

Mesozooplankton production, grazing and respiration in the Bay of Bengal: Implications for net heterotrophy

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ABSTRACT

Mesozooplankton samples were collected from the mixed layer depth along a central (along 88°E) and a western transect in the Bay of Bengal during four seasons covered between 2001 and 2006 in order to investigate spatio-temporal variability in their biomass. At these stations, grazing and respiration rates were measured from live zooplankton hauled in from the surface during December 2005. Akin to the mesozooplankton “paradox” in the central and eastern Arabian Sea, biomass in the mixed layer was more or less invariant in the central and western Bay of Bengal, even as the chl *a* showed marginal temporal variation. By empirical equation, the mesozooplankton production rate calculated to be 70- 246 mg C m⁻² d⁻¹ is on par with the Arabian Sea. Contrary to the conventional belief, mesozooplankton grazing impact was up to 83% on primary production (PP). Low PP coupled with very high zooplankton production (70% of PP) along with abundant bacterial production (50% of the PP; Ramaiah et al. 2009) is likely to render the Bay of Bengal net heterotrophic, especially during the spring intermonsoon. Greater estimates of fecal pellet-carbon egestion by mesozooplankton compared to the average particulate organic carbon flux in sediment traps, implies that much of the matter is recycled by heterotrophic communities in the mixed layer facilitating nutrient regeneration for phytoplankton growth. We also calculated that over a third of the primary production is channelized for basin-wide zooplankton respiration that accounts for ~ 52 M tC annually. In the current scenario of global warming, if low (primary) productive warm pools like the Bay of Bengal continue to be net heterotrophic, negative implications like enhanced emission of CO₂ to the atmosphere, increased particulate flux to the deeper waters and greater utilization of dissolved oxygen resulting in expansion of the existing oxygen minimum zone are imminent.

Key words: Biomass, abundance, copepods, growth rates, spatio-temporal variability

1. Introduction

Zooplankton are distributed throughout the world ocean and contribute 21 Gt to its living biomass (Conover 1978). These heterotrophs ingest organic carbon for their growth, production, and respiration and the unassimilated carbon is defecated. Zooplankton grazing is ascribed as the main process responsible for the steady-state of phytoplankton biomass in open-ocean oligotrophic regions (Venrick 1990). This means that phytoplankton is grazed on by zooplankton at the same rate as they are produced. Small bodied zooplankton such as the copepods exerts considerable grazing impact by virtue of their greater abundance (Turner 2004). This may also be the case in the tropics where this group is particularly abundant (McKinnon and Duggan, 2003).

Growth represents one of the most important trophodynamic processes in marine ecosystems (Kiørboe, 1997) is measured in many ways (Runge and Roff, 2000). Temperature, body size, and food availability have been demonstrated to have significant effects on copepod growth (Hirst and Lampitt, 1998). Using temperature and body weight as the important criteria, indirect estimates of zooplankton growth ranging from 0.08 to 0.18 d⁻¹ and production from 24 to 576 mg C m⁻² d⁻¹ were derived for the Arabian Sea (Roman et al. 2000). We used similar equation to derive the mesozooplankton community growth rate in the Bay of Bengal.

Closely coupled to growth, zooplankton respiration alone is reported to account for 42-72% of the total energy (Omori and Ikeda 1984). Del Giorgio and Duarte (2002) reported that respiration consumes more organic matter than estimated autotrophic biomass in the ocean. In tropical oceanic areas where abundances of food organisms for mesozooplankton are generally low *vis a vis* their neritic counterparts (Paffenhöfer et al. 2003), most of the primary production is mineralized through heterotrophic respiration. In a recent study by Duarte et al (2013) based on the Pacific, Atlantic and the South Indian Ocean estimate, increased respiration due to prevalence of heterotrophic communities is predicted in warmer regions dominated by riverine inputs and low gross primary production and chlorophyll *a*. However, such data is absent from the northern Indian Ocean.

Because of the significant role that zooplankton play in the transformation of organic matter (Marshall 1973), these rates must be quantified in order to understand the energy transfer and matter cycling through zooplankton in pelagic ecosystems. Grazing and metabolic rates have been extensively studied in the coastal and productive areas particularly from the Pacific and Atlantic oceans (Le Borgne 1982, Dam et al. 1995, Zhang et al. 1995, Roman and Gauzens 1997, Harrison et al. 2001, Huskin et al. 2001 a, b, Roman et al. 2002a, b; Calbet et al. 2009; Decima et al. 2011; Schukat et al. 2013), In the Indian

Ocean, such studies are scarce (Mullin 1966; Smith 1982, Petipa 1985, Sazhina 1985). Since the vast oligotrophic ocean contributes up to 80% of the global ocean production (Karl et al 1996), studies in these areas need urgent attention. However in the tropics where more than 50 copepod species exist in the surface layer at any given time (Grice and Hart 1962, Timonin 1971), it is impractical to emphasize on rates of individual species.

The Bay of Bengal Process Studies during 2001-2006 was an opportunity for us to carry out our first measurements on growth, production, grazing and respiration rates of copepods in an intensely stratified and low productive tropical ocean environment. For this, we collected mesozooplankton samples from the mixed layer during 4 different seasons during 2001 and 2006 and measured the vital rates during December 2005. Since the spatio-temporal variability in biological parameters in the central and western Bay is only minimal, the grazing and respiration rates measured on ship during winter monsoon period were applied to the mesozooplankton abundance measured during all four cruises undertaken in the Project. By doing this, we derived an annual picture of carbon flow through biological entities in the Bay of Bengal and attempted to answer a key question; whether the zooplankton production in the Bay of Bengal favor net heterotrophy?

2. Materials and Methods

2.1. Sampling and hydrographic characteristics

Sampling was carried out along 88°E in the central-(open ocean transect) and in the western (coastal transect) Bay of Bengal (Fig. 1) during July 6-August 2, 2001 (summer monsoon-SUM), September 14-October 12, 2002 (fall intermonsoon-FIM), April 10- May 10, 2003 (spring intermonsoon-SpIM) and November 25, 2005- January 7, 2006 (winter monsoon-WM). Temperature and salinity were recorded with a conductivity- temperature-depth (CTD; Seabird Electronics) rosette at every one degree interval between 9°N and 20°N in the offshore and coastal transects. These readings were used to discern the mixed layer depths.

*2.2. Chlorophyll *a**

Seawater for chlorophyll *a* (chl *a*) measurement was collected by 12-L Go-Flo bottles (General Oceanics, Miami, FL, USA) during CTD casts at 8 depths in the upper 120 m. Duplicate 1L samples were filtered through GF/F filters, to extract overnight in 90% acetone. Under dim lit conditions, chl *a* fluorescence was measured before and after acidification, by a fluorometer (Turner Designs, USA, 10-AU-005- CE; UNESCO, 1994) following the JGOFS Protocols (UNESCO, 1994).

2.3. Primary Productivity

Details of PP measurements carried out during different seasons from the top 120 m are published in Madhupratap et al (2003). In brief, water samples were collected from 8 depths at predawn in three light and one dark polycarbonate bottles (Nalgene, Germany), inoculated with one ampoule of $\text{NaH}^{14}\text{CO}_3$ (Board of Radiation and Isotope Technology, Mumbai; Specific activity 185 kBq) each and incubated *in situ* from sunrise to sunset. The contents of the bottles were filtered by GF/F filters (47 mm diameter, 0.7 μm pore size, Whatman, USA), fumed with 0.5 N HCl, and stored in scintillation vials. After adding liquid scintillation cocktail (Sisco Research Laboratory, Mumbai), ^{14}C incorporated in phytoplankton cells was measured in a scintillation counter (PerkinElmer Wallac 1409 DSA, USA) and expressed as $\text{mg C m}^{-2} \text{ day}^{-1}$ for 0–120 m column (UNESCO, 1994).

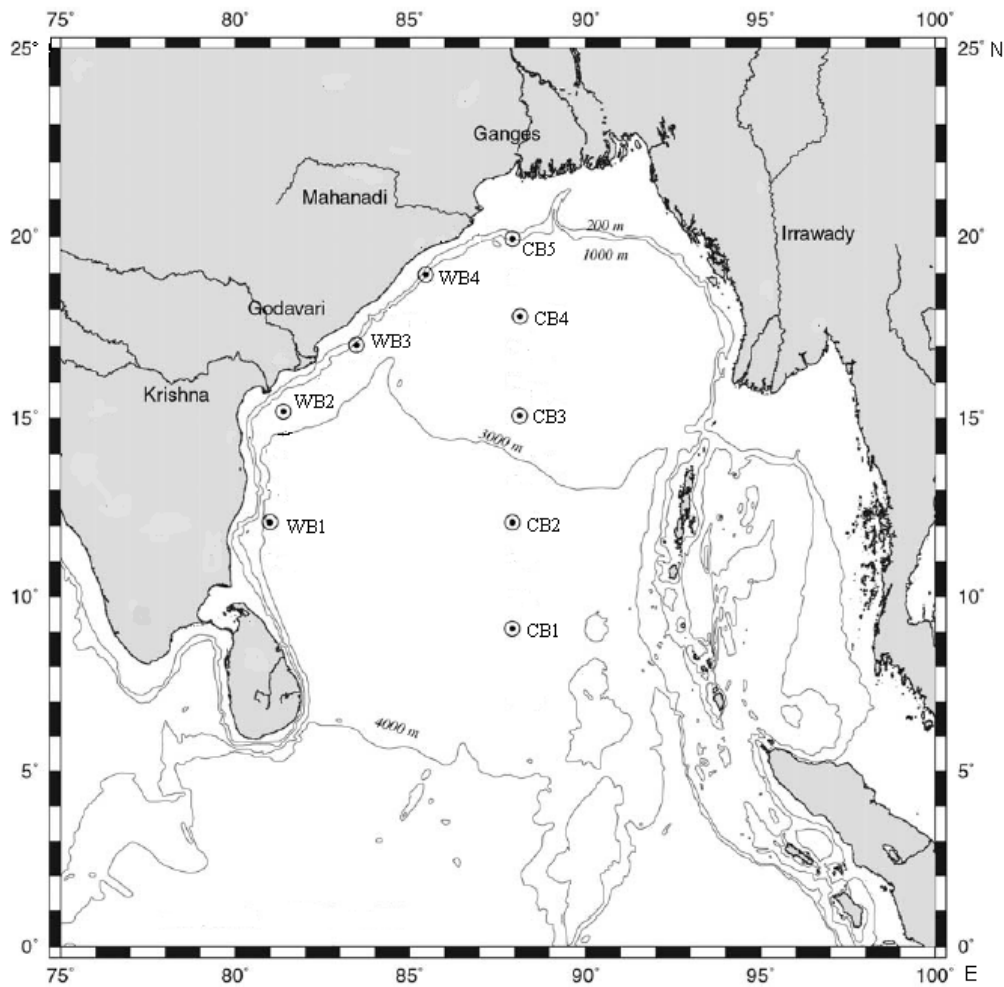


Fig. 1 Study area with sampling locations for mesozooplankton and other physico-chemical parameters. Stations CB1 to CB5 are along the central transect (88°E) and WB1 to WB4 are in the western Bay of Bengal.

2.4. Zooplankton collection, biomass, abundance and copepod species analysis

Mesozooplankton were collected during the day and the night by vertical tows of a multiple opening/closing plankton net (Multinet[®] Hydrobios; 200- μm mesh size; 0.25- m^2 mouth area) from 1000 m depth to surface. The net was hauled up at a speed of 0.8 m/s, and the volume of water filtered through the net was calculated from the product of depth and mouth area of the net. Only the mixed layer data has been used for this study.

Zooplankton biomass was determined by the displacement volume method (Harris et al. 2000). The biovolume was then converted to carbon equivalent using the relationship detailed by Madhupratap et al. (1981). Using $\leq 50\%$ sample, zooplankton abundances were estimated using stereozoom microscope (Olympus, Japan, 90x) and identified using standard identification keys (UNESCO 1968; Kasturirangan 1963).

2.5. Rate measurements

At each station, surface zooplankton samples were collected using a Bongo net during the WM cruise (November 2005- January 2006) for grazing and respiration measurements and were immediately transferred into 0.45- μm pre-filtered surface seawater.

2.5.1. Growth

The potential growth rate (g) of mesozooplankton was calculated indirectly by the method of Hirst and Shearer (1997). Average temperature of the upper 120 m water column was used in the equation considering that zooplankton as well experience the temperatures below the mixed layer during their descent during vertical migration. It was assumed that the predominant copepods comprised all of the measured mesozooplankton biomass after taking out macroscopic gelatinous individuals. Individual copepod weight for the 200-500 μm fraction was taken as 2.04 $\mu\text{g C}$ (Roman et al. 2000) and rates of copepod production were derived from the product of the estimated growth rate and biomass.

Intrinsic growth rate g (d^{-1}) = $0.0732 \times 10^{0.0246T} / W_c^{0.2962}$ where,

T ; $^{\circ}\text{C}$ is the average temperature of the top 120 m water column and W_c , $\mu\text{g C individual}^{-1}$ is the copepod carbon weight

Production P ($\text{mg C m}^{-2} \text{d}^{-1}$) = $B \times g$, where, B , mg C m^{-2} is the zooplankton biomass.

2.5.2. Grazing

Zooplankton grazing was measured employing the gut fluorescence technique (Mackas and Bohrer 1976) with some modifications. For measuring the gut pigments, at zero time itself, ~25 ml seawater was filtered by 200 µm mesh. Under low power and dim light, 30 copepods were picked and transferred into 10 ml 90 % cold acetone maintained at 4°C in the dark without homogenization (Morales et al. 1991) for extraction for 24 h. Similar number of copepods were picked every 15 min for 150 min and the same procedure was repeated. After extraction, the sample was thawed and chlorophyll (chl) *a* was measured in a fluorometer (AU-10 Turner designs, USA). The extract was then acidified with 0.1 ml of 10% HCl and fluorescence measured again for phaeopigments. The calculations for the gut pigments mentioned below were done according to (Harris et al. 2000).

$$\text{Chl } a \text{ (ng copepod}^{-1}\text{)} = (T / (T-1)) \times (R_b - R_a) \times F_d \times v / n$$

$$\text{Phaeopigment (ng copepod}^{-1}\text{)} = (T / (T-1)) \times ((T \times R_a) - R_b) \times F_d \times v / n$$

where; T = acidification coefficient (R_b/R_a obtained through the calibration of the fluorometer); R_b = reading before acidification; R_a = reading after acidification

F_d = fluorometer calibration factor (ng liter⁻¹); v = volume of extraction (ml);

n = number of copepods

$$\text{Gut content (G, ng pigment copepod}^{-1}\text{)} = (1.51 \times \text{conc. of phaeopigment}) + \text{conc. of chl } a.$$

The gut evacuation rate constant (K) was calculated from the decline in gut pigment content with time t: $G_t = G_0 \times e^{-Kt}$ where; G_t = pigment concentration at time t; G₀ = pigment concentration immediately after collection (time t₀).

Ingestion rates (I, ng chl eq. copepod⁻¹ h⁻¹) were calculated from the product of gut pigment content and gut evacuation rate constant: $I = G \times K$.

Egestion (fecal pellet production; E) was assumed to be 30% of I (Conover 1978). Daily grazing rate of the mesozooplankton community (mg C m⁻² d⁻¹) was estimated as the product of ingestion rate, copepod abundance and 24 hrs of a day. Here we assumed that copepods of similar body sizes have similar ingestion rates under the same environmental conditions (Morales et al. 1990). The carbon: chl *a* ratio was taken as 50 (Banse 1988).

2.5.3. Respiration

Respiration rate was measured following Mayzaud and Dallot (1973). For this, ~30 copepods and streptomycin (50 mg L⁻¹) were added to a set of two 125 ml bottles containing 0.2 µm filtered seawater. Replicates of experimental, and control bottles without copepods were incubated at room temperature (28 °C) in dark for 12 h. Care was taken to avoid any air bubble while filling the bottles or at the time of transferring the copepods. At the end of the incubation, it was ensured that the animals were swimming and alive. The bottles were fixed with Winkler A and B and the initial and the final concentrations of dissolved oxygen were estimated by the standard Winkler method (Grasshoff et al. 1983) using 665 Dosimat Metrohm, Switzerland. Oxygen respired by copepods was calculated according to Omori and Ikeda (1984):

$$R (\mu\text{l O}_2 \text{ copepod}^{-1} \text{ d}^{-1}) = ((C_0 - C_t) - (C_0 - C_t')) \times (V_e - V_z) / (t \times N)$$

Where C₀= Oxygen concentration (ml L⁻¹) at time 0, C_t= oxygen concentration (ml L⁻¹) in experimental bottle, C_t'= oxygen concentration (ml L⁻¹) in control, V_e= volume of experimental bottle in litres, V_z= volume of zooplankton, t= incubation time in days, N= number of copepods.

Since zooplankton are ammonotelic animals, a respiration quotient of 0.97 was used for converting oxygen consumed into carbon mineralized (Omori and Ikeda 1984). The values of respiration rate per copepod obtained during this cruise were multiplied with the number of copepods per square meter area sampled from the mixed layer during each of the four cruises to get the daily respiration rates for zooplankton community as done for ingestion rates.

2.6. Basin-wide energy conversion estimates

For obtaining the basin-wide estimates of carbon, data on zooplankton production (ZP), grazing, egestion, respiration and primary production (PP) in carbon units per meter square per day for four seasons using the above methods were extrapolated for 365 days of the year and basin-wide area of 2.2 x 10⁶ km² of the Bay of Bengal to yield values in M tC y⁻¹.

2.7. Data analysis

Differences in biomass and numerical abundance of zooplankton and all the physicochemical parameters in the study were tested separately for spatial and temporal differences with Friedman Anova using software *Statistica 6.0*. Correlation analysis was carried out to see the effect of environmental variables on the zooplankton vital rates with *Microsoft Excel Data analysis software*.

3. Results

3.1. Environmental data

Surface salinity varied from 27.7 to 33.9 in the central Bay and from 20.7 to 34.0 in the western Bay. Salinity was lower during SUM and FIM and was the highest during SpIM. Except during WM, the sea surface temperature (SST) was usually $>28^{\circ}\text{C}$ with the maxima generally during SpIM followed by FIM along both transects. The mixed layer varied between 2m and 55 m during the four sampling periods, mostly shoaling northwards during SUM and FIM periods. Details on the hydrography are given in Prasanna Kumar et al. (2007, 2010b).

Among seasons, the column-integrated chlorophyll (chl) *a* varied significantly from 9 to 23 mg m^{-2} in the central Bay (Chi sqr. [$N=5$, $df=3$]=9.7, $p<0.05$) with the highest concentration during winter monsoon. In the western Bay, chl *a* varied from 11 to 43 mg m^{-2} with the highest value during SpIM, and moderate during WM. However the variation was not significant (Chi sqr. [$N=4$, $df=3$]=3.9 $p>0.05$). The chl-carbon biomass ranged from 518 to 1023 mg C m^{-2} in the central- and from 688 to 1212 mg C m^{-2} in the western Bay (Ramaiah et al. 2010). The lowest Chl *a* biomass was observed during SUM in both transects. Subsurface Chl *a* maximum was found between 40 and 60 m in the central Bay and between 20 and 60 m in the western Bay and was deepest, at 80 m during the SpIM season in both transects.

Detailed values of primary productivity are available in Ramaiah et al. (2010). In brief, average column integrated primary production in the central Bay varied significantly from 144 $\text{mg C m}^{-2} \text{d}^{-1}$ during the SUM to 375 $\text{mg C m}^{-2} \text{d}^{-1}$ during WM (Chi Sqr. [$N = 5$, $df = 3$] = 8.28 $p < 0.05$). In the western Bay, PP varied marginally from 280 $\text{mg C m}^{-2} \text{d}^{-1}$ during the WM to 366 $\text{mg C m}^{-2} \text{d}^{-1}$ during SPIM (Chi Sqr. [$N = 4$, $df = 3$] = 3.60 $p > 0.05$).

3.2. Zooplankton biomass, abundance and composition in the mixed layer

Since zooplankton biomass (CB: Chi Sqr. [$N = 4$, $df = 4$] = 3.0 $p > 0.05$ and WB: Chi Sqr. [$N = 4$, $df = 3$] = 2.1 $p > 0.05$) and abundance (CB: Chi Sqr. [$N = 4$, $df = 4$] = 0.60 $p > 0.05$; WB: Chi Sqr. [$N = 4$, $df = 3$] = 0.30 $p > 0.05$) showed insignificant variability among stations in both transects sampled, the data presented hereafter will be average and standard deviation values of 5 stations in the central Bay and 4 stations in the western Bay for four sampling periods.

Zooplankton biomass integrated for the mixed layer varied insignificantly during the sampled periods. In the central Bay, it ranged from 360 mg C m^{-2} during WM (Table 1) to 812 mg C m^{-2} during SpIM (Chi

Sqr. [N = 5, df = 3] = 1.16 $p > 0.05$). In the western Bay, the biomass was low during SUM and FIM (295 and 291 mg C m⁻²) and was the highest during SpIM (1012 mg C m⁻², Chi Sqr. [N = 4, df = 3] = 1.50 $p > 0.05$).

Abundance of zooplankton individuals in the central Bay varied from 6785 to 22881 ind. m⁻² and from 10256 and 34763 ind. m⁻² in the western Bay (Table 1). In both transects, seasonal average was the highest for the intermonsoons and the lowest for SUM (Chi Sqr. [N = 5, df = 3] = 1.0 $p > 0.05$; WB: Chi Sqr. [N = 4, df = 3] = 6.0 $p > 0.05$). Also, the average zooplankton in the western Bay (27500 ind. m⁻²) was nearly double that in the central (15398 ind. m⁻²) Bay.

Zooplankton was represented by the predominant group Copepoda varying between 74 and 87% in the central- and 81-88% of the total numerical abundance in the western Bay (Table 1). The copepods were mostly small sized and *Oncaea venusta* was generally the most abundant species during all sampling periods. This species contributed 13-37% to the total copepod abundance in the central Bay with the maximum abundance during SUM and, in the western Bay, it ranged from 7% to 19%. In all other seasons when its abundance was relatively less, species such as *Paracalanus indicus*, *Clausocalanus arcuicornis* and *Acartia spinicauda* co-dominated.

3.3. Zooplankton growth and production rates

Growth rate, derived mostly as a function of temperature in the top 120 m, did not vary between stations in CB (Chi Sqr. [N = 4, df = 4] = 3.6 $p > 0.05$) and WB (Chi Sqr. [N = 4, df = 3] = 2.7 $p > 0.05$). The variation between seasons was significant only in the CB (Chi Sqr. [N = 5, df = 3] = 9.7 $p < 0.05$) where it averaged 0.24 d⁻¹ during SUM and FIM, and 0.26 d⁻¹ during WM and SpIM (Fig. 2a). In the western transect, it was the lowest at 0.23 d⁻¹ during WM, moderate at 0.25 d⁻¹ during FIM and higher at 0.26 d⁻¹ during SUM (Chi Sqr. [N = 3, df = 3] = 0.2 $p > 0.05$).

Using the growth rate and measured biomass in different seasons, we calculated the secondary/zooplankton production rate (Fig. 2b). It ranged from 94 to 225 mg C m⁻²d⁻¹ in the central Bay (Chi Sqr. [N = 5, df = 3] = 1.3 $p > 0.05$) and from 70 to 247 mg C m⁻²d⁻¹ in the western Bay, Chi Sqr. [N = 3, df = 3] = 1.0 $p > 0.05$). Zooplankton production greater during SpIM in both transects.

Table 1. Mean biomass (mg C m⁻²) and abundance (ind. m⁻²) of mesozooplankton, percentage (in parenthesis) of copepods* and their dominant species occurring in the mixed layer during different seasons.

	Summer 2001	monsoon	Fall intermonsoon 2002	Winter monsoon 2005	Spring 2003	Intermonsoon
Central Bay						
Biomass	552±381		544±390	360±247	812±892	
Abundance	6785(87)* ±7191		21973(74)* ±26448	9953(74)* ±9954	22881(78)* ±26805	
Dominant species	<i>Oncaea</i> (37)	<i>venusta</i>	<i>Paracalanus</i> (26) <i>O. venusta</i> (23)	<i>indicus</i> <i>O. venusta</i> (20), <i>C. arcuicornis</i> (10), <i>Oithona similis</i> (9)	<i>C. arcuicornis</i> (22), <i>O.venusta</i> (13)	
Western Bay						
Biomass	295±305		291±201	494±217	1012±1226	
Abundance	10256(88)* ±17014		34763(81)* ±14782	30565(82)* ±21766	34417(82)* ±49626	
Dominant species	<i>P. indicus</i> (17), <i>O. venusta</i> (15)		<i>O. venusta</i> (13), <i>Acartia spinicauda</i> (9)	<i>O. venusta</i> (19), <i>P. indicus</i> (8)	<i>O.venusta</i> (7), <i>C. arcuicornis</i> (7), <i>Pleuromamma indica</i> (7)	

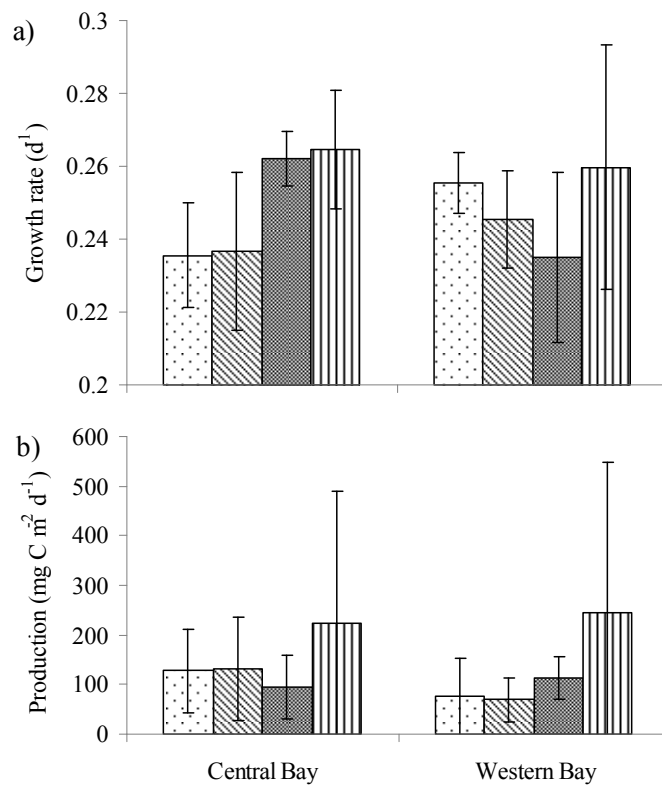


Fig. 2 Temporal variation of copepod growth and production rates in the central and western Bay of Bengal. Error bars indicate standard deviation of 5 stations in the central Bay and 4 stations in the western Bay during summer monsoon (SUM), fall intermonsoon (FIM), winter monsoon (WM) and spring intermonsoon (SpIM) season.

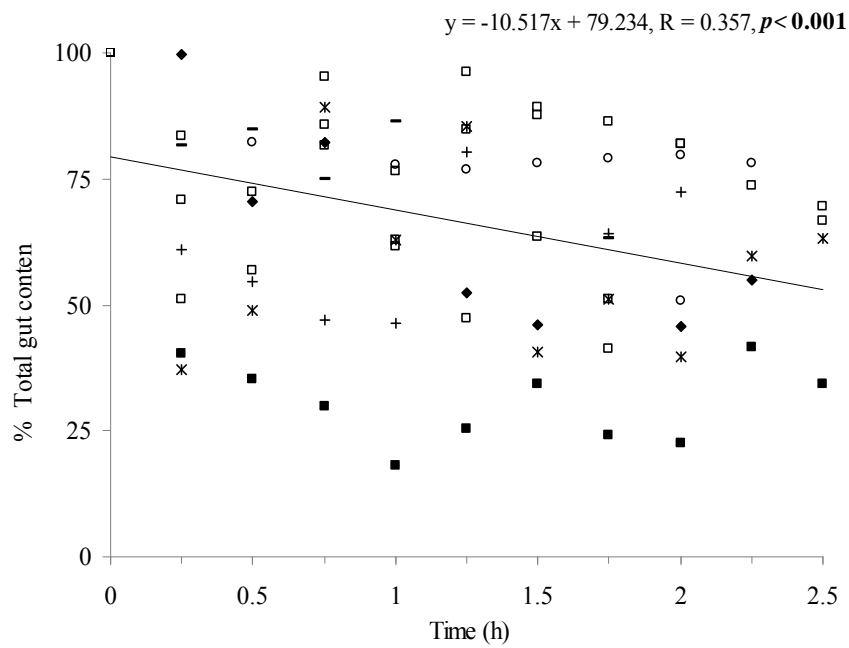


Figure 3. Variation in copepod gut pigment content (chl *a* and phaeopigments) with increasing starvation time

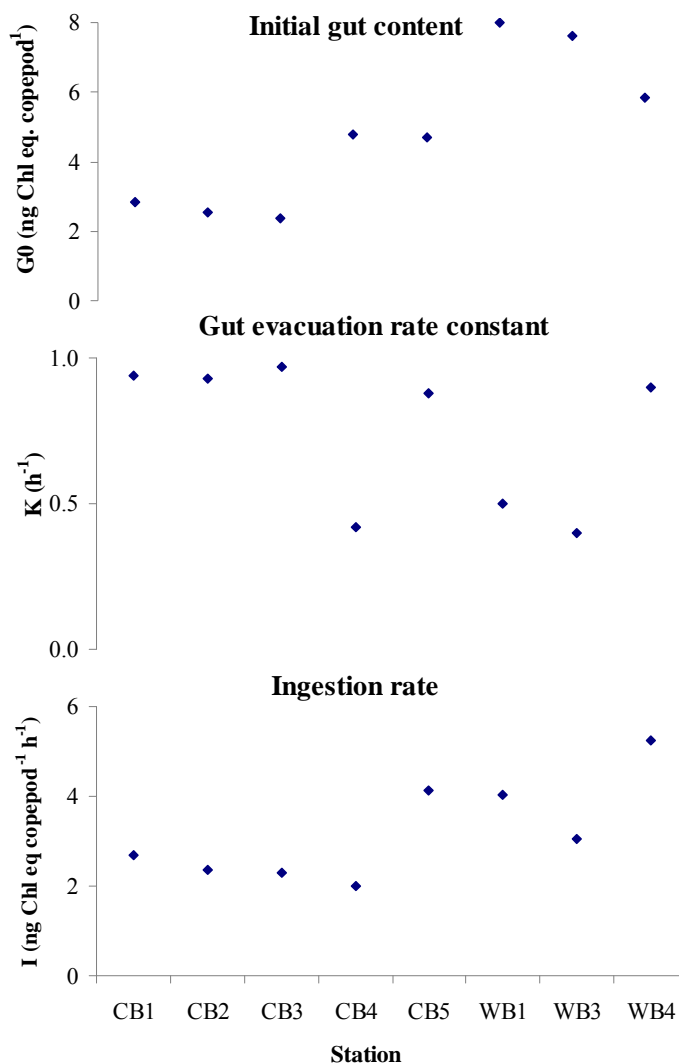


Fig.4 Spatial variability of initial gut content (G_0), gut evacuation rate constant (K) and ingestion rate (I) measured in copepods at different stations in the Bay of Bengal.

3.4. Gut pigments, ingestion and egestion rates of copepods

During the course of gut evacuation experiment, the gut content significantly decreased with increasing starvation time (Fig 3). Initial chl *a* concentrations from guts of freshly caught copepods during the measurements of gut fluorescence at various stations were found to be ranging from 1.8 to 5.2 ng copepod⁻¹. Similarly, the phaeopigment concentration ranged from 0.1 to 1.7 ng copepod⁻¹. The total initial pigment concentration (G_0) comprising the chlorophyll *a* and the phaeopigment in guts of live copepods ranged from 2.4 to 8 ng chl eq copepod⁻¹ (Fig. 4). In the central Bay, G_0 was higher at station

CB4 and CB5 and in the western Bay; it was higher at all the stations. The chlorophyll contained in the guts of the copepods in the western Bay was double than in the central Bay.

The gut evacuation rate (K) constant measured at different stations during WM cruise ranged from 0.4 to 0.94 h⁻¹, giving a gut clearance time estimate of 1.1-2.5 h (Fig. 4). The ingestion rate observed was 2.0-5.25 ng chl eq. copepod⁻¹ h⁻¹ and the rate of egestion of fecal pellets was assumed to be 0.6 and 1.58 ng chl eq. copepod⁻¹ h⁻¹. Complementing the abundance of zooplankton in various seasons, the daily grazing rate of the community ranged from 26-88 mg C m⁻² d⁻¹ in the central Bay and 39-133 mg C m⁻² d⁻¹ in the western Bay (Fig. 5a). Similarly, the fecal pellet egestion was estimated to be 8- 26 mg C m⁻² d⁻¹ in the central Bay and 12- 40 mg C m⁻² d⁻¹ in the western Bay (Fig. 5b). Correspondingly, the amount of phytoplankton-carbon ingested by grazers, and the amount lost to the surrounding water as fecal pellets was higher during both the intermonsoons in the central Bay and also during WM in the western Bay. Similarly, these rates in the western Bay were also twice that in the central Bay.

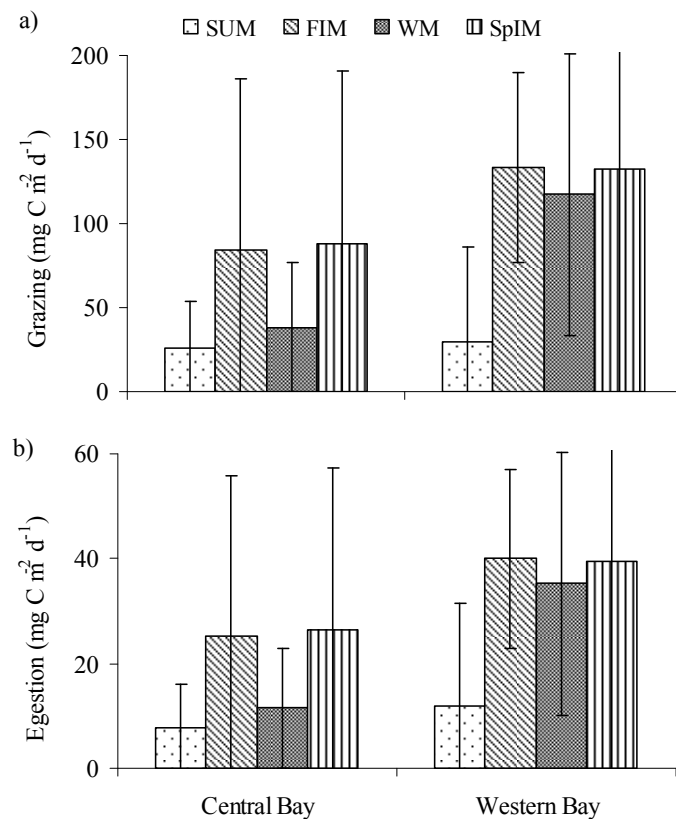


Fig. 5. Temporal variation in rates of copepod grazing and egestion of fecal pellets in the central and western Bay of Bengal. Error bars indicate standard deviation in each season of 5 stations in the central Bay and 4 stations in the western Bay.

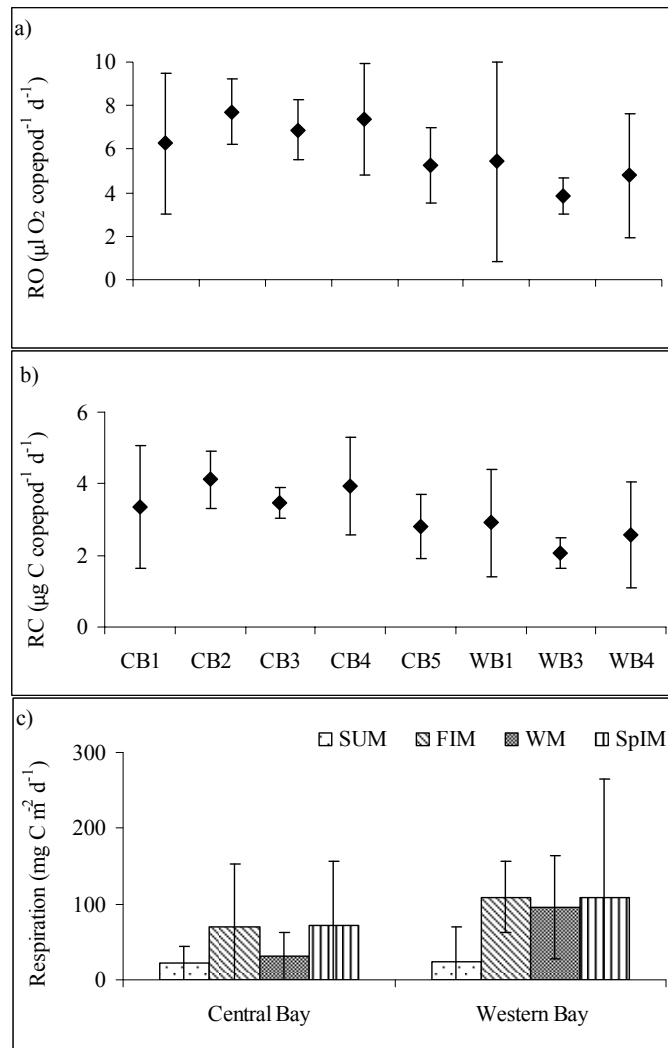


Fig. 6 Spatial variation in copepod respiration in terms of oxygen consumed (RO), carbon requirement (RC) and, temporal variation of respiration by zooplankton community in the mixed layer of central and western Bay of Bengal. Error bars in figures a) and b) indicate standard deviation of three measurements taken at each station. Error bars in figure c) indicate standard deviation in each season of 5 values (stations) in the central Bay and 4 stations in the western Bay.

3.5. Respiration rates of copepods

The oxygen consumption rates for respiration (RO; Fig. 6a) by copepods collected from the surface waters of the Bay of Bengal varied from 3.9 to 7.7 $\mu\text{l O}_2 \text{ copepod}^{-1} \text{ d}^{-1}$ at different stations during the WM period. The corresponding carbon requirement (RC; Fig. 6b) was 2.2-

4.1 $\mu\text{g C copepod}^{-1} \text{ d}^{-1}$. Higher values of respiration occurred in the central Bay and the lower values occurred in the western Bay. The carbon mineralized due to mesozooplankton community respiration in the mixed layer ranged from 21-71 $\text{mg C m}^{-2} \text{ d}^{-1}$ in the central Bay (Fig. 6c), with higher values during intermonsoons. This variation in zooplankton community respiration is mainly due to the variation in

zooplankton biomass during the various sampling periods. In the western Bay, the rate in the range of 24-109 mg C m⁻² d⁻¹ was similarly higher during all but SUM season.

3.6. Ratios of zooplankton grazing, respiration and production to primary production

The zooplankton grazing ratio (G: PP) ranged from 25% during WM to 83% during SpIM in the CB (Fig. 7a). In the WB, it ranged from 18% during SUM to 71% during WM. Varying similarly, the daily respiration rates (Fig. 7b) were 21%-68% of the daily PP in the CB with higher value in SpIM. In the WB, it ranged from 14% to 58% with higher values in WM and SpIM. Ratio of zooplankton production to primary production (ZP: PP) was a minimum of 50% during FIM and WM and 128% during SpIM in the CB (Fig.7c). In the WB, it was 26% in FIM to 118 % in SpIM. The variability was very large during SpIM, where aberrantly large biomass was found at only 2 stations.

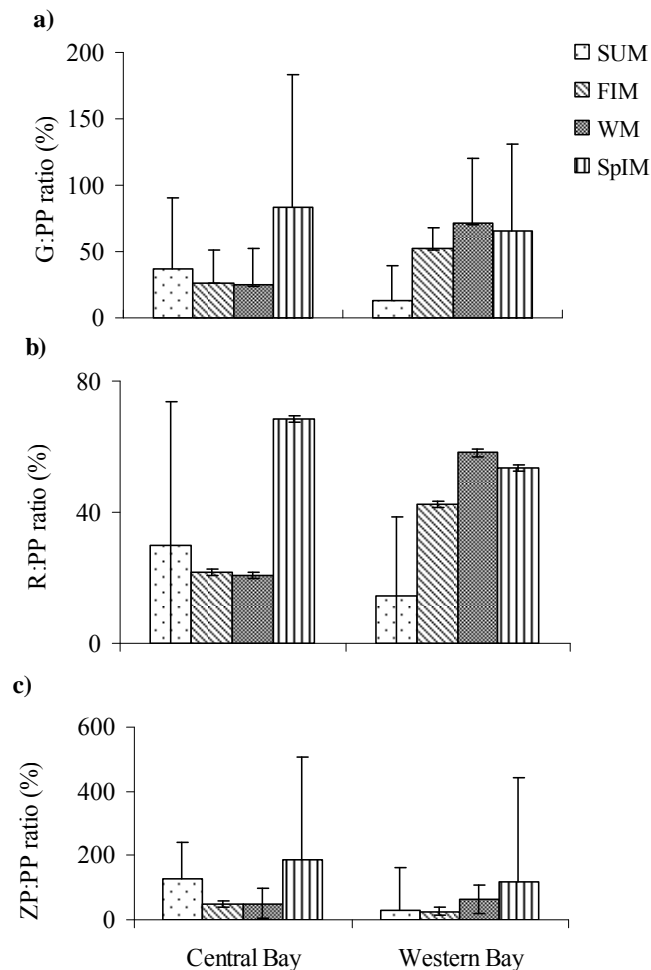


Fig. 7. Seasonal variation of ratios of zooplankton- production (ZP), grazing (G) and respiration (R) to primary production (PP) in the Bay of Bengal. Error bars indicate standard deviation in each season of 9 values (5 stations in the central Bay and 4 stations in the western Bay).

4. Discussion

4.1. Temporal variability in Zooplankton biomass

Spatial and/or temporal variability is largely governed by the seasonal changes in physico-chemical parameters, that affect concentrations of nutrients and chl *a*. Upwelling in the central Arabian Sea, and along the west coast of India during summer monsoon (June-August), leads to very high primary production supporting the extant zooplankton biomass (445-616 mg C m⁻²). From the earlier studies, eg., Joint Global Ocean Flux Study, it is observed that the mesozooplankton biomass in the mixed layer is more or less invariant (Madhupratap et al. 1996). Winter cooling during December-February and microbial loop during fall- (September-October) and spring- (March-May) intermonsoons help sustain such invariant biomass (Madhupratap et al. 1996).

Unlike in the western Indian Ocean as well as along the west coast of India, the Bay of Bengal –the eastern arm of the Indian Ocean- does not show signs of strong upwelling during any season (Vinayachandran and Shetye 1991). Observations during the International Indian Ocean Expedition (Panikkar and Rao 1973) and those later (see Madhupratap et al. 2003) highlight winter monsoon peaks in zooplankton biomass. Recently, spatial variability in zooplankton biomass, abundance and composition in the Bay during summer monsoon and fall intermonsoon seasons were reportedly attributed to mesoscale cold core eddies (Fernandes 2008; Fernandes and Ramaiah 2009; Fernandes and Ramaiah 2013).

After taking all the 4 study periods into account, we observed a general lack of significant spatial and temporal variability in mesozooplankton biomass and abundance in the Bay of Bengal. Incidentally, highest zooplankton biomass was found in the western bay during the spring intermonsoon, where the highest chlorophyll *a* concentrations were also noticed (Ramaiah et al 2010). The analysis of $\delta^{15}\text{N}$ values by Kumar and Ramesh (2005) has clearly shown that the phytoplankton in the central region was supported by new production through nutrients injected from the deep water and one such likely mechanism is cold core eddies as reported variously by Prasanna Kumar et al (2004, 2007, 2010). However in the western regions, terrestrial source was major. Some authors (Madhupratap et al. 1996; Jyothibabu et al. 2008) have frequently attributed the enhanced zooplankton stocks during SpIM to the microbial loop which dominates during this season in seas around India, when water column is thermally stratified. The same phenomenon was observed recently off the Gulf of Mannar and Palk Bay in the southern Bay of Bengal (Anjusha et al. 2013). There are not many studies reporting the seasonal variability in zooplankton biomass from the tropical open oceans. Most recent study by Yamaguchi et al

(2015) investigating epipelagic zooplankton in the top 150 m along 150°E has also shown that the biomass and its seasonality is lowest in the lower latitudes.

4.2. Grazing

Mesozooplankton grazing rate estimations in the tropical water are limited. In the Indian Ocean, the only grazing study was carried out in the Arabian Sea based on the dual isotope uptake method (Roman et al 2000). Scant biological measurements in the past half century reveal low primary production (reviewed in Prasanna Kumar et al 2010b) and zooplankton biomass (Achuthankutty et al 1980, Nair et al 1981, Rakshesh et al 2006) in the Bay of Bengal. However no mesozooplankton grazing measurements have ever been documented. From studies of Roman and Gauzens (1997), regions like this where diatoms and copepods predominate, hold a high grazing potential. The gut fluorescence method of estimating the ingestion rates of copepods is in use for more than 3 decades and comparisons with direct measurements of ingestion rates by other methods have yielded similar values (Peterson et al. 1990) To be contextual, we have compared the available data on grazing rates and ratios from the subtropical and temperate regions with the present observations (Table 2).

In this study, the gut fluorescence ranging from 1.8-5.2 ng chl *a* copepod⁻¹ in freshly caught copepods is comparable to the range of 0.1-16 ng chl *a* ind⁻¹ found in the temperate waters. Though higher gut fluorescence coinciding with higher chl *a* levels was found in the western Bay, the lack of significant positive correlation between them during WM is suggestive that gut pigment does not always relate to chlorophyll availability in the environment. As Besiktepe et al. (2005) and many others point out, such poor relationships are attributed to many factors such as evacuation of guts by copepods before freezing and even changes in phytoplankton composition at sampling stations. As the degree of pigment destruction during the digestion processes is highly variable in this method (Dam and Peterson, 1988; Head and Harris, 1996), no correction for pigment destruction was made on the assumption that there was little pigment destruction at the low food concentration (Penry and Frost, 1991). The number of phytoplankton cells found in the euphotic zone including all the study periods ranged from 40 – 23296 cells L⁻¹ (See Paul et al. 2008).

The values of gut evacuation rate constants (K : 0.4-0.94 h⁻¹) and gut transit times (1.1 to 2.5 h) are similar to those reported in the literature on subtropical copepods (Table 2). Dam and Peterson (1988) found a gut evacuation rate constant of 3.5 h⁻¹ for copepods at a temperature of 20 °C and have shown that the rate constant is higher at higher temperature. Relatively slower gut evacuation rates were observed by some in the temperate oceans (Dagg and Wyman 1983; Tsuda and Nemoto 1987). In

oceanic regions where temperature does not fluctuate rapidly, K varies with food concentration (Kjørboe et al. 1982). Dagg & Walser (1987) showed that gut passage time increased at progressively lower food concentrations. Shorter gut clearance time with increasing food concentration was shown in cladocerans (Murtaugh 1985), and in copepods (Baars and Oosterhuis 1984). We did not find significant correlation between K and Chl *a* concentration in this study. There are no gut fluorescence studies carried out on copepods from the Indian Ocean for comparison. Thus our study is useful in discerning the K values for estimating ingestion rates of copepods in the Indian Ocean.

The grazing impact of copepods is reported to account for as less as 1-12% of the primary production in the equatorial Pacific (Dam et al. 1995) and off NW Spain in the North Atlantic (Barquero et al. 1998) to moderate at 27-52 % in the Arabian Sea (Roman et al. 2000; Table 3). It is reported to be 35-66% in the Indian sector of the Southern Ocean (Mayzaud et al. 2002a). We found a large variability of 13-83% in the Bay of Bengal. Bautista and Harris (1992) explain that up to 40% of copepod grazing on PP is possible if the >10µm fraction of the phytoplankton increases. Within the oligotrophic Bay, the western transect has relatively higher nutrient concentrations and where larger phytoplankton cells such as *Chaetoceros lorenzianus*, *C. curvisetus*, *C. didymus*, *Bacteriastrum furcatum* and *B. comosum* were found irrespective of seasons (Paul et al. 2008). Incidentally, the ingestion rate in the range of 2- 5.3 ng chl eq. copepod⁻¹ h⁻¹ was also higher in this transect.

According to Calbet et al (2009), mesozooplankton grazing becomes important in regions of low primary productivity such as the Bay of Bengal. Similar to our observations, Huskin et al. (2001b) and Li et al. (2003) also found highly variable grazing rates, respectively 6-150% off Azores and 25- 141% in the Bohai Sea. As zooplankton standing stocks/live biomasses are often higher than those of phytoplankton, such extreme range is likely. The zooplankton ingestion rates measured in this study are based on phytoplankton consumption alone. This means that non-fluorescent organic matter of autochthonous/ allochthonous origin, protozoans and fecal pellets are not accounted for in the gut fluorescence. However, they may constitute an important part of the copepod diet in the Bay of Bengal especially in the western region as has been variously noted earlier (Dam et al. 1995, Verity and Paffenhöffer 1996, Roman and Gauzens 1997, Del Giorgio and Duarte 2002).

4.3. Respiration

Apart from defecation, respiration is the other means of direct mineralization of ingested carbon. Environmental temperature, body size and locomotion play a vital role in regulating the respiration rates (Ikeda 1985; Mazzocchi and Paffenhöfer 1999). Copepod respiration rates ranging from 3.9 to 7.7 µl O₂

copepod⁻¹ d⁻¹ obtained in this study are higher than those reported from temperate regions and compare quite closely with the ranges in the Pacific Ocean (Table 3). The higher rates in our study were in spite of the 12 h non-feeding during experimental duration, which according to Thor et al. (2003) can reduce the respiration by 50 %. Li et al. (2004) found that higher respiration rates in *Calanus sinicus* (5-20 $\mu\text{l O}_2 \text{ ind.}^{-1} \text{ d}^{-1}$) were often associated with high temperature in the Yellow Sea. Gaudy and Boucher (1983) found higher rates ranging from 5.5 to 31 $\mu\text{l O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ in the equatorial Indian Ocean. Greater specific respiration rates of zooplankton in the Bay of Bengal and in other tropical waters, as Hernandez-Leon and Ikeda (2005) highlight, are due to the combined effects of warmer temperatures and smaller body size of individuals.

Recently Bode et al (2013) found respiration rates of copepods in the northern Benguela system ranging from 1.44 ± 0.72 for small species to 38.4 ± 12 in larger ones like *Eucalanus*. From the morphological characteristics of feeding organs, Timonin (1971) reported that 50-80% of zooplankton in the Indian Ocean were carnivores and Motoda and Minoda (1972) reported that only 20-27% of zooplankton numbers in the Kuroshio region were herbivores. If a lower RQ such as 0.7 for the protein metabolism in zooplankton, the respiration would have been still smaller. But since they are ammonotelic organisms (Omori and Ikeda 1984), a value of 0.97 has been used in this study. Zooplankton community respiration ranging from 26 to 90 $\text{mg C m}^{-2} \text{ d}^{-1}$ in our study accounted for $\sim 50\%$ of carbon ingested through grazing (Fig.7). These rates are greater than the estimate of 33% suggested by Valiela (1984). Dam et al. (1995) found mesozooplankton respiration averaging 20% of the daily PP at the Bermuda Atlantic time-series station (BATS). In our study, respiration to PP ratios ranging from 22 – 68% were higher during SpIM. Teira et al. (2001) has found that phytoplankton release a higher percent of extracellular DOC in waters of low primary productivity release. This DOC is available for heterotrophic bacterial uptake. Therefore less productive ecosystems are more likely to have higher respiration to PP ratios.

4.4. Growth and Production rates

Zooplankton growth rates in the range of 0.33-0.45 d^{-1} are reported for smaller copepod species in the equatorial countercurrent of the Indian Ocean (Table 3; Sazhina 1985). The growth rates of 0.23- 0.26 d^{-1} in the Bay are higher than those obtained in the Arabian Sea (0.12 d^{-1} ; Roman et al. 2000) or, at BATS (0.15 d^{-1}) and Hawaiian ocean time-series (HOTS, 0.17 d^{-1} ; Roman et al. 2002 a). The higher growth rates which are mainly considered to be a function of temperature and body size in this study are higher because the Bay of Bengal is a warm pool almost throughout the year and the size of zooplankton

which are mostly copepods, small. For eg. the g , was as high as 0.9 d^{-1} for the nauplii of *Paracalanus* spp. in the near shore waters off Jamaica, at 28°C (Hopcroft et al. 1998). High growth rates were found in studies (Hopcroft and Roff, 1998) where warm waters accompanied with ample food supply allowed the copepods to grow rapidly. As also observed by Huntley and Lopez (1992) and Turner (2004), the mesozooplankton in the Bay of Bengal, comprising mostly small copepod species such as *Oncaea venusta*, *Paracalanus indicus*, *Oithona similis*, *Clausocalanus arcuicornis* and *Pleuromamma indica* appear to have high fecundity and growth rates at warmer SST of $\geq 28^\circ\text{C}$.

Zooplankton production rate derived in this study is similar in the central ($145 \pm 148 \text{ mg C m}^{-2} \text{ d}^{-1}$) and coastal (130 ± 164) waters of the Bay and are close to the estimates from the Arabian Sea ($156 \text{ mg C m}^{-2} \text{ d}^{-1}$; Roman et al. 2000). The average zooplankton production: primary production ratios estimated for the Arabian Sea (0.12; Roman et al. 2000), BATS (0.03; Roman et al. 2002a) and HOTS (0.05; Roman et al. 2002b) are lower than our estimates of 0.26-1.87 owing mainly to lower primary production in the Bay (Prasanna Kumar et al 2010 a, b).

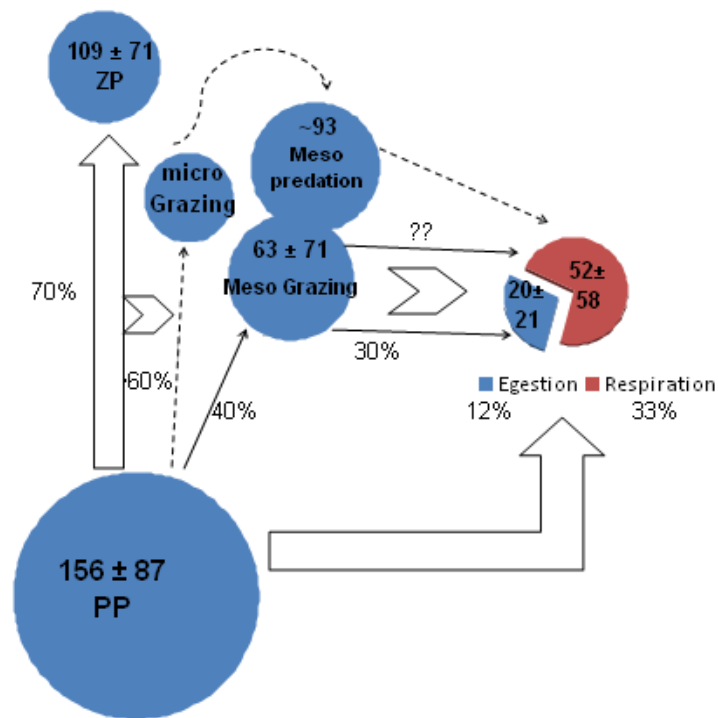


Fig.8. Basin-wide (2.2 million sq. km area) carbon flow in the Bay of Bengal through zooplankton, depicting in Mt C y^{-1} of primary production (PP), zooplankton production (ZP) and their grazing, egestion and respiration rates estimated from measurements during this study. The larger fraction of PP is presumed to be routed through the dotted pathway with microzooplankton as the key component (not measured in this study).

4.5. Basin-wide estimates of carbon transfer

Our first reports of mesozooplankton vital rates reveal that their contribution to the removal of carbon from photosynthesizers is enormous in the relatively less explored Bay of Bengal. Such contribution appears to be true for other regions as well (Hernandez-Leon and Ikeda 2005). It is evident from our previous studies (Prasanna Kumar et al. 2004, 2007, 2010a, b) that strong thermohaline stratification, perennial cloud cover, turbidity and weaker winds keep primary production low to moderate (156 Mt C y^{-1} , Fig. 8) in the Bay of Bengal. Of the 63 Mt C y^{-1} that is grazed by mesozooplankton, 30% is egested in the form of fecal pellets. But the respiration which accounts for 52 Mt C y^{-1} cannot be met through grazing alone. Isla and Anadón (2004) found that the phytoplankton ingested by mesozooplankton was not able to support their basal metabolism and had to be complemented by protein diet. As only few copepods are pure herbivorous, most are omnivorous, and heterotrophic flagellates, ciliates and nauplii may be an important food source for them (Lampitt & Gamble 1982, Tiselius 1989). Therefore, we propose that ~60% of the PP is routed to mesozooplankton *via* the microzooplankton.

Further, as shown by Khodse et al. (2009), the particulate matter predominantly of terrigenous origin during SpIM and from diatoms during SUM and FIM form the major source of organic carbon to the heterotrophs. The dominant copepods found throughout the study are *Oncaea venusta*, which are very versatile in their food habits (Turner 1986, Paffenhöfer 1993). Not only *Oncaea* but as stated above, most copepods are in fact omnivores. This seems to favor the mesozooplankton that can make the best use of available phytoplankton and microzooplankton from within the system and also subsidize with the detritus brought in by rivers. The very high zooplankton production projected at 109 Mt C y^{-1} together with basin-wide bacterial production ($\sim 90 \text{ Mt C y}^{-1}$; derived from Ramaiah et al. 2010) gives a heterotrophic production (without accounting for microzooplankton) that exceeds the primary production.

Our annual estimate of zooplankton fecal pellet egestion amounts to 8.8 gC m^{-2} for the study area and 20 Mt C for the entire basin. This is 3 times the particulate organic carbon flux estimated through sediment trap data ($3.3 \text{ gC m}^{-2} \text{ y}^{-1}$; Honjo et al. 2008). From studies of Isla and Anadón (2004), it is evidenced that the contribution of vertically migrating mesozooplankton to the active fluxes of organic matter below the photic zone is less in the oceanic waters. The lower value in the sediment traps may be due to fecal pellet recycling in the water column through coprophagy and coprohexy (Fortier et al. 1994) or, even due to rapid regeneration by prokaryotic /heterotrophic processes in the euphotic zone (Cushing 1989, Fernandes et al. 2008).

The annual respiration of 52 Mt C by mesozooplankton from the mixed layer in the Bay amounts to about 0.5% to the global ocean average of $10.4 \pm 3.7 \text{ Gt Cyr}^{-1}$ from the epipelagic layer (Hernandez-Leon and Ikeda 2005). Considering that the area of the Bay is $\sim 0.6\%$ of the global ocean, the carbon respiration we arrived at is apparently agreeable. It is also important to note that the mesozooplankton respiration in the Bay accounts for 33% of PP *vis a vis* the reported global range of 17-32%.

5. Conclusion

Our study indicates that the low (primary) productive Bay of Bengal is characterized by relatively high heterotrophic (zooplankton) production averaging 70% of the primary production. There is a clear temporal shift in zooplankton control of primary production, especially during SpIM in the central Bay (ZP: PP, 188% and Grazing: PP 83%) in both oceanic and coastal transects. In low PP regions, proportionally more carbon is transferred to zooplankton (Strömberg et al. 2009). This hypothesis was also tested in the open Atlantic Ocean by Calbet et al (2009), who believe that since the primary productivity in oligotrophic systems is primarily due to picoplankton, a size that is not feasible for the mesozooplankton feeding, they probably become conditioned to effective feeding on larger microphytoplankton cells. A relatively high zooplankton production is apparently fuelled by the allochthonous carbon inputs from the numerous rivers, resulting in an inverse plankton pyramid. Warm pool regions such as these, where the surface waters are stable and often depleted in nitrate are likely to support high zooplankton production and biomass *via* microbially mediated regenerated production and cyclonic eddy-generated new production in the oceanic waters and by terrestrial inputs in the coastal waters.

From our results it is possible to suggest that in this warm pool region, net heterotrophy is likely to prevail in the mixed layer during SUM in the central Bay and in both transects during the warmer SpIM season. Sarma et al. (2004) reported net heterotrophic conditions in the eastern Arabian Sea where zooplankton grazing exceeds phytoplankton growth mostly during the intermonsoons. Akin to findings of Regaudie-de-Gioux et al (2009), net heterotrophy could accelerate carbon export by zooplankton in the Bay in the form of carcass sinking/moulting/feces into the subsurface. The implications of this study is that if net heterotrophic conditions continue, the Bay of Bengal will become a source of carbon dioxide and sink of organic matter and oxygen- which might result in the expansion of the already large oxygen minimum zone.

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Table 2. Comparison of initial gut content (G_0), gut evacuation rate constant (K) and ingestion rate (I) of copepods from various regions of the world ocean

Area	G_0 (ng chl <i>a</i> ind ⁻¹)	K (h ⁻¹)	I (ng chl <i>a</i> eq. ind. ⁻¹ d ⁻¹)	References
<i>Temperate</i>				
50N 48W; Off Plymouth, coastal	0.1-0.9	0.05-0.36	10-200	Bautista and Harris 1992
47-60N, 20W; N. Atlantic	0.03-11.0	0.72-2.04	0.9-86	Morales et al. 1991
45N, 2W; Gironde estuary	0.2-0.5	2.4-12	20-88	Sautour et al. 2000
48-60S, 60-70E; Southern Ocean	6.0-16.0	0.66-1.13	9-65	Mayzaud et al. 2002 b
42-43N, 29-34E; SW Black Sea	0.1-9.1	2.4	3.1-22	Besiktepe 2001
<i>Subtropic</i>				
43-44N, 8-9W; NW Spain, N. Atlantic coast	0.1-0.6	0.72-1.4	20-80	Barquero et al. 1998
41N, 72W; Long Island Sound estuary, Atlantic	0.3-4.2	0.3-3.5	-	Dam and Peterson 1998
41N, 71W; Narrangansett Bay, Atlantic Ocean	0.7-1.7	1.87-2.8	19-145	Włodarczyk et al. 1992
39N, 141E; Otsuchi Bay	0.1-2.7	0.3-0.63	-	Tsuda and Nemoto 1987
37-40N, 118W; Bohai Sea	1.1-2.7	0.96-1.02	14-37	Li et al. 2003
27-39N, 19-33W; Azores	0.15-4.64	1.74-1.92	-	Huskin et al. 2001b
22-24N, 119-120W; SE Taiwan Strait	0.2-2.0	-	6-36	Tseng et al. 2008
<i>Tropic</i>				
9-20N, 81-88E; Bay of Bengal	2.4-8.1	0.4-0.94	48-126	This study*

‘-’ denotes no data. *This is the only study where these three copepod measurements have been made in the tropical ocean

Table 3 Comparison of rates of copepod grazing (G), Respiration (R) and growth rate (g) and ratios of Grazing to primary production (G:PP), zooplankton production to primary production (ZP:PP) and Fecal pellet to Total carbon flux from sediment trap (Fp:TcFlux) from different areas of world ocean.; AMT: Atlantic Meridional transient 50N-50S; BATS: Bermuda Atlantic Time Series Study; HOT: Hawaii Ocean Time Series; '-', no data

Area	G (mg C m ⁻² d ⁻¹)	R (μl ind ⁻¹ d ⁻¹)	g d ⁻¹	G: PP	ZP: PP	Fp: TcFlux	Reference
Long Island Sound; estuary	-	0.5-1.7	-	-	-	-	Thor et al. 2003
Antarctic Ocean	81-84	0.6-61	-	0.35-0.66	-	-	Mayzaud et al. 2002a, 2002b
Galician coast, NW Spain	25-350	0.1-1.6	-	0.02-0.12	-	-	Ikeda et al. 2001, Barquero et al. 1998
Gironde estuary	54-281	-	-	0.09-0.40	-	-	Sautour et al. 2000
Black Sea	9-246	-	-	0.07-0.17	-	-	Besiktepe 2001
Azores, Atlantic Ocean	2-85	-	-	0.06-1.50	-	-	Huskin et al. 2001b
AMT	1.6-252	-	-	0.08-0.13	-	-	Huskin et al. 2001a
BATS	37±12	-	0.15	0.09±0.13	0.03	0.42	Roman et al. 2002a
HOT	90±29	-	0.17	0.18±0.25	0.05	1.05	Roman et al. 2002a
North Atlantic	20-600	0.6-5.6	-	0.04-0.28	-	-	Calbet et al. 2009, Schneider and Lenz 1987
North Pacific	-	2.0-5.2	-	-	-	-	King et al. 1978
Bohai Sea	29-470	-	-	0.25-1.41	-	-	Li et al. 2003
Yellow Sea	-	5-20	-	-	-	-	Li et al. 2004
Equatorial Pacific	24-180	1.3-9.9	0.17	0.01-0.32	0.05	1.03	Roman & Gauzens 1997, Shushkina & Pavlova 1973
Equatorial Pacific	44-47	-	-	0.01-0.12	0.23	3.7	Dam et al. 1995
Equatorial Pacific	60-240	-	0.19	0.28-0.42	0.12	1.5	Roman et al. 2002b
Discovery Bay	-	-	0.65	-	-	-	Hopcroft and Roff 1998
Sargasso Sea	3-51	2.1-11	-	0.09-0.26	-	-	Roman et al. 1993, Menzel and Ryther 1960
Arabian Sea	120-1824	-	0.12	0.27-0.52	0.12	>1.0	Roman et al. 2000
Gulf of Aden	-	2.0-3.4	-	-	-	-	Schneider and Lenz 1991
Equatorial Indian Ocean	-	5.5-31	0.39	-	-	-	Sazhina 1985, Gaudy and Boucher 1983
Bay of Bengal	26-134	3.9-7.7	0.25	0.13-0.83	0.70	2.6	This study