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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

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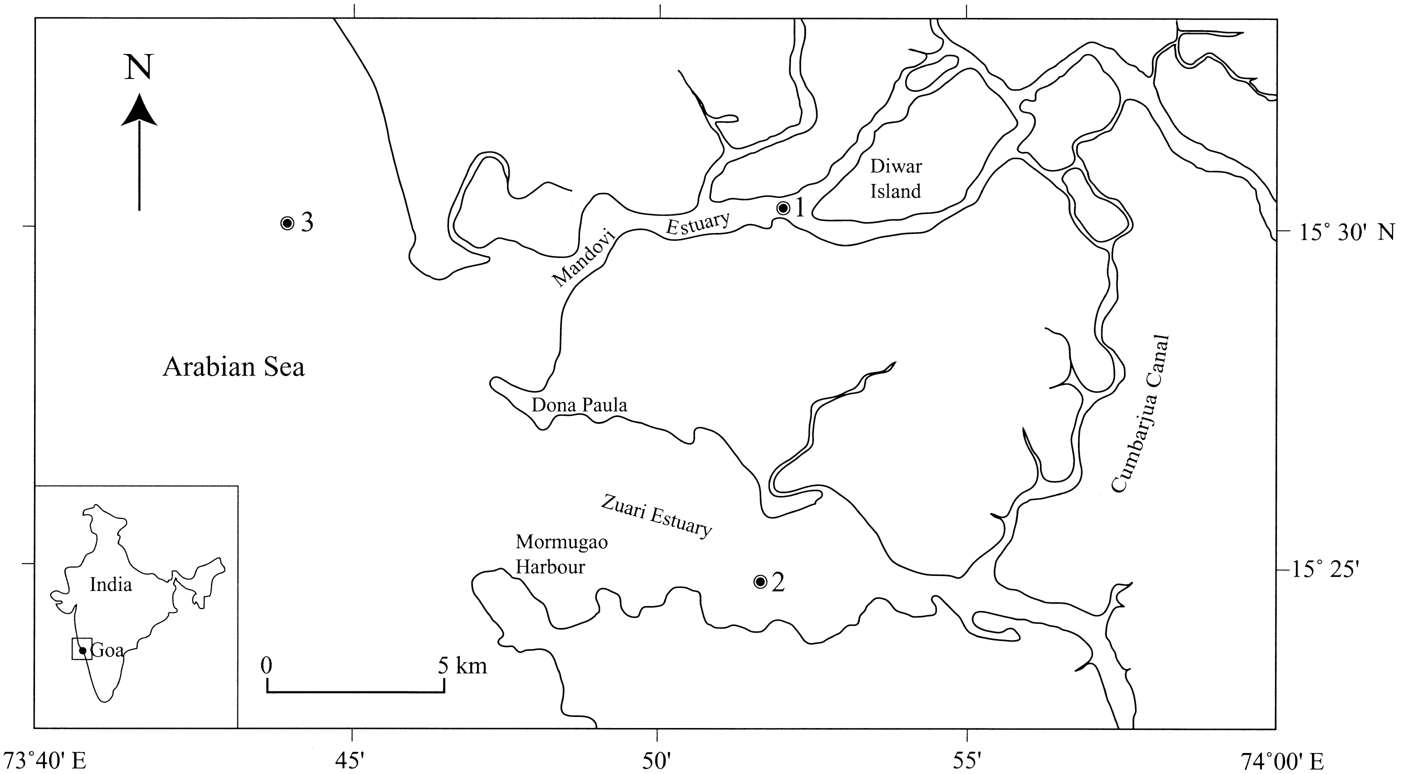

Fig. 1. Sampling stations in the Mandovi–Zuari estuarine system.

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, α = 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

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).

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

filled with water samples. The water samples were inoculated with labeled $NaH^{14}CO_3$ (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 ($<$100 mm Hg). Radio-labeled dissolved inorganic carbon ($DI^{14}C$) 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 ^{14}C 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 ^{14}C method to gross primary productivity (GPP), time series production experiments using both the approaches, i.e., ^{14}C and light–dark bottle technique, were carried out from dawn to dusk (12-h period). Results indicated that the productivity measured by the ^{14}C method was lower than the light–dark bottle technique (GPP) but not significantly lower ($\leq$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^{-2}. 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 ($p <$

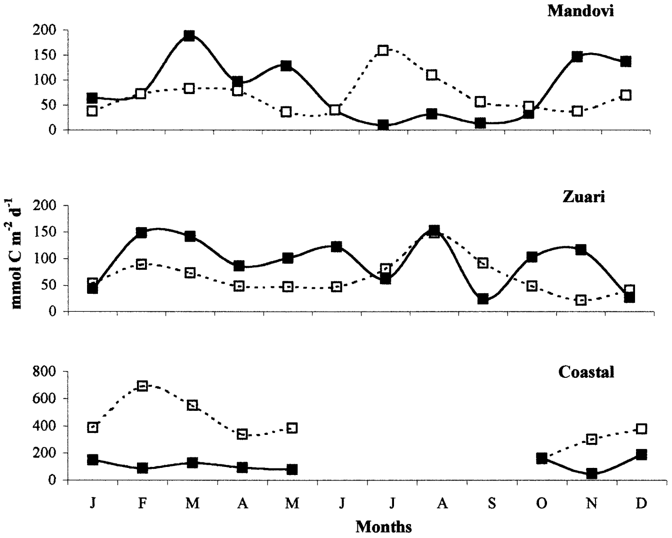

Fig. 2. Monthly variation in the production (smooth line; filled squares) and respiration (dotted line; open squares) measurements at the three stations.

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).

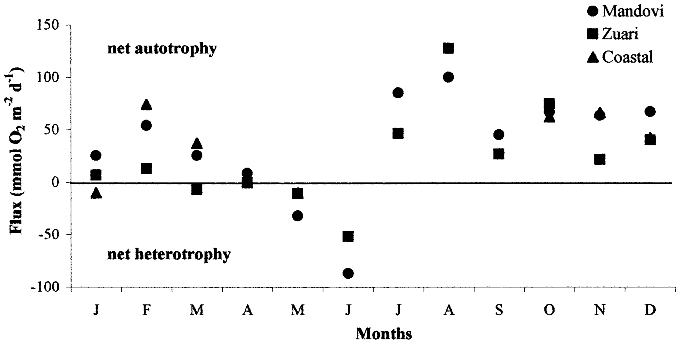

Fig. 3. Monthly variation in the net flux of oxygen across the air–sea interface.

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 CO_2 gas flux and net O_2 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 ^{14}C 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 ^{14}C technique (Davies and Williams 1984). Our results showed the same trend as the light–dark bottle technique method depending on the season. In

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.

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

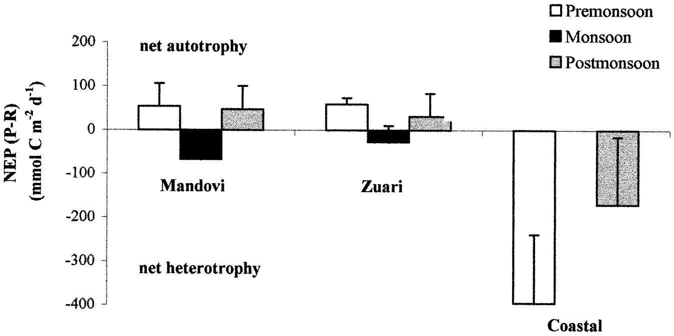

Fig. 4. Seasonal variation in the net ecosystem production (NEP) during premonsoon, monsoon, and postmonsoon season.

our study the ^{14}C method was only $\leq$5% of gross production (light–dark bottle technique). In our work we have not considered the benthic metabolism. Since the pelagic community metabolizes 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 the 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 (Soetaert 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-

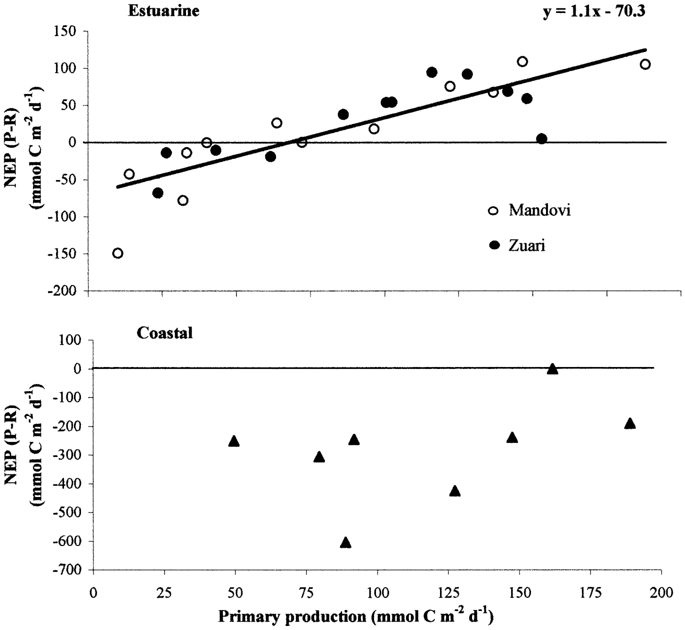

Fig. 5. Relationship between net ecosystem production and primary production at estuarine stations ($r^2 = 0.71$, $n = 24$, $p < 0.001$) and coastal station (r^2 value not significant).

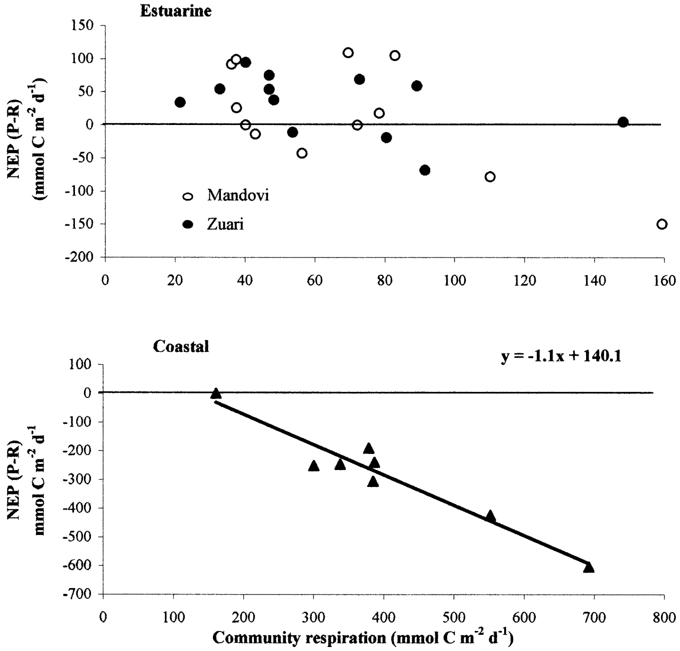

Fig. 6. Relationship between net ecosystem production and community respiration at estuarine stations (r^2 value not significant) and coastal station ($r^2 = 0.92$, $n = 8$, $p < 0.001$).

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 O_2 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 (O_2 and CO_2) 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 pCO_2 in surface waters can help to identify sources or sinks of atmospheric carbon dioxide. Although pCO_2 was not measured in the present study, recently Sarma et al. (2001) reported a high pCO_2 value of 1,153 μatm (at salinity $\leq$10), which is three times higher to that in the atmosphere during the southwest monsoon season in the Mandovi–Zuari estuarine system. High pCO_2 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 pCO_2 levels in these estuarine systems. High pCO_2 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 pCO_2 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 (carrying 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 phosphorous 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.

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