

**Bacterial Growth Efficiency in a Tropical Estuary: Seasonal Variability Subsidized
by Allochthonous Carbon**

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Abstract

Bacterial growth efficiency (BGE) is a key factor in understanding bacterial influence on carbon flow in aquatic ecosystems. We report intra annual variability in BGE, and bacteria mediated carbon flow in the tropical Mandovi and Zuari estuaries (southwest India) and the adjoining coastal waters (Arabian Sea). BGE ranged from 3 to 61% and showed clear temporal variability with significantly (ANOVA, $p < 0.01$) higher values in the estuaries (mean, $28 \pm 14\%$) than coastal waters (mean $12 \pm 6\%$). The greater variability of BGE in the estuaries than coastal waters suggest some systematic response to nutrient composition and the variability of dissolved organic matter pools, as BGE was governed by bacterial secondary production (BP). Monsoonal rains and its accompanied changes brought significant variability in BGE and bacterial productivity to primary productivity (BP/PP) ratio when compared to non-monsoon seasons in the estuaries and coastal waters. High BP/PP ratio (> 1) together with high carbon flux through bacteria ($> 100\%$ of primary productivity) in the estuarine and coastal waters suggests that bacterioplankton consumed dissolved organic carbon in excess of the amount produced *in situ* by phytoplankton of this region, which led to the mismatch between primary production of carbon and amount of carbon consumed by bacteria. Despite the two systems being subsidized by allochthonous inputs, the low BGE in the coastal waters may be due to the nature and time interval in the supply of allochthonous carbon.

Introduction

Heterotrophic bacterioplankton are the most abundant component in any aquatic system and are the major mineralizers of organic carbon (C) and nutrients. Consumption of dissolved organic carbon (DOC) by bacteria is one of the major pathways of material and energy flow in pelagic food webs [10]. DOC supporting bacterial metabolism originates either from in situ primary production (autochthonous C) or from external terrestrial inputs (allochthonous C) [31, 44]. This DOC can either be transformed to bacterial biomass (bacterial production, BP) or respired to inorganic carbon (bacterial respiration, BR), which is unlikely to reach higher consumers. In the marine offshore waters phytoplankton photosynthesis is a major source of organic carbon to bacterioplankton and there exists a balance between phytoplankton and bacterial production in time and space [6, 12], whereas in estuaries and adjoining coastal ecosystems this balance is lost due to the flow of allochthonous inputs from riverine discharge and terrestrial runoff [19, 26]. Bacterial growth efficiency (BGE, calculated using BP and BR) is a parameter that integrates various aspects of bacterial metabolism and is, in turn, affected by a variety of resource factors, such as nutrient and organic matter availability. BGE is tightly coupled to the physiological condition of bacteria, and in this respect may be an extremely sensitive index of the response of aquatic bacteria to their environment [15]. Values of BGE in aquatic systems are highly variable, and while there are a growing number of studies that have explored the environmental regulation of this variability, many important questions regarding resource control of BGE remain unanswered.

The coastal oceans, especially tidally influenced estuaries, have drawn much attention as they are the most geochemically and biologically active areas of the biosphere [21]. Estuaries being on the margin between the coast and land, by nature are dynamic regions characterized by steep gradients in temperature, salinity and nutrient concentrations [14]. They mediate the export of matter to the coastal waters. In such systems the relative importance of autochthonous versus allochthonous supporting bacterial metabolism is important to our understanding of C cycling in aquatic systems. Multiple lines of evidence suggest that Mandovi-Zuari tropical system is net heterotrophic especially in the monsoon season where respiration exceeds gross primary

production, which can only occur when external subsidies of organic C support estuarine metabolism [39]. This study area forms a part of the Northern Indian Ocean (southeastern Arabian Sea) is characterized by extreme wind forcing and seasonal monsoon winds which are an annual recurring phenomenon in these estuaries [29]. So, do the seasonal differences in monsoon winds affect the annual pattern in the BGE and carbon flow or not? To test the above hypothesis, the present study was carried out in tide dominated Mandovi-Zuari tropical estuary located in Goa on the southwest coast of India and was formed by the connection of two rivers, the Mandovi and Zuari into its adjoining coastal waters (Arabian Sea). Thus, this study addresses a question of significant interest to the field, and more so in a tropical marine environment for which such studies are especially scanty.

Material and Methods

Study site

The study stations in the Mandovi-Zuari estuarine system are (1) in the Mandovi estuary ($15^{\circ}30'N$, $73^{\circ}52'E$), (2) in the Zuari estuary ($15^{\circ}25'N$, $73^{\circ}51'E$) and (3) in the coastal waters ($15^{\circ}30'N$, $73^{\circ}44'E$) adjoining the Arabian Sea (Fig. 1). The detailed characteristics of the study stations have already been described elsewhere [39].

Sampling and Sample processing

Water samples from surface and close to the bottom (1 metre above the sediments) were collected at monthly intervals at the above-mentioned stations for a period of one year (January to December 1998) using Niskin water sampler (Miami, FL, USA). The water samples were pre-filtered through 220 μ m nylon mesh to remove larger organisms. Samples were kept cold and dark while transported to the laboratory for analysis. Sampling months were classified according to three distinct seasons namely, the pre-monsoon (February - May), monsoon (June - September) and post-monsoon (October - January) respectively. Depth- integrated approach was carried out to give a more accurate picture of flow and to analyze the relationships between parameters. Because of navigational constraints, the adjacent coastal station could not be sampled during the monsoon season (June-September).

Water transparency was measured using Secchi disc. Water temperature was measured by field thermometer and salinity was determined with a Guildline 8400

Autosal salinometer. Dissolved oxygen concentration (DO) was determined by Winklers method using starch endpoint titration with thiosulphate [8]. Nutrient (ammonia, nitrite, nitrate and phosphate) concentrations in water samples were determined spectrophotometrically using standard methods [35]. Organic carbon concentrations were determined by high temperature (680°C) carbon analyzer (Shimadzu TOC 5000) with potassium biphthalate standard [43]. Chlorophyll *a* (Chl *a*) concentration was estimated fluorometrically from in samples (250 ml) collected on GF/F filters (Whatman, Maidstone, England) and pigments extracted in 90% acetone overnight in the dark at 4°C [35].

All carboys, filtering devices, glasswares and tubings were acid washed (in 10% HCl) and rinsed (thrice) with de-ionized water prior to each use.

Primary Production

Primary productivity (PP) was estimated by the ¹⁴C assimilation method [28]. The light and dark acid washed bottles (125 ml capacity) containing the water samples and labeled NaH¹⁴CO₃ (Activity: 5 µCi ml⁻¹, BARC, Mumbai, India) were incubated using neutral density screens at *in situ* temperature in a deck incubator. The water samples after incubation were filtered immediately through 0.45 µm filter (Millipore, Danvers, MA, USA) under diffused light and low pumping pressure (<50 mm Hg). Radio labeled dissolved inorganic carbon (DI¹⁴C) was removed by exposing the filters to fumes of concentrated hydrochloric acid for one minute. The filters were then placed in scintillation vials and 5 ml of scintillation cocktail in dioxane (Spectrochem, Mumbai, India) were added. Radioactivity was measured in a liquid scintillation counter (LKB Wallac 1209, Perkin Elmer, Boston, MA, USA).

Bacterial productivity, Respiration, and Growth Efficiency

For the calculation of BGE, BP and BR were measured from the water samples that had been filtered through GF/F filter (Whatman, Maidstone, England). This coarse filtration removed essentially all the phytoplankton and bacterial grazers and reduced bacterial numbers by 15% (± 5). Filtration was done under a low differential pressure (< 50 mm Hg) to avoid disruption of fragile cells.

BP was determined by the incorporation of the nucleoside ³H-thymidine into bacterial DNA [20]. 30ml of GF/F filtered water samples (in triplicates) along with one

2% neutral buffered formalin killed control were incubated with ^3H -thymidine (^3H -TdR) at a final concentration of 15 nM (Specific activity = 52 Ci mmol⁻¹, BARC, Mumbai) and then incubated at in situ conditions in the dark for one hour. TdR incorporation was stopped by adding 2% neutral-buffered formalin. The samples were filtered through 0.22 μm filter (Millipore, Danvers, MA, USA) (pre-soaked with 5% trichloroacetic acid (TCA), extracted in cold 5% TCA and rinsed with 80% ethanol. The dried filters were placed in scintillation vials and 5 ml of dioxan based scintillator (Spectrochem, Mumbai, India) was added. Radioactivity was measured with a liquid scintillation counter (Wallac LKB 1209, Perkin Elmer, Boston, MA, USA) with external standards. Concentrations of kinetic experiments showed that isotopic dilution was negligible when using 15 nM thymidine. BP, calculated in moles of TdR incorporated into DNA, was converted into the number of bacterial cells produced by applying a conversion factor (1.96×10^{18} cells mole⁻¹) determined from the present study and to carbon by using a conversion factor of 2×10^{-14} g C cell⁻¹ [27].

We adopted size fractionation procedure and 24-h incubation of water samples to determine the BR rates [3, 39], as it could give us a more ecologically relevant data, especially in estuarine systems, as there can be a rapid turnover of organic matter. Size-fractionation approach by filtration procedure obviously alters prey-predator interactions [36] and can lead to release of inorganic and organic substrates if cells are broken during filtration. This technique is not without its share of potential problems associated with enclosure effects BR was estimated from the consumption of dissolved oxygen in BOD bottles (GF/F filtrate), assuming a respiratory quotient of 1. The bottle effect due to long incubation periods (> 24 hr) may induce changes of bacterial community composition [22, 30] and/or exhaust trophic resources [40]. In our study we tried to reduce the incubation time as much as possible to detect the significant decrease in dissolved oxygen in the samples, in order to minimize the bias in the BGE determination. The linear decrease in oxygen during incubation as observed in our previous study [40] and the present study suggests that size-fractionation artifacts were not substantial. The Winkler technique has been most commonly used technique to estimate BR. Water samples were collected in six 300 ml biological oxygen demand (BOD) bottles. Time zero control samples (in triplicates) were immediately fixed with Winklers reagents. Another set of

samples (in triplicates) was kept at the *in situ* temperature in darkness for 24 hours before fixation. It offers satisfactorily high sensitivity and precision [4, 5], even in oligotrophic waters, although it has the disadvantage of preventing continuous monitoring of oxygen concentration with time.

BGE was derived as the slope of bacterial production versus sum of bacterial production and bacterial respiration and expressed as percentage. The carbon flux through bacterioplankton (CFTB) is equal to BP + BR and expressed as percentage of PP [3].

All statistical analyses were performed using Minitab software for Windows (Release 12, Minitab Inc., 1999).

Results

A typical tropical monsoonal pattern was observed in water temperature, salinity, and dissolved oxygen over an annual cycle. Generally the estuaries are well mixed, except in the monsoon season (especially in Zuari estuary) when stratification is caused by salinity gradient. With the exception of salinity in the monsoon season (in Zuari estuary), stratification did not bring about any significant differences ($p > 0.05$) in the physico-chemical characteristics between surface and bottom waters. Dissolved oxygen concentration remained high ($> 4 \text{ mg l}^{-1}$) throughout the water column, suggesting that the system is well oxygenated. Significant differences in salinity, dissolved oxygen and dissolved inorganic nitrogen (DIN) were observed between monsoon and non-monsoon seasons (ANOVA, $p < 0.02$). The average concentrations (surface and bottom waters) of organic carbon, nutrients and C:N ratio during non-monsoon and monsoon seasons are summarized in Table 1.

During the study period the overall primary productivity (PP) was high in the Zuari ($22.8 \mu\text{g C l}^{-1} \text{ h}^{-1}$) than Mandovi estuary ($14.3 \mu\text{g C l}^{-1} \text{ h}^{-1}$). In both the estuaries the PP maxima was observed in the non-monsoon season. Heavy precipitation in the monsoon season, characterized by low salinity and high turbidity led to a significant decrease in PP in Mandovi (ANOVA, $p < 0.001$) and Zuari estuary (ANOVA, $p < 0.05$) when compared to non-monsoon seasons. The average PP in the Mandovi and Zuari estuaries during the monsoon season were $4.4 (\pm 2.5) \mu\text{g C l}^{-1} \text{ d}^{-1}$ and $18.2 (\pm 15.4) \mu\text{g C l}^{-1} \text{ d}^{-1}$ respectively (Table 1). PP related significantly ($p < 0.05$) to DOC at the coastal waters

only (Table 2). Unlike PP, chlorophyll *a* did not show any significant differences between the seasons.

Bacterial growth efficiency

BGE ranged from 3 to 61% with a majority (85%) of the measurements between 5 to 40%. The average BGE in the estuaries and coastal waters were 28% (± 14) and 12% (± 6) respectively. Temporal variability in BGE was more obvious in this tropical system with significantly higher ($p < 0.01$) BGE in the estuaries than coastal waters. BGE maxima for Mandovi (52%) and Zuari (61%) estuary were noted in monsoon months of August and September respectively, while the minima were noted in December (post-monsoon) for both the estuaries (Fig. 2). High variability in BGE was observed in the monsoon season ($CV = 71\%$) than non-monsoon seasons ($CV = 42\%$) at the estuaries. Zuari estuary alone showed significantly (ANOVA, $p < 0.03$) higher BGE values in the monsoon than non-monsoon seasons. BGE was inversely related to C:N ratio of organic matter (Table 2) alone at the estuaries ($p < 0.001$) and coastal waters ($p < 0.01$) and did not correlate with other environmental parameters that we measured (temperature, salinity DOC, nutrients and chlorophyll *a*). BGE did not correlate to BR in this tropical estuarine system, but could however be predicted from BP, and explained 85% and 57% of the variation of BGE in the estuaries and adjacent coastal waters respectively (Table 2). Good correlation between BGE and BP, especially at the estuaries is driven by the small range in BR over a wide range in BP resulting in the lack of correlation between BP and BR. In the coastal waters a significant correlation ($p < 0.01$) between BP and BR led to weaker relationship between BP and BGE in contrast to the estuaries.

BP ranged from 2 to 535 $\text{mmol C m}^{-2} \text{d}^{-1}$ ($CV = 181\%$) and 13 to 105 $\text{mmol C m}^{-2} \text{d}^{-1}$ ($CV = 60\%$) in estuaries and adjoining coastal waters respectively (Fig. 2). The variation in BP at the study stations was larger than BR. In the estuaries, BP related to dissolved inorganic phosphate (DIP) ($p < 0.01$) and, to PP ($p < 0.05$) in the pre-monsoon season only (Table 2). BR at the estuaries ranged from 21 to 344 $\text{mmol C m}^{-2} \text{d}^{-1}$ ($CV = 99\%$) and from 267 to 693 $\text{mmol C m}^{-2} \text{d}^{-1}$ ($CV = 34\%$) in the coastal waters (Fig. 2). BR exceeded BP by 4-8 folds and by an order of magnitude at the estuaries and coastal waters respectively. BR was significantly higher than BP in both the estuaries (ANOVA,

$p > 0.005$) and adjacent coastal waters (ANOVA, $p < 0.00001$). BR related to DOC ($p < 0.01$) and PP ($p < 0.05$) at the Mandovi and Zuari estuary respectively.

Carbon flux through bacteria

In the present study, the bacterial productivity: primary productivity (BP/PP) ratios were less than 1 in the non-monsoon season (pre- and post-monsoon) in contrast to monsoon season where the ratios were greater than 1 in the estuaries. The average BP/PP ratios observed during the study period at the study stations are shown in Table 3. Both the estuaries showed similar trend with respect to the processing of organic carbon. In the non-monsoon seasons, the percentage of carbon flux through bacteria (CFTB) in the Mandovi and Zuari estuary was calculated to be 87 and 76% of PP respectively (Table 3). In the monsoon season the CFTB was $>100\%$ of PP in both the estuaries with maximum values of 481 and 500% of PP in the Mandovi and Zuari estuary respectively. Unlike the estuaries, the adjoining coastal waters did not exhibit any pattern whenever the measurements were made. The CFTB in the coastal waters was 288% of PP in the non-monsoon seasons (Table 3).

Discussion

In marine ecosystems the balance between autotrophy and heterotrophy are considered to be important for assessing the transfer of organic carbon to higher trophic levels [2]. High BP/PP ratio (i.e. > 1) have been shown to increase as a direct linear function of terrestrial carbon and of the fraction of primary production processed by bacteria and inversely with respiration as a function of growth efficiency [37]. Review of studies conducted so far have indicate BP/PP ratio to be generally in the range of 0.20 and 0.30 in aquatic systems [12] but exceptionally wide variation from 0.01 to 4.69 in estuaries [19, 24, 41] due to allochthonous inputs, either from riverine or waste discharge . BP/PP in our tropical ecosystem varied with time. High BP/PP ratio at the estuaries especially during the monsoon with consistently high growth efficiency (35%) suggested bacteria to utilize exogenous organic material (the flow of labile organic matter) which was not consistent throughout the estuary due to high variability in BP. Intense precipitation and increased riverine discharge in the monsoon season led to the uncoupling of BP with PP, suggesting that bacteria could largely be supported by exogenous carbon sources which may further explain the fact that they can have larger

impact than primary production on net oxygen saturation in this tropical system. High bacterial carbon demand or CFTB ($> 100\%$ of PP) in the monsoon season at the estuaries suggested the shift in the trophic status to net heterotrophy i.e. the bacterial carbon demand is met either by the exogenous organic carbon or DOC reservoir source, in addition to those derived from local contemporaneous phytoplankton. This shift in the trophic status corroborates with our earlier findings using the alternative approach of net oxygen and CO_2 gas flux across air-sea interface in this estuarine system [40]. Significant relationship ($p < 0.01$) between BP and PP in the dry pre-monsoon season suggested PP to be the dominant source of carbon for bacterioplankton growth. The amount of PP supporting BP in marine environment is reported to vary from 10% to over 100% with a global mean value of 60% when reviewing data from a large number of marine systems [12, 18]. In our tropical estuaries the CFTB during the non-monsoon seasons varied from 65 to 91% (mean = 82%) of PP, which suggested that the net amount of organic carbon produced by phytoplankton was sufficient to support bacterial production in the photic zone. The adjoining coastal waters showed high percentage of bacterial utilization of PP, suggesting the flow of large proportion of carbon from primary production into the microbial food web, as proposed by Ducklow and Carlson [18] for oligotrophic waters.

Utilization of organic matter by bacterioplankton i.e. CFTB are largely dependent upon BGE, an index of organic carbon available to higher trophic levels [1]. Substantial variability in BGE is a common feature of natural bacterial assemblages [3, 7, 42]. The range (3 to 61%) and mean (28% for estuaries and 12% for coastal waters) for the observed BGE values in the present study agree well with values reported previously for marine communities [15]. Although the utility of BGE measurements has recently been questioned on the basis of potential large uncertainties resulting from methodological concerns [23], our results show that the observed variability in BGE represents an ecological meaningful pattern. This tropical ecosystem has been classified as highly productive system [29] as a result one would expect higher BGE. But contrary to our understanding the average BGE in this estuarine system was low, which is lower than the average (37%) reported for estuaries [16].

In our study, the high BGE ($> 50\%$) were obtained in the monsoon months of both the estuaries, where the system would be dominated by freshwater input due to high

riverine runoff and intense precipitation: a characteristic previously reported in this tropical estuarine system [38, 45]. The high BGE was due to the high BP, which coincided with high DIN concentration during the period. In the Zuari estuary, low DOC supported high BP (leading to high BGE) in the monsoon season, which suggested greater bioavailability of organic matter to the bacterial community unlike the high humic input in the Mandovi estuary. The high growth efficiency especially in the monsoon season would be unusual because one would expect bacterial growth on presumed recalcitrant organic material from terrestrial sources to be inefficient. Relatively high BGE in the monsoon season at the estuaries led to BP/PP ratio exceeding more than 1, thereby suggesting the efficient utilization of terrestrial organic matter (TOM) by the bacterial communities. Similar trend was observed in the river station of Delaware estuary [37]. Preen and Kirchman [37] argued that growth may be slow on TOM, but not necessarily be inefficient and TOM is a complex mixture of compounds that bacteria use at different rates and efficiencies. In the present study, large variability in BGE due to BP in the monsoon (CV = 71%) than non-monsoon season (CV = 42%) could be due to unbalanced growth [9], depending on the nature and supply of allochthonous carbon inputs, which can lead to high BGE for short time periods.

Variability in BGE results from the loose coupling between its two components i.e. BP and BR. A significant relationship between BGE and BP, (not BR) at the estuaries, as seen in the present study, has been reported previously [40, 42]. Across a range of aquatic ecosystems, BP was consistently shown to be more variable than BR [eg. 17], which has often led to the conclusion that variation in BGE are driven by those factors that regulate variations in BP. The high variability of BGE in the estuaries compared to coastal waters could be explained by the lack of significant relationship between BP and BR. Lack of relationship between BP and BR could also be due to nitrification, a bacterially mediated process that would lead to discrepancies and apparent inconsistencies, if nitrifying bacteria do not incorporate thymidine and leucine. Nitrification has been shown to make substantial contributions to oxygen demands in some estuarine systems [34] and minor contributions in others [32]. Lack of sufficient information exists pertaining to the above in this estuarine system, therefore we do not rule out the possibility that high respiration rates were due to nitrification.

The overall low BGE observed in the adjoining coastal waters than estuaries was due to high BR, which explains the fact that bacteria allocate a relatively higher fraction of the energy uptake to maintenance than to biosynthesis. Higher organic carbon levels accompanied by low BGE values in the coastal waters suggest bacteria to be limited by the quality rather than the quantity of organic matter. Inverse relationship of BGE with C:N ratios and the greater variability of BGE in the estuaries compared to the coastal waters suggest some systemic response to nutrient composition and the variable quality of DOM pools.

Based on our data, it was clearly evident that monsoonal changes had a strong impact on BGE and BP/PP ratio that led to high bacteria mediated carbon fluxes at the estuaries. Thus the general feature of this tropical estuarine ecosystem is that it is productive with loose auto-heterotrophic coupling. The annual integrated data clearly showed that the carbon flow through bacterioplankton was 286 and 435% of the primary production in these productive estuarine and coastal waters. Bacterioplankton are the core of biogeochemical cycles in estuarine dynamics, and this study clearly identifies them as principal players that bring about the changes in trophic status. The findings of the above study will not only be useful in assessing the relative contribution of specific system to large scale carbon budgets but could also lead to better understanding of food web interactions in the tropical ecosystems.

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Figure Legends

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

Fig. 2. Monthly variation in the bacterial production (BP), bacterial respiration (BR) and bacterial growth efficiency (BGE) at the study stations.

Fig. 1

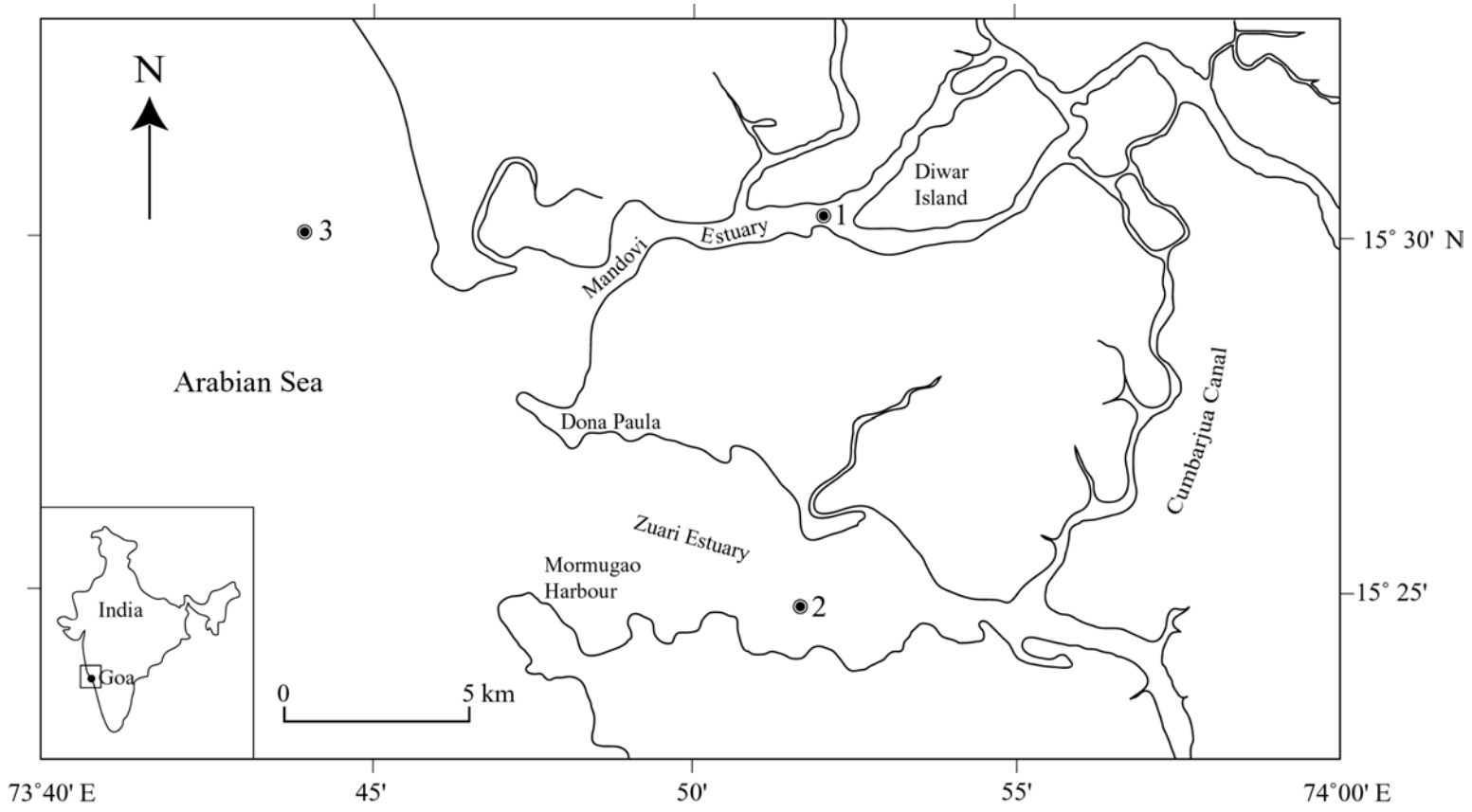


Fig. 2

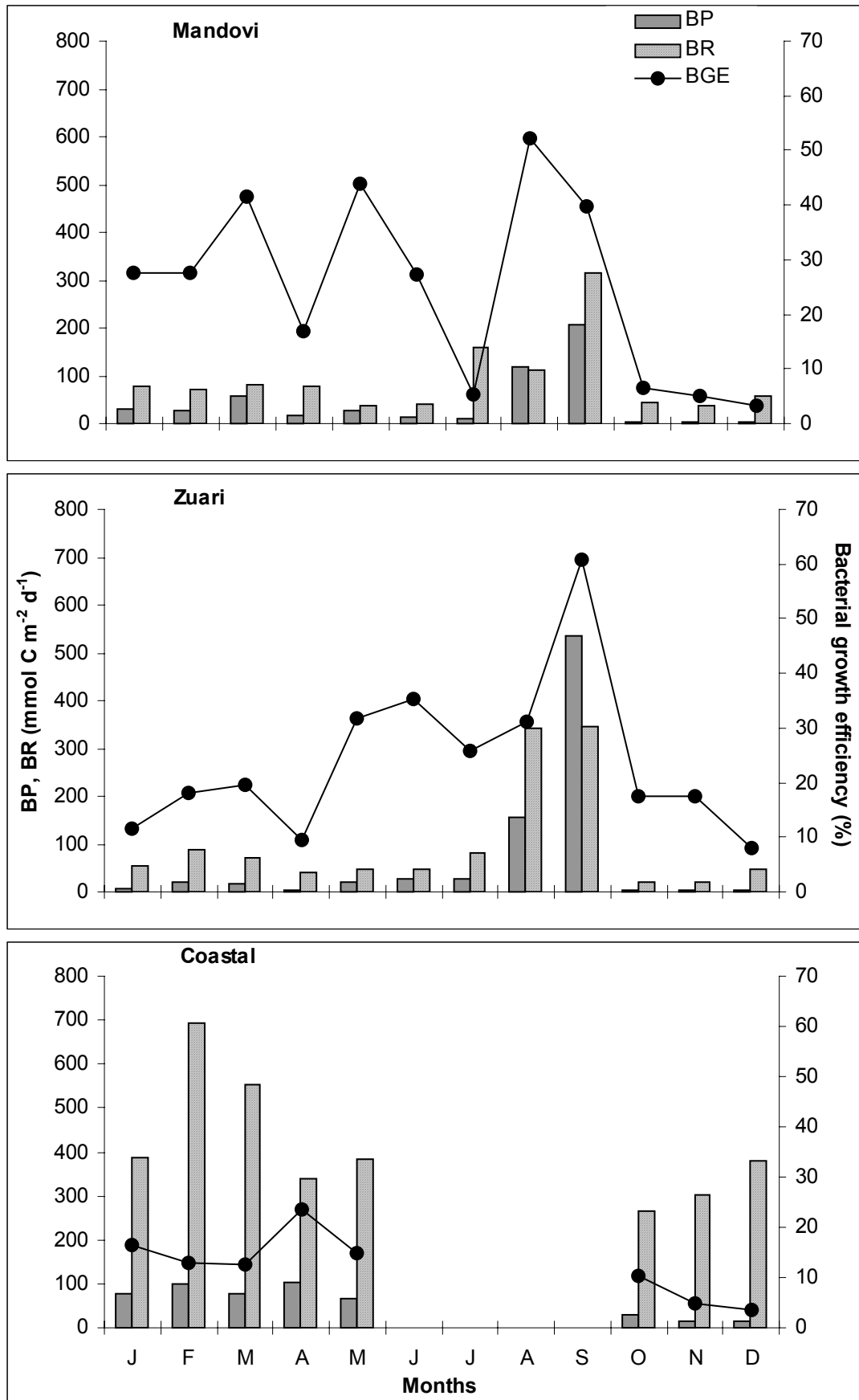


Table 1. Water characteristics of the study stations.Mean \pm Standard deviation of surface and bottom water samples.^a Non-mon: non-monsoon, Mon: monsoon.

DO: dissolved oxygen ; DOC: dissolved organic carbon ; DIN: dissolved inorganic nitrogen ; DIP: dissolved inorganic phosphate ; PP: primary productivity.

Parameters	Mandovi			Zuari			Coastal waters
	Average (n = 24)	Non-mon ^a (n = 16)	Mon ^a (n = 8)	Average (n = 24)	Non-mon (n = 16)	Mon (n = 8)	Non-mon (n = 16)
Temp. (°C)	28.5 (± 1.2)	29.9 (± 1.6)	27.1 (± 0.9)	28.6 (± 1.5)	29.4 (± 1.6)	27.4 (± 1.4)	28.2 (± 2.0)
pH	7.7 (± 0.2)	7.9 (± 0.1)	7.6 (± 0.2)	7.9 (± 0.1)	8.0 (± 0.1)	7.9 (± 0.2)	8.1 (± 0.1)
Salinity (psu)	12.7 (± 4.2)	23.2 (± 6.1)	2.1 (± 2.3)	25.6 (± 6.6)	29.9 (± 6.1)	21.2 (± 7.0)	31.1 (± 4.5)
DO (mg l ⁻¹)	5.8 (± 1.1)	5.4 (± 0.5)	6.2 (± 1.7)	5.0 (± 1.2)	4.5 (± 0.7)	5.6 (± 1.6)	5.1 (± 0.9)
C:N ratio	6.0 (± 1.6)	5.8 (± 1.3)	6.1 (± 1.9)	5.8 (± 1.6)	6.9 (± 1.8)	4.7 (± 1.5)	7.2 (± 3.1)
DOC (mg l ⁻¹)	4.6 (± 2.9)	4.0 (± 2.3)	5.2 (± 3.4)	3.6 (± 2.4)	3.8 (± 2.2)	4.3 (± 2.6)	3.3 (± 1.4)
DIN (μ M)	12.5 (± 5.0)	8.3 (± 6.5)	16.7 (± 3.5)	7.6 (± 6.7)	6.7 (± 5.9)	8.4 (± 7.6)	4.8 (± 3.2)
DIP (μ M)	1.6 (± 0.8)	1.6 (± 0.8)	1.6 (± 0.8)	1.7 (± 1.3)	2.1 (± 1.7)	1.3 (± 0.8)	1.8 (± 0.9)
PP (μ g C l ⁻¹ h ⁻¹)	14.3 (± 10.7)	24.2 (± 18.9)	4.4 (± 2.5)	22.8 (± 18.9)	27.3 (± 12.3)	18.2 (± 15.4)	7.9 (± 7.5)
Chl a (μ g l ⁻¹)	1.1 (± 0.7)	0.9 (± 0.8)	0.9 (± 0.1)	1.2 (± 0.7)	1.1 (± 0.7)	1.3 (± 0.5)	0.6 (± 0.5)

Table 2. Correlation between different variables.

The data set comprises of surface and bottom samples. BP: bacterial production; BR: bacterial respiration; BGE: bacterial growth efficiency; DIP: dissolved inorganic phosphate ; PP: primary productivity; DOC: dissolved organic carbon.

*p < 0.05, **p < 0.01, ***p < 0.001, ns = not significant.

^a pre-monsoon season only.

Parameters	Estuaries (n = 24)	Coastal waters ^a (n = 8)
BP and BGE	0.92***	0.75**
BP and BR	ns	0.75**
C/N ratio and BGE	0.69***	0.80**
DIP and BP	0.51**	ns
PP and DOC	ns	0.68*
PP and BP	0.64*	ns

Table 3. Seasonal variations of biological parameters used for bacteria mediated carbon flow.

Mean \pm Standard deviation of surface and bottom samples are shown.

^a Non-mon: Non-monsoon ; Mon: Monsoon.

BP: bacterial production; PP: primary productivity; BGE: bacterial growth efficiency;

CFTB: carbon flux through bacterioplankton.

Parameters	Mandovi estuary			Zuari estuary			Coastal waters
	Average (n = 24)	Non-mon ^a (n = 16)	Mon ^a (n = 8)	Average (n = 24)	Non-mon (n = 16)	Mon (n = 8)	Non-mon (n = 16)
BP/PP	0.84 (± 3.10)	0.19 (± 0.06)	1.49 (± 6.14)	1.02 (± 0.41)	0.13 (± 0.07)	1.90 (± 0.74)	0.59 (± 0.22)
BGE (%)	27 (± 16.0)	22 (± 12.0)	31 (± 20.0)	28 (± 11.2)	17 (± 6.9)	38 (± 15.5)	12 (± 5.6)
CFTB/PP (%)	284 (± 404)	87 (± 38)	481 (± 770)	288 (± 402)	76 (± 64)	500 (± 740)	435 (± 207)