provinces, where negative NCP was always measured together with O₂ supersaturation in the upper waters. A similar maintenance of O₂ supersaturation with net heterotrophy was observed in the euphotic zone of the stratified oligotrophic waters of the southern Bay of Biscay during the summer (Serret et al. 1999), which is consistent with a slow consumption of organic matter previously synthesized in the same water and highlights the differences in timescale of estimations of net community metabolism based on in vitro oxygen fluxes and in situ concentrations. In the ETRA region, where both NCP and the %O₂ sat exhibited stronger vertical gradients, not related to the subsurface Chl a maxima, an inverse relationship was found between these two variables.

Discussion

Data representativeness: the linkage between trophic dynamics and community structure—It is critical that the data used to derive meaningful GPP:CR relationships and to understand the functioning of an ecosystem, are representative of long-term averages (see Hairston and Hairston 1993). The biomass and activity of heterotrophs in a community are not only sustained by locally produced organic matter nor ex-
clusively controlled by substrate availability. Consequently, such activity is not always directly related to the concurrent activity of autotrophs (e.g., early or late spring bloom), and hence the relationship between GPP and CR in a transient community will not necessarily reflect the trophic dynamics of the ecosystem. Similarly, the relative abundance of the different species sharing an habitat at a certain time will not necessarily reflect the structure of the community or the organization of the food web. The obvious difficulty we face is the assessment of the representativeness of a set of instantaneous measurements without actually knowing the long term averages.

Various theoretical (e.g., Legendre and Lefevre 1991; Moloney and Field 1991; Kiørboe 1993) and field studies (e.g., Legendre et al. 1993; Nielsen and Hansen 1995; Pesant et al. 1998; Tamigneaux et al. 1999) have shown that the structure of a plankton community close to equilibrium can be predicted from the size distribution of phytoplankton. This occurs because, under equilibrium conditions, the factors regulating the relative growth and loss rates of the different populations (and hence also the net metabolism of the community)—i.e., competitive aptitude for nutrients and light uptake, sinking rate, predator-prey interactions, susceptibility to grazing control, and DOM exudation—are all dependent on cell size. A combination of the adequate representation of the structure of planktonic food webs by the size structure of phytoplankton and the existence of a link between community structure and food web fluxes in functional communities (e.g., Hairston and Hairston 1993) has enabled several conceptual models to relate the percentage of export (Legendre and Lefevre 1989; Tremblay and Legendre 1994; Legendre and Rassoulzadegan 1996; Boyd and Newton 1999) or new production (Tremblay et al. 1997) to the relative dominance of particular food webs. Predictions of these models have been frequently satisfied in the field (e.g., Heiskanen et al. 1996; Pesant et al. 1998; Tamigneaux et al. 1999; Pesant et al. 2000), except when the scale of study did not match that of the functioning of the ecosystem (e.g., Rivkin et al. 1996). Within this conceptual framework, but by simply reversing the logic, we have investigated the representativeness of our data set by analyzing the relation between community structure (as summarized by phytoplankton size) and ecological energetics (summarized by NCP) in our sampled communities.

The latitudinal variation of the euphotic zone integrated percentage of particulate carbon incorporated by phytoplankton <2 μm (%PO4CP < 2 μm) and integrated NCP shows a clear inverse relationship along the AMT-6 transect (Fig. 7A). Such a significant relationship is described by the equation (reduced major axis) NCP = -276.5 log (%PO4CP < 2 μm) + 972.9, r2 = 0.761, n = 21, P < 0.0001 (Fig. 7B). This relationship does not reveal whether community structure affects plankton GPP:CR balance, because that could simply result from the respective covariation of both NCP and phytoplankton size with total GPP. What such a strong relationship between trophic structure and functioning does suggest is that our data are representative of different ecological communities, and, specifically, that the plankton communities from oligotrophic and eutrophic provinces were functionally distinct. This is an important observation that will help us to interpret our results of community metabolism.

GPP : CR relationships: the influence of community structure—Because the derivation of GPP and CR from in situ changes in dissolved oxygen in this study is almost identical to that employed in Williams (1998), a direct comparison can be made, thus overcoming the interpretative problems associated with comparing different analytical methods (i.e., the 14C technique used in del Giorgio et al. 1997 and Duarte et al. 1999). Using the same method of data analysis as Williams (1998), we found that integrated DCR was remarkably constant over a range of integrated GPP of almost three orders of magnitude (Fig. 8A), which agrees with the results of del Giorgio et al. (1997) and supports their conclusion that microbial CR exceeds GPP in unproductive systems (see...
also Duarte et al. 1999). We found that, at integrated rates of GPP below ~100 mmol O$_2$ m$^{-2}$ d$^{-1}$, heterotrophy prevailed. This contrasts with the results of Williams (1998), who, from data collected from five open ocean regions derived the point of metabolic balance to be 16.7 mmol O$_2$ m$^{-2}$ d$^{-1}$. Figure 8A also shows that the constancy of integrated DCR only occurs through the sampling of both distinct eutrophic (black circles) and oligotrophic (open triangles and circles) communities, which suggests that our discrepancy with Williams (1998) may result from a different coverage of planktonic communities. Of the data sets examined by Williams (1998), only those from the North Pacific Central Gyre may be considered as representing real oligotrophic communities, but these were only 5 out of a total of 65 profiles used in the analysis.

Comparison of the low GPP parts of the integrated GPP: DCR plots in Williams (1998) and the present study confirms that such a discrepancy does not arise from the different range of GPP. Of his 33 stations with integrated GPP <100 mmol O$_2$ m$^{-2}$ d$^{-1}$ (range, ~25–100 mmol O$_2$ m$^{-2}$ d$^{-1}$) only 5 values of DCR were >100 mmol O$_2$ m$^{-2}$ d$^{-1}$, and the average DCR was ~55 mmol O$_2$ m$^{-2}$ d$^{-1}$ (Fig. 2a in Williams 1998). Conversely, in our data set, five out of a total of six stations within the same range of integrated GPP (25–100 mmol O$_2$ m$^{-2}$ d$^{-1}$) had integrated DCR >100 mmol O$_2$ m$^{-2}$ d$^{-1}$, and the average DCR was 141 ± 18 mmol O$_2$ m$^{-2}$ d$^{-1}$; the only station with DCR <100 mmol O$_2$ m$^{-2}$ d$^{-1}$ (GPP = 95 ± 8, DCR = 75 ± 6 mmol O$_2$ m$^{-2}$ d$^{-1}$) corresponded to the Benguela upwelling region. This observation is sustained when all our stations with GPP <100 mmol O$_2$ m$^{-2}$ d$^{-1}$ are considered: eight of nine stations had DCR >100 mmol O$_2$ m$^{-2}$ d$^{-1}$ (average DCR 146 ± 12 mmol O$_2$ m$^{-2}$ d$^{-1}$).

Williams (1998) found that the water-column integration of his volumetric data tended to move the GPP: DCR relationship toward the 1:1 line, whereas our data show exactly the opposite trend (Fig. 8A,B). The explanation given by Williams (1998) for the change in the slope between his volumetric and areal GPP: DCR relationships was the compensation of imbalances over the vertical profile, but in our data from oligotrophic provinces, heterotrophy prevailed throughout the water column (Figs. 6 and 8B). Although the ranges of volumetric GPP overlap between oligotrophic and eutrophic environments (Fig. 8B), vertical integration tends to segregate the values from the different regions (Fig. 8A). That is, volumetric data combines low GPP values from two very different origins: functionally oligotrophic communities and locally growth-limited eutrophic communities. In eutrophic regions, heterotrophic balances at some depths tend to be compensated by autotrophic balances at other depths (usually near the surface); thus, the integrated value tends toward metabolic balance (Williams 1998) (Fig. 8A). However, this does not occur in oligotrophic regions, so inclusion of data from oligotrophic communities in our analysis causes the observed constancy of integrated DCR.

Such imbalances in the ETRA and NAST require allochthonous supplies of organic matter. Various studies have shown a seasonal accumulation of dissolved organic carbon (DOC) in the upper waters of both open ocean (Hansell and Carlson 1998) and coastal ecosystems (Álvarez-Salgado et al. 2001). The possible fate for accumulated DOC is delayed local consumption, local downward export associated with winter convective mixing or horizontal transport, or a combination of any of these. Hence, within the winter mixed layer, there will be areas where or seasons when net consumption of allochthonous DOC must take place to enable the DOC concentrations to return to those present before the seasonal accumulation. Whenever such consumption occurs concurrently with low local primary production, a net heterotrophic metabolism can develop. Net heterotrophy measured during the summer in some temperate seas therefore has been explained as a result of the consumption during the oligotrophic season of DOC accumulated during the preceding spring bloom (Serret et al. 1999 and references therein).

Hansell and Carlson (1998) have shown that DOC accumulation at the BATS station in the Sargasso Sea (NAST-W) may reach 39%–70% of the spring bloom NCP; however, it is unlikely that organic matter locally accumulated in the unproductive NAST-E and ETRA can sustain the rates of net heterotrophy presented here. Nonetheless, Hansell et al. (1995) measured rates of DOC mineralization exceeding concurrent primary production rates in the Sargasso Sea and concluded that either GPP had been underestimated or that previously produced DOC was supporting periods of net heterotrophy in this region. Rates of DOC mineralization in the Sargasso Sea were ~0.45 mmol C m$^{-3}$ d$^{-1}$ (Hansell et al. 1995), whereas, following the method of Hansell and Carlson (1998), the net consumption of DOC in the upper 250 m of the BATS station after the 1995 spring bloom can be estimated to be ~0.2 mmol C m$^{-3}$ d$^{-1}$. These values represent ~45% and 20% of the negative NCP rates in the euphotic zone of the NAST-E presented here. In the Azores Front region, Doval et al. (2001) have measured rates of DOC accumulation in the upper 100 m during August 1998 of 0.47 mmol C m$^{-3}$ d$^{-1}$, i.e., ~50% of our negative NCP rates in the NAST-E. However, a significant contribution of photoheterotrophy to community metabolism, by reducing the respiratory energy requirements in bacterial DOM assimilation (Béja et al. 2000; Kolber et al. 2000), would further increase the demand of DOM in relation to our measurements of O$_2$ consumption. A lateral input of DOC to the eastern Atlantic from the neighboring upwelling system off the northwest African coast (Hansell and Carlson 1998; Álvarez-Salgado et al. 2001), aeolian inputs (Cornell et al. 1995), and possibly river discharge are also potentially important in the ETRA and NAST provinces. The limited quantitative information on these large-scale and episodic supply mechanisms means that it is difficult to completely account for the carbon demand required for the NCP data presented here.

**Plankton community structure influences net ecosystem metabolism: constraining the global estimation of NCP**—We have shown that volumetric and areal GPP: DCR relationships change when data from characteristic oligotrophic communities are included, irrespective of the ranges of GPP. We therefore suggest that community structure, and not only the amount of photosynthesis, influences the degree of heterotrophy of marine plankton ecosystems. Hypotheses derived from empirical relationships can only be tested through...
their predictions (e.g., Peters 1991). We have hence compared the predictive ability of the integrated GPP:CR empirical relationship presented here with that in Williams (1998). These two empirical relationships, which differ most in the range of communities sampled but not in the magnitude of GPP, are used to predict the behavior of systems environmentally similar but taxonomically, geographically, and temporally different from those included in either model derivation (Tom et al. 1990). Given that our empirical model is based on the large-scale spatial variability of NCP, its most rigorous test would be the prediction of the temporal variation of NCP at a single location (Burke et al. 1997). We have used data from the only comprehensive seasonal study of euphotic zone NCP found in the literature (Serret et al. 1999) (Fig. 9). The prediction of our model, derived from a wide range of distinct plankton communities, fairly reproduces the measured seasonal cycle of integrated NCP at three stations across the coastal transitional zone of the southern Bay of Biscay, and in particular, the characteristic spring-summer auto-heterotrophic transition. By contrast, the model based on a similar range of GPP, but a single type of community (Williams 1998), failed to predict any net heterotrophy throughout the entire seasonal cycle, even during the summer, when characteristic oligotrophic communities prevail in the region. Furthermore, a GPP:DCR relationship close to 1 : 1 (Williams 1998) would require disproportionately high values of GPP to justify the measured rates of NCP during, e.g., the northern Atlantic spring phytoplankton bloom (e.g., Kiddon et al. 1995; Serret et al. 1999). Following the empirical GPP:DCR relationship in Williams (1998), integrated rates of GPP close to 760 mmol O₂ m⁻² d⁻¹ (>9 g C m⁻² d⁻¹) would be necessary to sustain measured NCP rates of ~200 mmol O₂ m⁻² d⁻¹ (Serret et al. 1999).

We therefore suggest that food web fluxes can be predicted in pelagic ecosystems, despite their enormous taxonomic and functional complexity and diversity, only when proper consideration of the influence of community structure on trophic dynamics is made—that is, when the model used is derived from a representative range of community structures. This is consistent with analyses of the control of ecological efficiencies by trophic structure in freshwater and terrestrial ecosystems (Hairston and Hairston 1993) and with microcosm experiments that revealed an increase in decomposition rates with the complexity of aquatic microbial webs (McGrady-Steed et al. 1997; Petchey et al. 1999). Such a trophic constraint on empirical GPP:CR relationships may help us understand the functional relationship between food web organization and net metabolism in pelagic ecosystems and should be considered for interpretation of NCP predictions. Although our results indicate that net heterotrophy prevails where total GPP < ~100 mmol O₂ m⁻² d⁻¹ and the %PO₄:CP attributable to <2-μm cells exceeds 33%, they also highlight the difficulties in extrapolating observations beyond the studied range of pelagic ecosystems. This precludes an estimation of the metabolic balance of the global ocean from the empirical GPP:CR relationship presented here, which is based on a spring-summer sampling of systems located in either the marginal regions of the subtropical gyres or close (150–500 nm) to highly productive coastal provinces.

References


Primary productivity of reef-building crustose coralline algae

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Abstract

The primary productivity of four species of crustose coralline algae was measured as a function of depth (0–18 m) and irradiance on samples collected from and growing upon the windward coral reef at Lizard Island, northern Great Barrier Reef, Australia. Significantly higher productivities were measured in the field than in the laboratory. Maximum gross oxygen production in situ varied from 12.8 to 22.8 mmol m⁻² h⁻¹; dark respiration consumed between 2.7 and 4.5 mmol O₂ m⁻² h⁻¹. Integration of photosynthesis–irradiance models with half sine curve approximations of whole-day irradiance yielded estimated in situ net productivities of 15–132 mmol O₂ m⁻² d⁻¹. When multiplied by previously determined photosynthetic quotients, in situ net carbon fixation was estimated to vary from 0.2 to 1.3 g m⁻² d⁻¹. Multiplying these rates by measured surface relief factors of 3.1 for the reef crest and 5.0 for the windward slope yielded estimated contributions to reef organic production of ~0.9–5 g C (net) planar m⁻² d⁻¹ over the depth interval 0–18 m, given 100% cover. These data suggest that crustose coralline algae make a larger contribution to organic production on coral reefs than has been thought to this time. A curvilinear model is presented that enables their primary productivity to be estimated from measurements of in situ irradiance at the solar zenith.

Although it is recognized that crustose coralline algae may make a significant overall contribution to coral reef primary production by virtue of their high abundance, they are regarded as low rate producers of organic carbon (Larkum 1983). If this is true, it is surprising that some species are able to calcify their tissues at rates of up to 9.1 g CaCO₃ m⁻² d⁻¹ (Chisholm 2000), since this would require significant concomitant production of organic carbon. Given that specific rates of photosynthesis by crustose coralline algae have seldom been measured in the field and only once in a high-energy environment where conditions favor their development (Chisholm et al. 1990), it is possible that their organic productivity has been underestimated.

The organic productivity of crustose coralline algae is no less important to the maintenance of coral reefs than is their inorganic production, as the latter depends on the former. Calcification occurs within the cells walls of coralline algae and not externally, as in corals and other invertebrates; thus, photosynthesis creates the organic environment in which the calcite crystals are deposited. The rate at which coralline algae are able to bind loose substrata and provide protective barriers to bioerosion is therefore a function of their primary productivity.

Coralline algae are ubiquitous and often dominant components of coral reef communities (e.g., Littler 1973a; Stearn et al. 1977; Glynn et al. 1996; Keats et al. 1997), and their abundance in cryptic and shaded environments can be greatly underestimated (Littler 1973a). They also provide food for herbivores with hardened mouthparts (e.g., Steneck and Dethier 1994; Steneck 1997 and references given therein) and surfaces for settlement of invertebrate larvae (Ady 1998).

Analysis of how reefs will respond to major changes in the environment, such as increased ocean temperature or UV penetration, cannot be achieved without comprehensive data on their sources and sinks for organic carbon (Crossland et al. 1991 and references given therein). Estimation of the contributions made by different reef communities to whole-reef production and of coral reefs to global ocean production is complicated by a lack of data on the metabolic activity of outer reef slopes, which are thought to be zones of elevated production (Kinsey 1985; Crossland et al. 1991). Since productivity measurements cannot be accomplished on reef slopes using flow respirometry or open-top enclosures, the target organisms or communities must either be sampled and measured in the laboratory or examined in situ using incubation chambers (Chisholm 2000).

In order to estimate the organic productivity of crustose coralline algae on an outer reef slope, I measured their rates of oxygen production and consumption using laboratory- and field-based respirometers and converted the data into equivalent units of carbon using simultaneously determined metabolic quotients (Chisholm 2000). I selected four important reef-building species for study whose vertical distributions overlap on the windward reef at Lizard Island, northern Great Barrier Reef (GBR), Australia (14°40'S: 145°27'E) to encompass a total depth range of 0–18 m. I measured their laboratory productivities in late August through September 1985 and their in situ productivities between late March and early July 1986, thus 4–5 months before and 2–6 months after the sun passed overhead.

Methods

Samples—The samples selected for study comprised: Hydrolithon onkodes (Heydrich) Penrose and Woelkerling (for-
Crustose coralline productivity

formerly *Porolithon onkodes*) at depths of 0 and 2 m; *Neogoniolithon brassica-floridea* (Harvey) Satchell and Mason (formerly *Neogoniolithon fosliei*) at depths of 0, 3, and 6 m; *Hydrolithon reinboldii* (Weber van Bosse and Foslie) Foslie at depths of 3 and 6 m; and *Neogoniolithon conicum* (Dawson) Gordon, Masaki, and Akioka (formerly *Paragoniolithon conicum*) at depths of 0, 6, and 18 m. Crusts were selected at random at the given depth intervals, except when they were growing in locations too confined to sample or to measure in situ. Thus, crusts growing in cryptic or shaded environments were examined along with crusts on exposed reef surfaces.

**Laboratory respirometry**—Target crusts were located on the reef and tagged with colored ribbons to facilitate retrieval. The percentages of sea surface irradiance incident upon their upper surfaces at noon were determined under cloudless conditions using a pair of intercalibrated quantum sensors (Li-Cor 190SB and 192SB) connected to a light meter (Li-Cor 188B).

Crusts were bored to a depth of approximately 5 mm using a 17-mm internal diameter (ID) diamond-tipped core drill, driven by compressed air supplied from a SCUBA tank. The cores were left attached to the reef for at least 7 d to ensure repair of tissues cut by the core drill. Crusts were dislodged from the reef with a small chisel and carefully cleaned of noncoralline basal substratum using a grinding stone. Finally, the samples were transported to the laboratory and immersed for 30 min in filtered seawater (0.45-µm Milipore) containing 60 µg ml⁻¹ penicillin G and 100 µg ml⁻¹ streptomycin N (Commonwealth Serum Laboratories, Australia). The decision to pretreat with antibiotics resulted from pilot experiments that revealed a significant rise in respiration over the course of incubations. Extended tests revealed no significant alterations in the rates of photosynthesis or respiration after addition of the antibiotics.

Rates of O₂ production and consumption were determined in a clear acrylic, purpose-built incubation chamber (15-ml volume; Fig. 1a). The chamber possessed a circumferential jacket, through which water of constant temperature (25°C ± 0.1°C) was circulated. It also contained a port that traversed the water jacket for insertion of a sample holder or Li-190 SB quantum sensor. The sample holder was filled with soft wax (Tray Wax, Sybron Kerr) into which the sample was pressed and thus held stable in the path of a horizontal light beam in a manner that simulated attachment to the reef surface. The chamber was built to mate with an acrylic base-plate, containing a central polarographic O₂ electrode (Rank Bros. Pty. Ltd.). The electrode was connected via a signal amplifier to a chart recorder (Shimadzu R-112M) and calibrated daily in a saturated solution of Na₂SO₃ (zero O₂) and air-saturated seawater. The O₂ content of the air-saturated seawater was interpolated from the solubility tables of Carpenter (1966) under measured conditions of atmospheric pressure, salinity, and temperature and constant stirring.

Samples were irradiated with a 300 W quartz-halogen slide projector lamp. The lamp was fitted with a glass infrared heat filter to reduce heat output and to adjust the spectral distribution of the artificial illumination to better approximate that of sunlight in the shallow ocean. Irradiance was varied during experiments using neutral density filters. The irradiance transmitted by each of the filters was measured by inserting a Li-Cor 190SB sensor in place of the sample holder.

All measurements of photosynthesis were made between 0730 and 1800 h. Dark respiration was measured at the beginning, middle, and end of the light incubations. Incubation water volume was measured by tipping the contents of the chamber into a volumetric cylinder before removing the sample.

**In situ respirometry**—In situ samples were prepared by boring through crusts to a depth of 10–15 mm with a 36-mm ID diamond-tipped core drill. Small amounts of surrounding substratum were removed with a hammer and chisel to render the cores marginally proud of the surrounding reef surface. Tray Wax was smeared around their sides and stainless steel bands (316 Grade) were fitted so that their uppermost edges lay just beneath the pigmented layers of the crusts (see Chisholm et al. 1990; or Chisholm 2000). Crusts were then left undisturbed for 7–10 d.

A small, domed, UV-transparent, acrylic incubation chamber was fitted over the stainless steel band surrounding each coralline sample, and sensors were inserted through acrylic
fixtures bonded to the sidewall of the chamber (see Fig. 1b and Chisholm et al. 1990 for specifications). Rates of net photosynthesis and dark respiration were measured over 24 h with a galvanic oxygen electrode fitted with a long stirrer bar attachment (50 mm, Kent EIL). The stirrer bar attachment traversed the chamber and coupled magnetically with a motor-driven magnet that rotated in a stainless steel housing positioned diatomically opposite. Seawater temperature was measured to ±0.1°C with a thermistor encased in a stainless steel tube (Analog Devices AC2626K4). Irradiance was measured with an underwater quantum sensor (Li-192SB, Li-Cor, Ltd.), fitted inside a replica chamber mounted adjacent.

The O₂ electrode was calibrated at the temperature of the ocean before each experiment in air-saturated seawater and zeroed against a saturated solution of Na₂SO₄. The temperature sensor was calibrated against a quartz thermometer (±0.01°C, traceable to the National Bureau of Standards). The quantum sensor was calibrated underwater against a second, manufacturer-calibrated, Li-192SB sensor, connected to a light meter (Li-188B). A data logger, protected within a pressure-resistant housing, interrogated the sensors every 6 s and recorded their mean outputs at 1-min intervals. A centrifugal pump periodically pumped fresh seawater through the chamber for 3 min in every 18–30-min period.

After incubation, the sample was clipped from the reef and taken to the laboratory. Incubation water volume was determined by refilling the chamber with seawater, refitting the coralline sample and sensors, and then withdrawing one sensor to allow the seawater to run into a volumetric cylinder.

Data normalization—The surface areas of the samples were estimated using the foil skin technique of Marsh (1970).

Samples were then frozen in a vapor stream of dry ice (CO₂ at −32°C), crushed in a stainless steel percussion press that had been chilled to 4°C, and finally ground to a fine powder on ice. Non–water soluble pigments were extracted successively into three volumes (5 ml) of 20% tetrahydrofuran (THF) in methanol (MeOH). During extraction, samples were partially immersed in beakers containing ice-water slurry (0°C) and ultrasonicated for 5 min to assist release of membrane-bound pigment fractions. The extracts were centrifuged at 3,000 × g for 10 min at 4°C to separate solid and liquid phases. Absorbances of the liquid phases at 665 nm were determined immediately in a spectrophotometer (Hitachi U-3200). Chlorophyll a (Chl a) was quantified according to the method of Chalker and Dunlap (1982) using an extinction coefficient for Chl a at 665 nm (ε₆₆₅ a(CHL)) in 20% THF/MeOH of 77.015 L g⁻¹ cm⁻¹ (B. E. Chalker, Australian Institute of Marine Science, unpubl. data). The reliability of the resulting estimates of Chl a was checked by freeze-drying three THF/MeOH extracts, redissolving the residues in equivalent volumes of 90% acetone in water, and requantifying Chl a using the equation of Jeffrey and Humphrey (1975).

Examination of the quantities of Chl a extracted into successive volumes of THF/MeOH indicated contributions from at least two different sources. That is, Chl a did not extract exponentially, as in single-phase systems. Inspection of the samples revealed variable quantities of endolithic algae, predominantly cyanobacteria, in the skeletal carbonate below the living coralline layer.

Effort was made to quantify the amount of Chl a derived from endolithic algae by searching for specific accessory pigments that could be used as proxies for the associated Chl a. Pigments were extracted from samples of pure coralline tissue and pure endolithic algal tissue into 20% THF/MeOH. Pure coralline tissue was obtained by scraping the upper surfaces of coralline crusts with a scalpel in a cold room at −20°C. Pure endolithic algal samples were obtained by continuing this procedure after microscopic examination revealed no further traces of the red, phycoerythrin-containing cell layers of the coralline crusts. The two fractions were then crushed, ground, and extracted as before to remove Chl a and accessory pigments. Aliquots of the extracts were injected onto an RP-18 (Spheri-5, 25 cm) column and separated by solvent gradient HPLC using a Waters liquid chromatograph (ALC/GPC 204). Pigment fractions were detected by visible wavelength absorption at 436 nm (0.01 units full scale) using a Waters data module (730).

Data analysis—Rates of O₂ flux were plotted against irradiance and modeled using the general exponential function of Chalker (1980):

\[ \frac{\partial P}{\partial I} = \alpha(P_m^* - P) \left(1 + \frac{\epsilon P}{P_m^*}\right) + R \]  

where \( P_m^* \) is the maximal rate of gross photosynthesis; \( R \) (negative in sign) is the absolute rate of dark respiration; \( I_s \) is the irradiance at which the initial slope intercepts the horizontal asymptote; and \( \epsilon \) is the rate of transition from light-limited to light-saturated photosynthesis (i.e., the degree of curve inflexion). When \( \epsilon = -1 \), Eq. 1 integrates to the right-rectangular hyperbola:

\[ P = P_m^* \frac{I}{I_s + R} \]  

When \( \epsilon = 0 \), Eq. 1 integrates to a simple exponential function:

\[ P = P_m^*(1 - e^{-\eta I}) + R \]  

When \( \epsilon = 1 \), Eq. 1 integrates to the hyperbolic tangent function:

\[ P = P_m^* \tanh \frac{I}{I_s} + R \]  

For limits \(-1 < \epsilon < 1 \) and \( \epsilon \neq 0 \), Eq. 1 integrates to a general exponential function:

\[ P = P_m^* \left[ \frac{e^{\epsilon(I_s+\eta I)} - 1}{e^{\epsilon(I_s+\eta I)} + \epsilon} \right] + R \]

which can define any rate of curvature intermediate to those of the right-rectangular hyperbola and the hyperbolic tangent. Curves were fitted by the method of least squares (JMP v3 Statistics Made Visual, SAS Institute). When \( \epsilon \) converged upon an integer value characterizing Eqs. 2, 3, or 4 (−1, 0,
Crustose coralline productivity

Table 1. Percent coefficients of variation (=SD/mean × 100) for maximal rates of gross and net photosynthesis by coralline algae under laboratory and field conditions after normalization to different parameters.

<table>
<thead>
<tr>
<th></th>
<th>Planar area</th>
<th>Crust area</th>
<th>Chlorophyll a</th>
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<tr>
<td></td>
<td>$P_{g}$</td>
<td>$P_{n}$</td>
<td>$P_{g}$</td>
</tr>
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<td></td>
<td></td>
</tr>
<tr>
<td>H. onkodes</td>
<td>15.2</td>
<td>17.4</td>
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<tr>
<td>N. brassica-florida</td>
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<td>16.6</td>
<td>9.5</td>
</tr>
<tr>
<td>H. reinboldii</td>
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<td>13.2</td>
<td>9</td>
</tr>
<tr>
<td>N. conicum</td>
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<td>26.3</td>
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</tr>
<tr>
<td>Mean</td>
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<td>11.6</td>
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<tr>
<td>In situ</td>
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<tr>
<td>Mean</td>
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<tr>
<td>Grand mean</td>
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Results

Data normalization—The Chl a contents of samples calculated using the extinction coefficient of Chalker for Chl a in 20% THF/MeOH differed by less than 1% from the quantities calculated using the extinction coefficient and equation of Jeffrey and Humphrey (1975) for Chl a in 90% acetone, thus confirming the accuracy of Chalker's unpublished extinction coefficient.

Estimates of photosynthesis were least variable when data were normalized to crust surface area and most variable when normalized to Chl a (Table 1). The amount of Chl a extracted from the skeletal carbonate underlying the living coralline tissue represented a substantial proportion of the total Chl a (Table 2). Although extracts made from pure endolithic algal fractions contained several unidentified accessory pigments that did not occur in the coralline tissues, their concentrations relative to the associated Chl a were highly variable and thus could not be used to partition the chlorophyll sources (Fig. 2).

Microscopic examination of endolithic algal populations present in the core samples after staining with 1% acridine orange indicated that much of their Chl a was inactive; that is, it fluoresced pale orange, not deep red. This is consistent with the observation that the Chl a content of core samples is significantly lower than the Chl a content of coralline algae (Table 2). Although extracts made from pure endolithic algal fractions contained several unidentified accessory pigments that did not occur in the coralline tissues, their concentrations relative to the associated Chl a were highly variable and thus could not be used to partition the chlorophyll sources (Fig. 2).

Fig. 2. Example chromatograms of photosynthetic pigments extracted from coralline algae, whole core samples, and endolithic algae into THF/MeOH (20:80, v:v) and separated by gradient flow HPLC; shaded regions identify accessory pigments unique to endolithic fractions.
with the very low rates of photosynthesis that have been reported for endolithic algae, in spite of their high Chl $a$ contents (Hawkins and Lewis 1982). Indeed, rates of photosynthesis by endolithic algae present in cores from which the living coralline tissue had been removed were only just sufficient to compensate for respiratory consumption at the highest light levels applied during treatments. These data presumably explain why Chl $a$ proved to be a poor standard for photosynthetic rate, and they indicate that assimilation numbers for coralline algae, if calculated, would be erroneously low. For this reason, rates of photosynthesis are not given per unit of Chl $a$.

**Laboratory respirometry—**$P-I$ curves were fitted to individual sample data sets with coefficients of determination ($r^2$) of 0.99–1.00. Between the limits of −1 and 1, $e$ tended to become more positive with increasing depth and decreasing irradiance, indicating increased rates of transition from light-limited to light-saturated photosynthesis (Fig. 3). In two of the four species, $e$ varied inversely with the natural logarithms of the precollection percentages of surface irradiance at their surfaces when the sun was at its zenith (Fig. 4). Maximum noontime irradiance varied from 1,689 µmol m$^{-2}$ s$^{-1}$ at 0 m to 35 µmol m$^{-2}$ s$^{-1}$ at 18 m.

Mean rates of maximal gross oxygen production varied from 7.9 to 20 mmol m$^{-2}$ h$^{-1}$ (Table 3). Mean rates of dark oxygen consumption varied from 1.9 to 4.6 mmol m$^{-2}$ h$^{-1}$ (Table 3). Maximum net oxygen production varied from 6 to 15 mmol m$^{-2}$ h$^{-1}$ (Table 3). Mean ratios of maximal gross photosynthesis to dark respiration varied from 3.2:1 to 5.4:1 (Table 3).

Multiplication of daytime oxygen data by photosynthetic quotients of the four species and nighttime data by their reciprocals provided mean estimates of maximal gross C fixation that ranged from 0.11 to 0.23 g m$^{-2}$ h$^{-1}$, dark C consumption that ranged from 0.02 to 0.05 g m$^{-2}$ h$^{-1}$, and net C production that ranged from 0.09 to 0.19 g m$^{-2}$ h$^{-1}$, dark C consumption that ranged from 0.02 to 0.06 g m$^{-2}$ h$^{-1}$, and maximal net C production that ranged from 0.07 to 0.15 g m$^{-2}$ h$^{-1}$.

Integration of the $P-I$ equations with half sine curve approximations of daily irradiance indicated that the coralline species could increase their mean organic C biomass by 0.12–1.2 g m$^{-2}$ d$^{-1}$, on average (Table 4). Multiplying the rates given in Table 4 by surface relief factors of 3.1 for the reef crest and 5.0 for the reef slope at Lizard Island (Chisholm 2000) indicates planar area productivities of 2–4 g C m$^{-2}$ d$^{-1}$ on the crest and 0.6–4 g C m$^{-2}$ d$^{-1}$ on the slope, given 100% cover.

**In situ respirometry—**Seawater temperature inside the specimen chamber varied from 30°C to 23°C over the course of experiments and by up to ±0.7°C during any single incubation. Maximum noontime irradiance varied from 1,516 µmol m$^{-2}$ s$^{-1}$ at 0 m to 30 µmol m$^{-2}$ s$^{-1}$ at 18 m.

$P-I$ curves were fitted to individual sample data with coefficients of determination ($r^2$) of 0.92–1.00. Full light-saturation of photosynthesis was uncommon, even among reef crest samples, and the $P-I$ responses of crusts in low-light environments were often nearly linear (Fig. 5). There was little difference in the fitting power of the various $P-I$ models (Eqs. 2–5) due to variability in the data.

Mean rates of maximal gross oxygen production varied from 12 to 23 mmol m$^{-2}$ h$^{-1}$ (Table 3). Mean rates of dark oxygen consumption varied from 2.7 to 4.5 mmol m$^{-2}$ h$^{-1}$ (Table 3). Maximum net oxygen production varied from 9.1 to 20 mmol m$^{-2}$ h$^{-1}$ (Table 3). Mean ratios of maximal gross photosynthesis to dark respiration varied from 4.5:1 to 7:1 (Table 3).

Estimates of maximal gross and net oxygen production, dark respiration, and the irradiance required for the onset of saturation ($I_0$) were in almost all instances significantly higher in situ than in the laboratory (Table 5); the mean differences were 52%, 54%, 26%, and 37%, respectively (Table 3). The differences tended to be less pronounced among reef crest samples. Although in situ samples exhibited larger values for $I_0$, they were not necessarily acclimated to higher incident irradiance (Table 4). Lower rates of dark respiration in the laboratory were likely due, at least in part, to suppression of bacterial respiration by treatment with antibiotics.

Multiplication of daytime oxygen data by the photosynthetic quotients of the four species and nighttime data by their reciprocals provided mean estimates of maximal gross C fixation that ranged from 0.03 to 2.1 g m$^{-2}$ h$^{-1}$, dark C consumption that ranged from 0.02 to 0.05 g m$^{-2}$ h$^{-1}$, and net C production that ranged from 0.09 to 0.18 g m$^{-2}$ h$^{-1}$.

Integration of the $P-I$ equations with half sine curve approximations of daily irradiance indicated that the coralline species could increase their mean organic C biomass by 0.17–1.3 g m$^{-2}$ d$^{-1}$ (Table 4). Multiplying the rates given in Table 4 by surface relief factors of 3.1 for the reef crest and 5.0 for the reef slope indicates planar area productivities of 3–4 g C m$^{-2}$ d$^{-1}$ on the crest and 0.9–5 g C m$^{-2}$ d$^{-1}$ on the slope, given 100% cover. The rates of net 24-h C fixation for the four species varied curvilinearly with noontime irradiance (Fig. 6).

**Discussion**

Under tightly controlled irradiance and temperature, inverse relationships were observed in two of the four species between the rates of $P-I$ curve inflexion and the natural logarithms of the percentages of surface irradiance upon the samples when the sun was at its zenith. Some species therefore reduce the optical thickness of their photosynthetic layers as the seawater column attenuates light, just as terrestrial plants adjust the thickness of their leaves beneath shade canopies (Arnold and Murray 1980; Littler 1980). The physical support provided by cell wall calcification presumably allows coralline algae to develop extremely thin tissues to complement their green light harvesting capacity, thus enabling them to live at extreme depths in the water column (Littler and Littler 1985).

Rates of photosynthesis were significantly lower in the laboratory than in situ. The differences were most likely due to either seasonal adjustment of the photosynthetic apparatus or to detachment of crusts from the reef matrix. It is unlikely that chance was responsible for the differences, as in situ
Crustose coralline productivity

Fig. 3. Mean P-I curves for samples of *Hydrolithon reinboldii* and *Neogoniolithon brassica-florida* in the laboratory, modeled using the right-rectangular hyperbola ($e = -1$); a simple exponential function ($e = 0$); the hyperbolic tangent function ($e = 1$); and a general exponential function (noninteger values between $-1$ and 1). Error bars are 95% confidence intervals. Inserts expand the regions of curve inflexion to illustrate differences in the fitting power of the models, whereby the hyperbolic tangent simulates the fastest rate of transition from light-limited to light-saturated photosynthesis, the right-rectangular hyperbola simulates the slowest, the simple exponential function simulates an intermediate rate, and the general exponential function simulates all other intervening rates. When only three curves are shown, the general exponential model was not fitted because $e$ converged upon an integer value characteristic of one of the three-parameter models. The value shown for $e$ in the insert indicates the model that most accurately described the data.

Rates were higher in every comparable instance (Table 6). Suppression of cyanobacterial metabolism via antibiotic treatment also appears an unlikely explanation for the inferior rates of productivity in the laboratory, since tests demonstrated that core samples lacking coralline tissue exhibited maximum rates of photosynthesis that were only just sufficient to compensate for respiratory consumption. Equally, inadequate simulation of the spectral distribution of light to which samples had become adapted does not explain the lower photosynthetic capacities of laboratory samples, since
they received sufficient white light to fully saturate their photosynthetic apparatus (Fig. 3). The lower values for \( I_s \) among laboratory samples might, nonetheless, indicate differences in their seasonally adapted states relating to measurement before the austral summer, or they may have become light saturated at lower irradiance due to a supply of greater amounts of red light than are available at depth in the seawater column.

Seasonal considerations aside, it is significant that all species except for *Hydrolithon onkodes*, which shows a marked preference for high light and shallow water (e.g., Littler 1973a; Hawkins and Lewis 1982), exhibited higher rates of primary production in situ than have been reported in simulated in situ studies (Table 6). It would be interesting to investigate whether coralline production is supported by nutrients (and/or CO\(_2\)) diffusing out of reef pore waters (see Rougerie and Wauthy 1988) or fixed by cyanobacteria resident in the underlying reef carbonate, since the enhanced growth of coralline algae near sewage outlets suggests that they may be strongly nutrient limited in the open ocean (Littler 1973a; Kindig and Littler 1980; Littler et al. 1991).

The net productivities of coral reef plant communities have been estimated as follows: benthic fleshy algae 0.1-4 g C m\(^{-2}\) d\(^{-1}\); phytoplankton 0.1-0.5 g C m\(^{-2}\) d\(^{-1}\); sand algae 0.1-0.5 g C m\(^{-2}\) d\(^{-1}\); sea grasses 1-7 g C m\(^{-2}\) d\(^{-1}\); turf algae 1-6 g C m\(^{-2}\) d\(^{-1}\); and zooxanthellae 0.6 g C m\(^{-2}\) d\(^{-1}\) (Larkum 1983). After adjustment for reef surface relief, the rates reported here for coralline algae of 0.9-5 g C m\(^{-2}\) d\(^{-1}\) equate with the rates given for fleshy and turf algae. Without adjustment for surface relief, coralline algae have similar net productivities (0.17-1.3 g C m\(^{-2}\) d\(^{-1}\)) to turf-dominated epilithic algal communities growing upon coral settlement plates in the central GBR (0.06-1.26 g C m\(^{-2}\) d\(^{-1}\), Klumpp and McKinnon 1989).

It is estimated that highly productive coral reef flats fix C  

### Table 3. Parameters describing the P-I curves of crustose coralline samples in the laboratory and in situ. 

<table>
<thead>
<tr>
<th>Species</th>
<th>Depth (m)</th>
<th>N</th>
<th>n</th>
<th>( P_{lb} ) (mmol O(_2) m(^{-2}) h(^{-1}))</th>
<th>( P_{ln} ) (mmol O(_2) m(^{-2}) h(^{-1}))</th>
<th>( R ) (( \mu )mol m(^{-2}) s(^{-1}))</th>
<th>( I_s ) (( \mu )mol m(^{-2}) s(^{-1}))</th>
<th>( P_{lb}/R )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Laboratory</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>H. onkodes</em></td>
<td>0</td>
<td>6</td>
<td>6</td>
<td>19.5 (4.9)</td>
<td>14.9 (4.1)</td>
<td>4.6 (1.2)</td>
<td>124</td>
<td>4.3</td>
</tr>
<tr>
<td><em>N. brassica-florida</em></td>
<td>0</td>
<td>4</td>
<td>4</td>
<td>14.4 (1.4)</td>
<td>10.1 (1.2)</td>
<td>4.5 (0.7)</td>
<td>85</td>
<td>3.2</td>
</tr>
<tr>
<td><em>N. conicum</em></td>
<td>0</td>
<td>5</td>
<td>5</td>
<td>13.2 (3.2)</td>
<td>10.1 (3.0)</td>
<td>3.1 (0.5)</td>
<td>84</td>
<td>4.2</td>
</tr>
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<td><em>H. reinboldii</em></td>
<td>0</td>
<td>5</td>
<td>5</td>
<td>14.2 (1.1)</td>
<td>9.7 (2.0)</td>
<td>4.5 (1.0)</td>
<td>59</td>
<td>3.2</td>
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<tr>
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<td>3</td>
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<td>4</td>
<td>15.6 (0.6)</td>
<td>11.9 (0.7)</td>
<td>3.6 (0.5)</td>
<td>85</td>
<td>4.3</td>
</tr>
<tr>
<td><em>N. brassica-florida</em></td>
<td>3</td>
<td>4</td>
<td>4</td>
<td>11.9 (2.4)</td>
<td>8.5 (2.2)</td>
<td>3.4 (0.4)</td>
<td>57</td>
<td>3.5</td>
</tr>
<tr>
<td><em>H. reinboldii</em></td>
<td>3</td>
<td>4</td>
<td>4</td>
<td>12.5 (3.0)</td>
<td>9.9 (2.2)</td>
<td>2.6 (1.0)</td>
<td>59</td>
<td>4.8</td>
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<td><em>N. brassica-florida</em></td>
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<td>5</td>
<td>5</td>
<td>11.4 (1.3)</td>
<td>8.9 (1.2)</td>
<td>2.6 (0.3)</td>
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<td>5</td>
<td>9.8 (3.0)</td>
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<td>2.4 (0.4)</td>
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<td>4.2</td>
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<tr>
<td><em>H. reinboldii</em></td>
<td>6</td>
<td>4</td>
<td>4</td>
<td>11.3 (0.9)</td>
<td>9.2 (1.3)</td>
<td>2.1 (0.5)</td>
<td>63</td>
<td>5.4</td>
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<td>18</td>
<td>5</td>
<td>5</td>
<td>7.9 (1.1)</td>
<td>6.0 (1.3)</td>
<td>1.9 (0.3)</td>
<td>31</td>
<td>4.1</td>
</tr>
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<td>In situ</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>H. onkodes</em></td>
<td>0</td>
<td>5</td>
<td>5</td>
<td>22.8 (2.7)</td>
<td>18.4 (2.7)</td>
<td>4.5 (0.4)</td>
<td>205</td>
<td>5.1</td>
</tr>
<tr>
<td><em>N. brassica-florida</em></td>
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<td>4</td>
<td>4</td>
<td>18.4 (1.6)</td>
<td>14.6 (1.8)</td>
<td>3.9 (0.6)</td>
<td>157</td>
<td>4.8</td>
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<td><em>N. conicum</em></td>
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<td>4</td>
<td>19.6 (2.1)</td>
<td>15.3 (1.6)</td>
<td>4.3 (0.5)</td>
<td>85</td>
<td>4.6</td>
</tr>
<tr>
<td><em>H. onkodes</em></td>
<td>2</td>
<td>4</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>3</td>
<td>4</td>
<td>4</td>
<td>21.1 (3.6)</td>
<td>16.6 (3.2)</td>
<td>4.5 (0.5)</td>
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<td>4.7</td>
</tr>
<tr>
<td><em>H. reinboldii</em></td>
<td>3</td>
<td>4</td>
<td>4</td>
<td>20.1 (2.7)</td>
<td>16.5 (3.1)</td>
<td>4.2 (0.8)</td>
<td>129</td>
<td>5.0</td>
</tr>
<tr>
<td><em>N. brassica-florida</em></td>
<td>6</td>
<td>4</td>
<td>4</td>
<td>12.1 (1.8)</td>
<td>9.1 (2.4)</td>
<td>2.7 (0.8)</td>
<td>68</td>
<td>4.5</td>
</tr>
<tr>
<td><em>N. conicum</em></td>
<td>6</td>
<td>4</td>
<td>2</td>
<td>16.7 (0.6)</td>
<td>13.8 (0.7)</td>
<td>2.9 (0.7)</td>
<td>65</td>
<td>5.8</td>
</tr>
<tr>
<td><em>H. reinboldii</em></td>
<td>6</td>
<td>4</td>
<td>4</td>
<td>22.8 (1.4)</td>
<td>19.6 (1.3)</td>
<td>3.3 (0.3)</td>
<td>117</td>
<td>7.0</td>
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<tr>
<td><em>N. conicum</em></td>
<td>18</td>
<td>4</td>
<td>2</td>
<td>12.8 (0.7)</td>
<td>10.0 (1.6)</td>
<td>2.7 (0.3)</td>
<td>52</td>
<td>4.7</td>
</tr>
</tbody>
</table>
Crustose coralline productivity

Table 4. Estimated production and consumption of organic carbon by crustose coralline algae over 24 h based on laboratory and in situ measurements; rates are means of \( n \) samples; half 95% confidence intervals in parentheses; \( I_{\text{max}} \), the irradiance incident upon the coralline samples at noon.

<table>
<thead>
<tr>
<th>Species</th>
<th>Depth (m)</th>
<th>( n )</th>
<th>( P_{\text{u}} ) (g C m(^{-2}) d(^{-1}))</th>
<th>( P_{\text{b}} ) (g C m(^{-2}) d(^{-1}))</th>
<th>( -R ) (( \mu )mol m(^{-2}) s(^{-1}))</th>
<th>( I_{\text{max}} ) (( \mu )mol m(^{-2}) s(^{-1}))</th>
</tr>
</thead>
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<tr>
<td>( \text{Laboratory} )</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( H. onkodes )</td>
<td>0, 4</td>
<td>6</td>
<td>2.31 (0.41)</td>
<td>1.21 (0.35)</td>
<td>1.1 (0.19)</td>
<td>1,689</td>
</tr>
<tr>
<td>( N. brassica-florida )</td>
<td>0, 5</td>
<td>4</td>
<td>1.68 (0.1)</td>
<td>0.66 (0.12)</td>
<td>1.02 (0.1)</td>
<td>1,683</td>
</tr>
<tr>
<td>( N. conicum )</td>
<td>0, 5</td>
<td>5</td>
<td>1.78 (0.27)</td>
<td>0.93 (0.22)</td>
<td>0.84 (0.08)</td>
<td>1,629-1,633</td>
</tr>
<tr>
<td>( H. reinboldii )</td>
<td>0, 5</td>
<td>5</td>
<td>1.55 (0.07)</td>
<td>0.56 (0.21)</td>
<td>0.99 (0.14)</td>
<td>1,636-1,638</td>
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<tr>
<td>( H. onkodes )</td>
<td>3, 4</td>
<td>4</td>
<td>1.69 (0.17)</td>
<td>0.82 (0.21)</td>
<td>0.86 (0.07)</td>
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<td>3, 4</td>
<td>4</td>
<td>1.27 (0.26)</td>
<td>0.49 (0.24)</td>
<td>0.78 (0.06)</td>
<td>130-864</td>
</tr>
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<td>( H. reinboldii )</td>
<td>3, 4</td>
<td>4</td>
<td>1.33 (0.19)</td>
<td>0.76 (0.12)</td>
<td>0.57 (0.14)</td>
<td>389-974</td>
</tr>
<tr>
<td>( N. brassica-florida )</td>
<td>6, 5</td>
<td>5</td>
<td>1.25 (0.1)</td>
<td>0.67 (0.07)</td>
<td>0.58 (0.05)</td>
<td>170-535</td>
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<tr>
<td>( N. conicum )</td>
<td>6, 5</td>
<td>5</td>
<td>0.73 (0.02)</td>
<td>0.12 (0.7)</td>
<td>0.64 (0.06)</td>
<td>43-107</td>
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<tr>
<td>( H. reinboldii )</td>
<td>6, 4</td>
<td>5</td>
<td>0.77 (0.26)</td>
<td>0.32 (0.3)</td>
<td>0.45 (0.06)</td>
<td>43-234</td>
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<td>( N. brassica-florida )</td>
<td>6, 4</td>
<td>4</td>
<td>0.69 (0.09)</td>
<td>0.16 (0.09)</td>
<td>0.53 (0.04)</td>
<td>35-129</td>
</tr>
<tr>
<td>( \text{In situ} )</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( H. onkodes )</td>
<td>0, 5</td>
<td>5</td>
<td>2.37 (0.09)</td>
<td>1.31 (0.11)</td>
<td>1.06 (0.08)</td>
<td>1,441-1,516</td>
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<tr>
<td>( N. brassica-florida )</td>
<td>0, 4</td>
<td>4</td>
<td>1.82 (0.14)</td>
<td>0.94 (0.25)</td>
<td>0.88 (0.15)</td>
<td>1,347-1,359</td>
</tr>
<tr>
<td>( N. conicum )</td>
<td>0, 4</td>
<td>4</td>
<td>2.33 (0.22)</td>
<td>1.18 (0.09)</td>
<td>1.15 (0.15)</td>
<td>1,250-1,257</td>
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<td>2, 4</td>
<td>4</td>
<td>1.12 (0.24)</td>
<td>0.35 (0.3)</td>
<td>0.77 (0.09)</td>
<td>50-120</td>
</tr>
<tr>
<td>( N. brassica-florida )</td>
<td>3, 4</td>
<td>4</td>
<td>1.95 (0.45)</td>
<td>0.95 (0.42)</td>
<td>1.02 (0.11)</td>
<td>650-1,130</td>
</tr>
<tr>
<td>( H. reinboldii )</td>
<td>3, 4</td>
<td>4</td>
<td>1.74 (0.09)</td>
<td>0.83 (0.24)</td>
<td>0.9 (0.17)</td>
<td>615-1,000</td>
</tr>
<tr>
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<td>6, 4</td>
<td>4</td>
<td>1.0 (0.1)</td>
<td>0.43 (0.16)</td>
<td>0.57 (0.14)</td>
<td>70-390</td>
</tr>
<tr>
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<td>6, 4</td>
<td>4</td>
<td>1.44 (0.21)</td>
<td>0.66 (0.16)</td>
<td>0.78 (0.19)</td>
<td>130-550</td>
</tr>
<tr>
<td>( H. reinboldii )</td>
<td>6, 4</td>
<td>4</td>
<td>1.58 (0.33)</td>
<td>0.87 (0.31)</td>
<td>0.71 (0.07)</td>
<td>54-355</td>
</tr>
<tr>
<td>( N. conicum )</td>
<td>18, 4</td>
<td>5</td>
<td>0.9 (0.17)</td>
<td>0.17 (0.12)</td>
<td>0.73 (0.08)</td>
<td>30-80</td>
</tr>
</tbody>
</table>

At gross rates of close to 7 g m\(^{-2}\) d\(^{-1}\) (Kinsey 1985), with whole reefs averaging around 3 g m\(^{-2}\) d\(^{-1}\) (Crossland et al. 1991). At a gross production rate of 6.9 g C m\(^{-2}\) d\(^{-1}\), given 100% cover and a surface relief factor of 5, the coralline algae investigated here could substitute for the high rate category. At a more moderate cover of around 40% (e.g., Stearn et al. 1977), they could account for the average productivity of whole reefs.

Although coralline algae are often dominant components of Caribbean and Indian Ocean reefs and can attain surface...
covers approaching 100% on true algal crests and exposed oceanic reef margins, it would be unrealistic to suggest that their average global cover is anywhere near this level. Also, in areas where they do cover 90%-100% of the reef, surface relief factors of five are abnormal. Thus, when I have given in areas when they do cover 90%-100% of the reef, surface oceanic reef margins, it would be unrealistic to suggest that covers approaching 100% on true algal crests and exposed differences between the group means for location X depth x species interactions; ns, nonsignificant.

### Table 5. Statistical comparison of parameters describing the P-I curves of coralline algae in situ and in the laboratory (LSD test; α = 0.05), after confirmation of normality and variance homogeneity and three-way ANOVA (F_{1,47} = 22.6, p < 0.00005); probabilities are for differences between the group means for location X depth X species interactions; ns, nonsignificant.

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>Species</th>
<th>( P_g )</th>
<th>( P_m )</th>
<th>(-R)</th>
<th>( I_a )</th>
</tr>
</thead>
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<tr>
<td>0</td>
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<td>&lt;0.05</td>
<td>&lt;0.05</td>
<td>ns</td>
<td>&lt;0.000001</td>
</tr>
<tr>
<td></td>
<td>N. brassica-florida</td>
<td>&lt;0.05</td>
<td>&lt;0.01</td>
<td>ns</td>
<td>&lt;0.000001</td>
</tr>
<tr>
<td></td>
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<td>&lt;0.00005</td>
<td>&lt;0.005</td>
<td>&lt;0.01</td>
<td>ns</td>
</tr>
<tr>
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<td>&lt;0.000001</td>
<td>&lt;0.05</td>
<td>&lt;0.000001</td>
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<tr>
<td></td>
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<td>&lt;0.000001</td>
<td>&lt;0.05</td>
<td>&lt;0.000005</td>
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<td>&lt;0.000001</td>
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<td>&lt;0.0005</td>
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<tr>
<td></td>
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<td>&lt;0.0005</td>
<td>ns</td>
<td>&lt;0.05</td>
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</tbody>
</table>

Even with regular flushing, samples experience abnormal excursions from normal seawater \([O_2], [CO_2]\), and pH, and when confined within chambers they are not continuously influenced, to their benefit or detriment, by chemical changes produced by the surrounding benthos (see McConnaughey et al. 2000; Small and Adey 2001). In spite of these deficiencies, rates greatly above those presented here do not appear to be the norm in open reef environments (Kinsey 1985) or in coral reef microcosms (Griffith et al. 1987; Atkinson et al. 1999).

R. Steneck very generously provided me with recent and as yet unpublished estimates of crustose coralline cover on reefs in the GBR, Palau, and Guam; they vary from around 10% to 30% (pers. comm.). These estimates are higher than McLanahan (1997) obtained on a fringing reef in Kenya (0.1%-18.3%), lower than Little (1971) reported for a fringing reef in Hawaii using line transect and photographic methods (mean estimates of 31.9% and 45.6% cover, respectively), and far below what can be observed on true algal ridges in the Caribbean and on Pacific atoll rims (e.g., Adey 1975; Steneck and Adey 1976; Andréfotiet et al. pers. comm.).

Steneck derived his estimates from line transects by measuring the uppermost species cover. Multiplying the mean gross production rate obtained here for the four species on the windward reef slope at Lizard Island of 1.4 g C m\(^{-2}\) d\(^{-1}\) (data for in situ samples in Table 4, averaged over the interval 2–18 m) by Steneck’s estimates yields rates of 0.1–0.4 g C m\(^{-2}\) crust d\(^{-1}\) and 0.7–2 g C m\(^{-2}\) planar d\(^{-1}\). The latter rates thus represent 23%–67% of the estimate of Crossland et al. (1991) for average whole-reef gross production.

However, coralline cover beneath coral canopies and in crevices was not included in Steneck’s survey. This cover can be considerable on oceanic reef margins (pers. obs.). Although the average productivity of heavily shaded corallines will be lower, it will not be negligible. Also, as light is more strongly attenuated by the water column at Lizard Island, a midshelf reef system, than by the open ocean, the rates of production given here are likely lower than would be measured at equivalent depths on barrier and atoll reef systems. When all of these factors are taken into account, it would appear that crustose coralline algae are not low rate producers of organic carbon. Given their abundance on coral reefs, the conclusion of Larkum (1983) that coralline algae

![Graph](image-url)
could make a significant contribution to overall production appears to be well supported.

Larkum (1983) proposes that 8 g C m⁻² d⁻¹ is the maximum sustainable limit to net primary production on coral reefs, which is equivalent to a gross productivity of 12 g C m⁻² d⁻¹ according to Kinsey (1985). Kinsey (1985) argues against Larkum’s theoretical limit on the basis of a few higher rate measurements, made over extended periods: 17 g C m⁻² d⁻¹ on a coral shoal in the Houtman Abrolhos reefs (Smith 1981) and 30 g C m⁻² d⁻¹ on an inner reef flat at St. Croix (Adley 1983; Adley and Steneck 1985). Kinsey’s arguments may be justified because data are almost entirely lacking for outer reef slopes, which frequently have high living cover, complex three-dimensional structures, and higher rates of water advection, mixing, and nutrient supply than other reef zones (Smith 1981; Kinsey 1985). The outer slopes of barrier reefs on the GBR regularly have high cover of coralline algae beneath canopies of branching corals; thus, total live cover can significantly exceed 100% on a projected area basis (pers. obs.). Coralline algae could contribute up to half of the suggested maximum sustainable gross production (12 g C m⁻² d⁻¹) at 70%–85% cover on a reef slope with high surface relief. When combined with coral production, it would not be surprising to find rates in excess of the

### Table 6. Reported mean rates of maximal gross and net photosynthesis by tropical coralline algae, including data given here (in situ rates in bold text), in descending order with priority given to net production. In this study, planar area rates are for planar areas of crust, rather than for planar areas of reef, since the rates were calculated by scaling up from the cross-sectional areas of the core samples (i.e., from 7πr²), which exhibited comparatively little variation in surface topography (maximum real area: projected area ratio of 1.4:1). Empty cells indicate rates not provided or incalculable from the information given. Note that *Hydrolithon onkodes*, *Hydrolithon gardineri*, *Neogoniolithon brassica-floride*, and *Neogoniolithon conicum* may be better known by their former names of *Porolithon onkodes*, *Porolithon gardineri*, *Neogoniolithon fosilii*, and *Paragoniolithon conicum*, respectively (see Chisholm 2000 for references to taxonomic revisions).

<table>
<thead>
<tr>
<th>Source</th>
<th>Species</th>
<th>Depth (m)</th>
<th>n</th>
<th>Max. photosynthesis (mg O₂ m⁻² h⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Net Crust Planar Gross Crust Planar</td>
</tr>
<tr>
<td><strong>In situ</strong></td>
<td><em>Hydrolithon reinboldii</em></td>
<td>6</td>
<td>4</td>
<td>627</td>
</tr>
<tr>
<td>Littler (1973a)</td>
<td><em>Hydrolithon onkodes</em></td>
<td>0</td>
<td>4</td>
<td>589</td>
</tr>
<tr>
<td><strong>In situ</strong></td>
<td><em>Neogoniolithon brassica-floride</em></td>
<td>3</td>
<td>4</td>
<td>531</td>
</tr>
<tr>
<td><strong>In situ</strong></td>
<td><em>Hydrolithon reinboldii</em></td>
<td>3</td>
<td>4</td>
<td>528</td>
</tr>
<tr>
<td><strong>In situ</strong></td>
<td><em>Neogoniolithon conicum</em></td>
<td>0</td>
<td>4</td>
<td>490</td>
</tr>
<tr>
<td>Laboratory</td>
<td><em>Hydrolithon onkodes</em></td>
<td>0</td>
<td>6</td>
<td>477</td>
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<tr>
<td><strong>In situ</strong></td>
<td><em>Neogoniolithon brassica-floride</em></td>
<td>0</td>
<td>4</td>
<td>467</td>
</tr>
<tr>
<td><strong>In situ</strong></td>
<td><em>Neogoniolithon conicum</em></td>
<td>6</td>
<td>3</td>
<td>442</td>
</tr>
<tr>
<td>Littler and Doty (1975)</td>
<td><em>Hydrolithon gardineri</em></td>
<td>0</td>
<td></td>
<td>533</td>
</tr>
<tr>
<td>Littler (1973b)</td>
<td><em>Hydrolithon gardineri</em></td>
<td>0</td>
<td>2</td>
<td>600</td>
</tr>
<tr>
<td>Littler (1973b)</td>
<td><em>Hydrolithon onkodes</em></td>
<td>0</td>
<td>12</td>
<td>517</td>
</tr>
<tr>
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<td><em>Hydrolithon onkodes</em></td>
<td>0</td>
<td></td>
<td>480</td>
</tr>
<tr>
<td>Hawkins and Lewis (1982)</td>
<td><em>Hydrolithon onkodes</em> (dominant species)</td>
<td>0</td>
<td>10</td>
<td>380</td>
</tr>
<tr>
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<td><em>Hydrolithon onkodes</em></td>
<td>3</td>
<td>4</td>
<td>381</td>
</tr>
<tr>
<td>Marsh (1970)</td>
<td><em>Hydrolithon onkodes</em> (probable identity)</td>
<td>0</td>
<td>32</td>
<td>360</td>
</tr>
<tr>
<td><strong>Laboratory</strong></td>
<td><em>Neogoniolithon solubile</em></td>
<td>0.5–3</td>
<td>17</td>
<td>340</td>
</tr>
<tr>
<td>Laboratory</td>
<td><em>Neogoniolithon conicum</em></td>
<td>0</td>
<td>5</td>
<td>323</td>
</tr>
<tr>
<td>Laboratory</td>
<td><em>Neogoniolithon brassica-floride</em></td>
<td>0</td>
<td>4</td>
<td>323</td>
</tr>
<tr>
<td><strong>In situ</strong></td>
<td><em>Neogoniolithon conicum</em></td>
<td>18</td>
<td>2</td>
<td>320</td>
</tr>
<tr>
<td>Laboratory</td>
<td><em>Hydrolithon reinboldii</em></td>
<td>3</td>
<td>4</td>
<td>317</td>
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<tr>
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<td><em>Hydrolithon reinboldii</em></td>
<td>0</td>
<td>5</td>
<td>310</td>
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<tr>
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<td><em>Hydrolithon onkodes</em></td>
<td>2</td>
<td>4</td>
<td>301</td>
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<td><em>Hydrolithon reinboldii</em></td>
<td>6</td>
<td>4</td>
<td>294</td>
</tr>
<tr>
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<td><em>Neogoniolithon brassica-floride</em></td>
<td>6</td>
<td>2</td>
<td>291</td>
</tr>
<tr>
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<td><em>Neogoniolithon brassica-floride</em></td>
<td>6</td>
<td>5</td>
<td>285</td>
</tr>
<tr>
<td>Laboratory</td>
<td><em>Neogoniolithon brassica-floride</em></td>
<td>3</td>
<td>4</td>
<td>272</td>
</tr>
<tr>
<td>Littler (1973b)</td>
<td><em>Sporolithon erythraeum</em></td>
<td>0</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>Littler et al. (1986)</td>
<td>Unidentified sp.</td>
<td>81</td>
<td>4</td>
<td>267</td>
</tr>
<tr>
<td>Laboratory</td>
<td><em>Neogoniolithon conicum</em></td>
<td>6</td>
<td>5</td>
<td>237</td>
</tr>
<tr>
<td>Wanders (1976)</td>
<td><em>Hydrolithon pachydermum</em></td>
<td>0.5–3</td>
<td>21</td>
<td>220</td>
</tr>
<tr>
<td>Wanders (1976)</td>
<td><em>Lithophyllum sp. 3</em></td>
<td>0.5–3</td>
<td>25</td>
<td>200</td>
</tr>
<tr>
<td>Laboratory</td>
<td><em>Neogoniolithon conicum</em></td>
<td>18</td>
<td>5</td>
<td>192</td>
</tr>
<tr>
<td>Wanders (1976)</td>
<td><em>Lithophyllum intermedium</em></td>
<td>0.5–3</td>
<td>18</td>
<td>190</td>
</tr>
<tr>
<td>Wanders (1976)</td>
<td><em>Lithophyllum sp. 4</em></td>
<td>0.5–3</td>
<td>19</td>
<td>150</td>
</tr>
<tr>
<td>Vooren (1981)</td>
<td><em>Hydrolithon boergesenii</em></td>
<td>11</td>
<td>2</td>
<td>120</td>
</tr>
<tr>
<td>Vooren (1981)</td>
<td><em>Hydrolithon boergesenii</em></td>
<td>.25</td>
<td>.3</td>
<td>120</td>
</tr>
<tr>
<td>Vooren (1981)</td>
<td><em>Archaeolithothamnion dimotum</em></td>
<td>25</td>
<td>7</td>
<td>110</td>
</tr>
</tbody>
</table>
suggested 12 g m⁻² d⁻¹ limit, although Larkum’s arguments would appear to be reasonable in most other reef situations in the absence of eutrophication.

Eutrophication can favor the development of crustose and articulated coralline algae (Littler 1973a; Kindig and Littler 1980; Littler et al. 1991), and there is ample evidence that anthropogenic nutrient enrichment is affecting nearshore reefs in many parts of the world (Wilkinson 2000). An increase in the abundance of crustose coralline algae is much preferable to the development of large fleshy algae, since the latter make no contribution to carbonate production or reef consolidation and they deprive carbonate-secreting organisms of irradiance. However, coralline algae may not increase in abundance under nutrient enrichment if concomitant restructuring of the grazing community leads to arrestment of the algal successional series at the stage of filamentous turf algae (McClanahan 1997).

While many coralline algae depend upon grazers to limit turf algal competition (e.g., Steneck and Dethier 1994; Adey 1998), grazers remove substantial amounts of their tissue and skeletal carbonate (e.g., Steneck 1983; Steneck 1985; Chisholm 2000). Although coralline algae shed tissue by epidermal sloughing (e.g., Keats et al. 1997; Steneck 1997), their generally slow rates of accretion indicate that they make important trophic contributions to coral reef development.

In conclusion, the primary productivity of reef-building coralline algae might have been underestimated because of the difficulties associated with making measurements in situ. The higher rates of productivity measured in situ raise the possibility that coralline crusts derive nutrients from the underlying reef matrix. In estimating the importance of coralline algae to reef organic production, their cover in shaded environments must be considered. The combination of relatively high instantaneous productivity and low rates of long-term accretion indicates that coralline algae make substantial contributions to the food supply within reef systems. Within broad limits, the data provided here enable the productivity of reef-building coralline algae to be estimated from measurements of in situ irradiance near the solar zenith (Fig. 6).

References


———. 1980. Morphological form and photosynthetic performanc-


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Seasonal shift in net ecosystem production in a tropical estuary

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Abstract

Net ecosystem production was examined in the Mandovi and Zuari estuaries (southwestern India) and the adjoining coastal waters for a period of 1 yr (January to December 1998). The study period encompassed premonsoon, monsoon, and postmonsoon seasons. At the estuarine stations, net ecosystem production showed monthly variation and a transition from net autotrophy of 49 mmol C m\(^{-2}\) d\(^{-1}\) during the nonmonsoon seasons (premonsoon and postmonsoon) to net heterotrophy of \(-46\) mmol C m\(^{-2}\) d\(^{-1}\) in the monsoon season. Seasonal monsoon-driven changes such as increased allochthonous inputs resulted in enhanced heterotrophic respiration and reduced primary production in the estuaries. In the coastal station, the monthly variation in net ecosystem production was not significant, and net heterotrophy was prevalent whenever measurements were made, thereby potentially serving as the net source of carbon dioxide to the atmosphere. Results suggest that the excess organic matter from these tropical estuaries supports heterotrophy in the adjacent coastal ecosystem.

The overall metabolic balance in any aquatic system depends on the sum of two fundamental and complementary variables: primary production (P) and community respiration (R). Measurements of these variables are a prerequisite to assess the trophic status of aquatic ecosystems. Del Giorgio et al. (1997) suggested that metabolic balance depends on the primary productivity of the system. The rate of plankton growth efficiency and respiration are important factors that determine the fate of primary production. Recently, heterotrophy has been reported from euphotic layers of the subtropical Northeast Atlantic (Duarte et al. 2001; Hoppe et al. 2002), and heterotrophy is not restricted to oligotrophic systems. Of late, there has been considerable debate on the role of planktonic communities as sources (del Giorgio et al. 1997; Duarte et al. 2001) or sinks (Williams 1998) of carbon in subtropical and temperate waters.

The coastal ecosystems, especially tidally influenced estuaries, have drawn much attention, since they are the most geochemically and biologically active areas. They receive inputs of terrestrial organic matter and nutrients through riverine runoff, which establishes a variable nutrient gradient in time and space. There is even a debate on whether coastal systems are nominally heterotrophic or autotrophic on a net annual basis (Smith et al. 1991). We hypothesize that nutrient load during the monsoon would increase autotrophy and excess organic matter would be transported to the coastal waters. Thus there may be a temporary shift in status (net autotrophic to net heterotrophic) of the coastal ecosystem.

To test this hypothesis, the present study was carried out in the Mandovi–Zuari estuarine system, which has been considered productive based on its primary production (Devassy and Goes 1989). This study area, which forms a part of the Northern Indian Ocean (southeastern Arabian Sea), is characterized by extreme wind forcing and seasonal reversal monsoon winds, which is an annual recurring phenomenon in these estuaries. This region experiences a spell of heavy precipitation of the order of 250–300 cm yr\(^{-1}\), much of it occurring during the southwest monsoon (June–September). During the dry season (November–May), the total precipitation drops to less than 10 cm (Shetye and Murty 1987). Large amounts of materials are transported through these estuaries following heavy rains during the monsoon period. This extent of input of organic matter might have a significant effect on the metabolism of the system. In the present study, the following questions were addressed. Is this tropical estuarine system autotrophic and subsidizing adjacent coastal waters? Or, is it heterotrophic and consequently dependent on allochthonous organic inputs from surrounding areas? Are inputs consumed by the resident heterotrophs, thus supporting their growth and respiration, or are they exported to the adjacent coastal waters? Does this input govern the trophic status of the system?

The importance of organic matter outwelling from Mandovi–Zuari estuaries to the adjacent coastal waters was assessed by measuring primary production and community respiration. In this study, we also examined whether there was a seasonal change in the trophic status in tropical estuaries and the adjacent coastal waters of the Arabian Sea. Assessment of the relative contributions of these estuaries to large-scale carbon budgets could lead to a better understanding of the role of tropical estuaries in general.

Methods

Study site—The coastal ocean region selected for our study was the Mandovi–Zuari estuarine system, located in Goa on the southwest coast of India (Northern Indian
Ocean), and was formed by the connection of two rivers the Mandovi and Zuari into its adjacent coastal waters (Arabian Sea) (Shetye et al. 1995). It has been classified as a tide-dominated tropical coastal plain estuary and geomorphologically identified as drowned river valley estuaries (Murty et al. 1976). It is homogeneously mixed, except in the monsoon season when the rivers become stratified forming a salt wedge. In both the estuaries, freshwater influx through riverine runoff is maximum during the monsoon months, with discharges of 175 and 125 m$^3$s$^{-1}$ in the Mandovi and Zuari estuaries, respectively (Unnikrishnan et al. 1997). During the nonmonsoon period, the input of fresh water is negligible and is regulated by the semidiurnal tides. The residence time of the water in the Mandovi estuary is 5–6 d during the monsoon season and about 50 d during in the nonmonsoon seasons (October–May), and in the Zuari estuary it is relatively longer (Qasim and Sengupta 1981).

**Sampling stations**—The study stations are (1) in the Mandovi estuary (15°30'N, 73°52'E), (2) in the Zuari estuary (15°25'N, 73°51'E), and (3) in the coastal zone (15°30'N, 73°44'E) adjoining the Arabian Sea (Fig. 1). The depth-integrated approach was used in our study since it overcomes some of the bias in the data and gives a more accurate picture of the balance of autotrophy and heterotrophy in these coastal zones.

Water samples from surface and close to the bottom were collected at monthly intervals for a period of 1 yr from January to December 1998. The sampling months were classified according to three distinct seasons, namely, the premonsoon, monsoon, and postmonsoon, respectively. Because of navigational constraints, the coastal station could not be sampled during the monsoon season (June–September).

Light transparency was measured using a Secchi disc. Salinity was determined with a Guildline 8400 Autosal salinometer. Dissolved oxygen concentration was determined by Winkler's method using starch endpoint titration with thiosulphate (Carpenter 1965). The net flux ($F$) of oxygen across the air–sea interface was calculated from the equation (Wanninkhof 1992)

$$F = k(C_w - \alpha C_a)$$

where $C_w$ = the gas concentration in the bulk of the water near the interface, $C_a$ = concentration of gas in the air phase near the interface, $\alpha$ = Ostwald's solubility coefficient, and $k$ = transfer velocity. $k$ (k for Schmidt number of 660) was estimated as a function of wind speed. Since the annual average wind speed for this region is 4 m s$^{-1}$ (Hastenrath and Lamb 1979), $k$ was calculated from the steady winds using the equations of Wanninkhof (1992). For flux measurements we have used positive values to denote the addition of oxygen to the system and negative ones for removal.

Total organic carbon concentrations were determined by high temperature (680°C) carbon analyzer (Shimadzu TOC 5000) with potassium biphthalate standard. Inorganic nutrient analyses for ammonia, nitrite, nitrate, and phosphate were carried out spectrophotometrically following the methods of Parsons et al. (1984).

**Primary productivity** ($P$)—Primary production was measured by $^{14}$C assimilation method (Lohrenz et al. 1992). Light and dark acid-washed bottles (125-ml capacity) were
Net tropical ecosystem production

Table 1. Seasonal variation in the water characteristics. Mean (±SD). DO = dissolved oxygen, TOC = total organic carbon, DIN = dissolved inorganic nitrogen, DIP = dissolved inorganic phosphate. Salinity measurements are indicated as average values (±SD).

<table>
<thead>
<tr>
<th>Stations</th>
<th>Secchi depth (m)</th>
<th>Salinity</th>
<th>Percent oxygen saturation</th>
<th>TOC (mol m⁻²)</th>
<th>DIN (mmol m⁻²)</th>
<th>DIP (mmol m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mandovi</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Premonsoon</td>
<td>0.5 (±0.2)</td>
<td>30.8 (±4.3)</td>
<td>106 (±16)</td>
<td>1.5 (±0.5)</td>
<td>27.3 (±15.4)</td>
<td>9.9 (±2.4)</td>
</tr>
<tr>
<td>Monsoon</td>
<td>0.3 (±0.1)</td>
<td>2.1 (±2.3)</td>
<td>114 (±33)</td>
<td>2.3 (±0.8)</td>
<td>32.4 (±13.7)</td>
<td>5.3 (±3.9)</td>
</tr>
<tr>
<td>Postmonsoon</td>
<td>0.8 (±0.3)</td>
<td>15.6 (±7.9)</td>
<td>126 (±3)</td>
<td>1.5 (±0.7)</td>
<td>28.4 (±23.7)</td>
<td>0.7 (±0.5)</td>
</tr>
<tr>
<td>Zuari</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Premonsoon</td>
<td>0.5 (±0.3)</td>
<td>29.7 (±6.8)</td>
<td>99 (±5)</td>
<td>1.1 (±0.3)</td>
<td>28.7 (±25.8)</td>
<td>9.3 (±8.3)</td>
</tr>
<tr>
<td>Monsoon</td>
<td>0.4 (±0.2)</td>
<td>21.2 (±7.0)</td>
<td>114 (±29)</td>
<td>1.4 (±0.8)</td>
<td>18.4 (±17.2)</td>
<td>6.4 (±3.4)</td>
</tr>
<tr>
<td>Postmonsoon</td>
<td>1.0 (±0.5)</td>
<td>30.0 (±5.3)</td>
<td>120 (±11)</td>
<td>1.7 (±0.4)</td>
<td>29.0 (±17.5)</td>
<td>4.2 (±0.7)</td>
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<tr>
<td>Coastal</td>
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<td></td>
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<tr>
<td>Premonsoon</td>
<td>1.0 (±0.2)</td>
<td>35.4 (±0.7)</td>
<td>112 (±17)</td>
<td>5.2 (±1.3)</td>
<td>51.8 (±34.0)</td>
<td>38.4 (±11.7)</td>
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<tr>
<td>Postmonsoon</td>
<td>2.0 (±0.8)</td>
<td>26.8 (±8.3)</td>
<td>125 (±5)</td>
<td>5.1 (±1.0)</td>
<td>67.8 (±35.4)</td>
<td>2.0 (±1.34)</td>
</tr>
</tbody>
</table>

filled with water samples. The water samples were inoculated with labeled NaH¹⁴CO₃ (Activity: 5 μCi ml⁻¹, BARC), incubated for 4 h at in situ light intensity, and cooled by running seawater. On retrieval, the water samples were filtered immediately through a 0.45-μ filter (Millipore, GS type) under diffused light and low pumping pressure (<100 mm Hg). Radio-labeled dissolved inorganic carbon (DIC) was removed by exposing the filter papers to fumes of concentrated hydrochloric acid for a minute. The filters were then placed in scintillation vials, and 5 ml of scintillation cocktail in dioxane (Spectrochem) were added. Radioactivity was measured in a liquid scintillation counter (LKB Wallac 1209). Production rates were calculated based on a 12-h photoperiod, and the results were expressed as mmol C m⁻² d⁻¹.

In the present study, the estimated dissolved inorganic carbon (DIC) concentration was used in the calculation for primary productivity. The ¹⁴C assimilation method was preferred to the light–dark bottle technique (oxygen method) to measure primary productivity because of its sensitivity and wider application in the estuarine and coastal environments. In order to validate the contribution of the ¹⁴C method to gross primary productivity (GPP), time series production experiments using both the approaches, i.e., ¹⁴C and light–dark bottle technique, were carried out from dawn to dusk (12-h period). Results indicated that the productivity measured by the ¹⁴C method was lower than the light–dark bottle technique (GPP) but not significantly lower (<5%) depending on the season.

Community respiration (R)—Community respiration rates were measured as oxygen consumption by the plankton community in dark bottles incubated for 24 h. Water samples were collected in six 300-ml dark biological oxygen demand (BOD) bottles. Three bottles were fixed immediately with Winkler's reagents for estimating initial dissolved oxygen concentration, and the remaining bottles were fixed after a 24-h incubation period at in situ temperatures. Dissolved oxygen concentration was determined using starch endpoint titration with thiosulphate (Carpenter 1965). The oxygen used up was converted to carbon respired assuming a respiratory quotient (RQ) of 1 (Biddanda et al. 1994). Results were integrated with depth and expressed as mmol C m⁻² d⁻¹. All statistical analyses were performed with Minitab software for Windows (Release 12, Minitab).

Results

There was a typical tropical monsoonal pattern in salinity and dissolved oxygen during the annual cycle. A significant variation in value in these parameters was observed during monsoon and nonmonsoon period (p < 0.02). In the estuaries the salinity dropped to about zero during the monsoon period. The nutrient concentration in these waters is generally high. The coastal waters recorded higher dissolved inorganic nitrogen (DIN = 52 to 68 mmol m⁻², DIP = 2 to 38 mmol m⁻²) (Table 1). Since these estuaries have a regular flow of river water, the total organic carbon (TOC) ranged from 1.5 to 2.3 mol m⁻³. The coastal waters showed higher concentration of TOC (Table 1) than the estuarine stations.

The annual variation in primary production (P) and respiration (R) at these three stations is shown in Fig. 2. The net flux (F) of oxygen calculated across the air–sea interface ranged from −87 to +128 mmol m⁻² d⁻¹ in the estuarine and −11 to +74 mmol m⁻² d⁻¹ in the coastal waters (Fig. 3). Although primary productivity was higher in the estuarine stations than the coastal station, it did not vary significantly. Primary productivity at the estuarine stations ranged from 72 to 188 mmol C m⁻² d⁻¹. The Mandovi estuary showed significant variation (p < 0.02) in primary production between monsoon and nonmonsoon seasons. Like Mandovi, the primary productivity in the Zuari estuary was low during the monsoon season but did not significantly vary with the nonmonsoon season.

The mean depth-integrated primary production at the three stations is shown in Table 2. Community respiration rates at the coastal station ranged from 161 to 692 mmol C m⁻² d⁻¹ with a value of 492 mmol C m⁻² d⁻¹ in the premonsoon season (Table 2). The respiration rates at the coastal station were one to twofold higher than estuarine stations (p <
0.05). There was no significant difference in respiration between the two estuaries. The seasonal values in NEP in Mandovi were 54, −34, and 47 mmol C m⁻² d⁻¹ in the premonsoon, monsoon, and postmonsoon seasons (Fig. 4). The production and respiration varied by an order of magnitude (Fig. 4 and Table 2).

The ratio of P: R for estuarine stations was >1 during the nonmonsoon season (Table 2) reflecting autotrophy. The monsoon period reflected heterotrophy of a lower magnitude in the Zuari estuary than the Mandovi estuary. In this period the net carbon balance was negative during the monsoon and positive in the nonmonsoon months. On average, the overall net trophic balance in both the estuaries was −46 mmol C m⁻² d⁻¹ during the monsoon season. The coastal station exhibited heterotrophy whenever measurements were made. Net ecosystem production of the estuaries increased with primary production, whereas in the coastal waters heterotrophy increased with community respiration (Figs. 5, 6).

Table 2. Median and range of the integrated primary production (P), community respiration (R), and production to respiration ratio (P: R) at the study sites.

<table>
<thead>
<tr>
<th>Stations</th>
<th>Integrated primary production (P) (mmol C m⁻² d⁻¹)</th>
<th>Integrated community respiration (R) (mmol C m⁻² d⁻¹)</th>
<th>Production : respiration (P: R)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mandovi</td>
<td>Pmensoon 112.4 (72.2–188.2)</td>
<td>75.3 (36.2–83.0)</td>
<td>1.49</td>
</tr>
<tr>
<td></td>
<td>Monsoon 23.0 (10.1–40.1)</td>
<td>83.3 (40.2–159.4)</td>
<td>0.28</td>
</tr>
<tr>
<td></td>
<td>Postmonsoon 100.4 (33.3–146.7)</td>
<td>42.3 (37.5–69.5)</td>
<td>2.37</td>
</tr>
<tr>
<td>Zuari</td>
<td>Premonsoon 122.2 (86.2–148.2)</td>
<td>48.3 (46.9–89.2)</td>
<td>2.53</td>
</tr>
<tr>
<td></td>
<td>Monsoon 61.7 (23.6–153.2)</td>
<td>91.6 (46.9–148.2)</td>
<td>0.67</td>
</tr>
<tr>
<td></td>
<td>Postmonsoon 72.9 (26.5–116.1)</td>
<td>44.2 (21.4–53.7)</td>
<td>1.65</td>
</tr>
<tr>
<td>Coastal</td>
<td>Premonsoon 90.3 (79.6–127.3)</td>
<td>468.3 (337.7–692.5)</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td>Postmonsoon 154.7 (49.7–188.9)</td>
<td>339.5 (161.0–386.7)</td>
<td>0.46</td>
</tr>
</tbody>
</table>

Fig. 2. Monthly variation in the production (smooth line; filled squares) and respiration (dotted line; open squares) measurements at the three stations.

Discussion

The contribution of any biological system to the global carbon budget relies on the balance between organic carbon production and consumption. The balance between primary production (P) and community respiration (R) in a particular ecosystem is a measure of its trophic status (Odum 1956). This balance indicated by the difference between P and R or the ratio of P: R is termed as net ecosystem production (NEP) (Howarth et al. 1996; Smith and Hollibaugh 1997). NEP can be estimated using different approaches such as net CO₂ gas flux and net O₂ gas flux (Cole et al. 2000). We used a P-R approach to make a conservative evaluation of the importance of allochthonous organic matter for the estuarine system. A system’s trophic status thus depends on the accurate measurements of primary production and respiration. The use of the ¹⁴C method has inherent limitations, since it measures net rather than gross production. This production, however, depends on the system. Peterson (1980) found that net production almost equals the gross primary production in a highly productive system. A similar observation was made where the surrogate method (light–dark bottle technique) agreed well with the ¹⁴C technique (Davies and Williams 1984). Our results showed the same trend as the light–dark bottle technique method depending on the season. In
our study the $^{14}$C method was only $\leq$5% of gross production (light–dark bottle technique). In our work we have not consid-
ered the benthic metabolism. Since the pelagic community metabo-
lizes a larger percentage of organic matter, the benthic metabolism may have limited influence on the overall NEP. It was observed that the negative NEP was at least consistent with the oxygen under saturation. Moreover, light penetration in these estuaries is only up to 2 m during the nonmonsoon period. Cole et al. (2000) have shown that irrespective of the method adopted, the pattern emerging for the system is the same.

Studies in temperate waters have indicated that NEP is highly variable with the seasons (Kemp et al. 1992; Smith and Hollibaugh 1997), salinity (Swaney et al. 1999), and/or depth (Caffrey et al. 1998) irrespective of the methods used. With the bottle method, the NEP in the coastal and estuarine waters exhibited seasonality. In the estuaries (Mandovi and Zuari estuaries), $R$ exceeded $P$ (>1) during the monsoon season and vice versa in the nonmonsoon seasons. Thus the trophic status of the ecosystem shifted between net heterotrophy and autotrophy. The shift was more pronounced in the Mandovi, which is shallower than the Zuari estuary. However, a seasonal study in San Francisco Bay indicated net autotrophy in shallow areas in spring months and net heterotrophy in the deeper regions during other seasons (Caffrey et al. 1998). During the monsoon period there is an increased freshwater flow from riverine discharge carrying a large amount of allochthonous matter. The increase in freshwater inflow led to decreased salinity and increased turbidity, thereby reducing light penetration and consequently primary production during the monsoon (Table 1). Qasim and Sengupta (1981) have also emphasized that one of the characteristics of this tropical estuary is high riverine runoff during the monsoon season. Low productivity due to high turbidity was reported in the Schelde estuary (Sectaert and Herman 1995). During sediment resuspension events in Lake Michigan, Cotner et al. (2000) found that primary productivity was reduced due to high turbidity, whereas heterotrophic activity was greatly enhanced due to nutrients released from the sediments as well as fluvial inputs.

During the same season there was significant enhancement of respiration, which may be due to allochthonous input. Increased community respiration in the Chesapeake Bay was attributed to use of labile organic matter (Howarth et al. 1996). In our present study, it is clear that the estuaries are autotrophic with a shift to heterotrophy during the monsoon. The percentage oxygen saturation in this estuarine system mostly ranged from 105% to 125%. The general trend of the estuaries toward autotrophy during nonmonsoon may be due to the nutrient concentration, which may increase primary productivity. In contrast, increased turbidity may decrease the amount of light available, thus limiting primary produc-

Fig. 4. Seasonal variation in the net ecosystem production (NEP) during premonsoon, monsoon, and postmonsoon season.

Fig. 5. Relationship between net ecosystem production and primary production at estuarine stations ($r^2 = 0.71, n = 24, p < 0.001$) and coastal station ($r^2$ value not significant).

Fig. 6. Relationship between net ecosystem production and community respiration at estuarine stations ($r^2$ value not significant) and coastal station ($r^2 = 0.92, n = 8, p < 0.001$).
tion regardless of nutrient concentrations (Young and Huryn 1996).

In the present study the NEP data were corroborated with the net oxygen gas flux approach. The oxygen gas flux in this estuarine system ranged from −87 to +128 mmol O₂ m⁻² d⁻¹. The pattern and magnitude inferred by this approach coincided with NEP measurements during most of the nonmonsoon months. These findings provide some support to our bottle measurements used for determining primary production and respiration. However, during the monsoon season there is a discrepancy between oxygen gas flux data and NEP. This could be due to the physical processes or to the benthos that may alter significantly at different times. The other factor that could also contribute to the above includes the metabolism of allochthonous organic carbon. Independent approaches to determine the lake metabolism using NEP and gas fluxes (O₂ and CO₂) and the factors regulating the above have already been discussed and carried out (Cole et al. 2000). From the present study, it was evident that most of the time the percentage of oxygen saturation was >100%, indicating the system acts as a net source for oxygen to the atmosphere, a condition that is consistent with net autotrophy (positive NEP).

In addition to the above, investigation of the distribution of pCO₂ in surface waters can help to identify sources or sinks of atmospheric carbon dioxide. Although pCO₂ was not measured in the present study, recently Sarma et al. (2001) reported a high pCO₂ value of 1,153 μatm (at salinity ≤10), which is three times higher to that in the atmosphere during the southwest monsoon season in the Mandovi–Zuari estuarine system. High pCO₂ in the monsoon coincided with high community respiration rates, indicating that the system is net heterotrophic. Sarma et al. (2001) have shown that pH influences the pCO₂ levels in these estuarine systems. High pCO₂ and low pH levels in the monsoon season could be due to the bacterial degradation of allochthonous organic matter from terrestrial and riverine inputs (del Giorgio et al. 1997). Thus, overall trophic status of the estuaries depends on biology, with physical process exerting a dominant influence during the monsoon season. Cole et al. (2000) also demonstrated net heterotrophy in Paul Lake, Wisconsin, where the pCO₂ values were found to be greater in the water than in the atmosphere, with the values ranging from 600 to 1,500 μatm seasonally.

In the coastal station, R exceeded P whenever measurements were made (i.e., premonsoon and postmonsoon seasons), indicating the trophic status of the ecosystem to be net heterotrophic, that is, NEP is negative. Since data could not be collected during the monsoon period for logistic reasons, no NEP picture could be given during this period. We speculate that during the monsoon season, coastal heterotrophy may be enhanced by increased riverine runoff (carring terrigenous carbon) compensating for any reduction in estuarine primary productivity. Thus it could be pointed out with high probability but not with certainty that coastal heterotrophy may be persistent throughout the year. However, Sarma et al. (1998) have reported that the central and eastern Arabian Sea is a perennial source of atmospheric carbon dioxide. The coastal waters showed no relationship between P and R, suggesting that this uncoupling could be due to the input of organic carbon from allochthonous sources.

The external organic sources entering the coastal waters are through the estuaries. When community respiration in the coastal system is subsidized from the estuarine inputs, any shift to net autotrophy requires a large increase in local primary production. Moreover, physical factors operating at the coastal station could also play a role in regulating NEP, as has been shown in Tomales Bay, where coastal upwelling led to net heterotrophy (Smith and Hollibaugh 1997). Azam et al. (1994) observed net heterotrophy temporarily during the intermonsoon season in the highly productive Arabian Sea and attributed it to the slow degradation of the dissolved organic carbon pool.

From the present study it is evident that the coastal waters are net consumers of organic matter, rather than producers, and that these systems might be expected to release inorganic nutrients (Table 1). It has been reported that the net heterotrophy leads to the release of dissolved inorganic phosphorus to the ocean and dissolved inorganic carbon to the atmosphere (Smith and Hollibaugh 1993; Sarma et al. 2001). Our studies suggest that the persistence of net autotrophy during the nonmonsoon in estuaries could have resulted in production of organic matter from inorganic nutrients, and this organic matter along with the allochthonous input could have been ultimately transported or exported hydrologically to the adjacent coastal regions, thereby supporting the outwelling hypothesis proposed by Odum (1968) or the coastal heterotrophy hypothesis proposed by Hopkinson (1985).

The outwelling hypothesis presumes that primary production of estuaries greatly exceeds local degradation and storage of carbon, and that the excess organic matter from the estuarine region is exported to the adjacent waters where it is finally degraded and incorporated into the offshore food web. Similar observations pertaining to the present study have been reported in the Georgia Bight (Hopkinson 1985). By measuring the level at which community respiration exceeds primary production, the import of allochthonous material is directly observed. Thus, organic carbon of terrestrial origin is likely to play a major role in this metabolic imbalance. Our findings should be of particular relevance to low-latitude coastal ocean regions where the bulk of the world’s river discharge occurs (Ittekot 1998). Our study suggests that seasonal changes in the NEP in the estuarine system can contribute substantially to the carbon dynamics in the adjacent coastal ecosystem.

References


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