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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 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 Mt C 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 CO_2 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.

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 representing 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 a 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

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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., 2001a, 2001b, Roman et al., 2002a, 2002b; 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 though biological entities in the Bay of Bengal and attempted to answer a key question; whether the zooplankton production in the Bay of Bengal favors 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

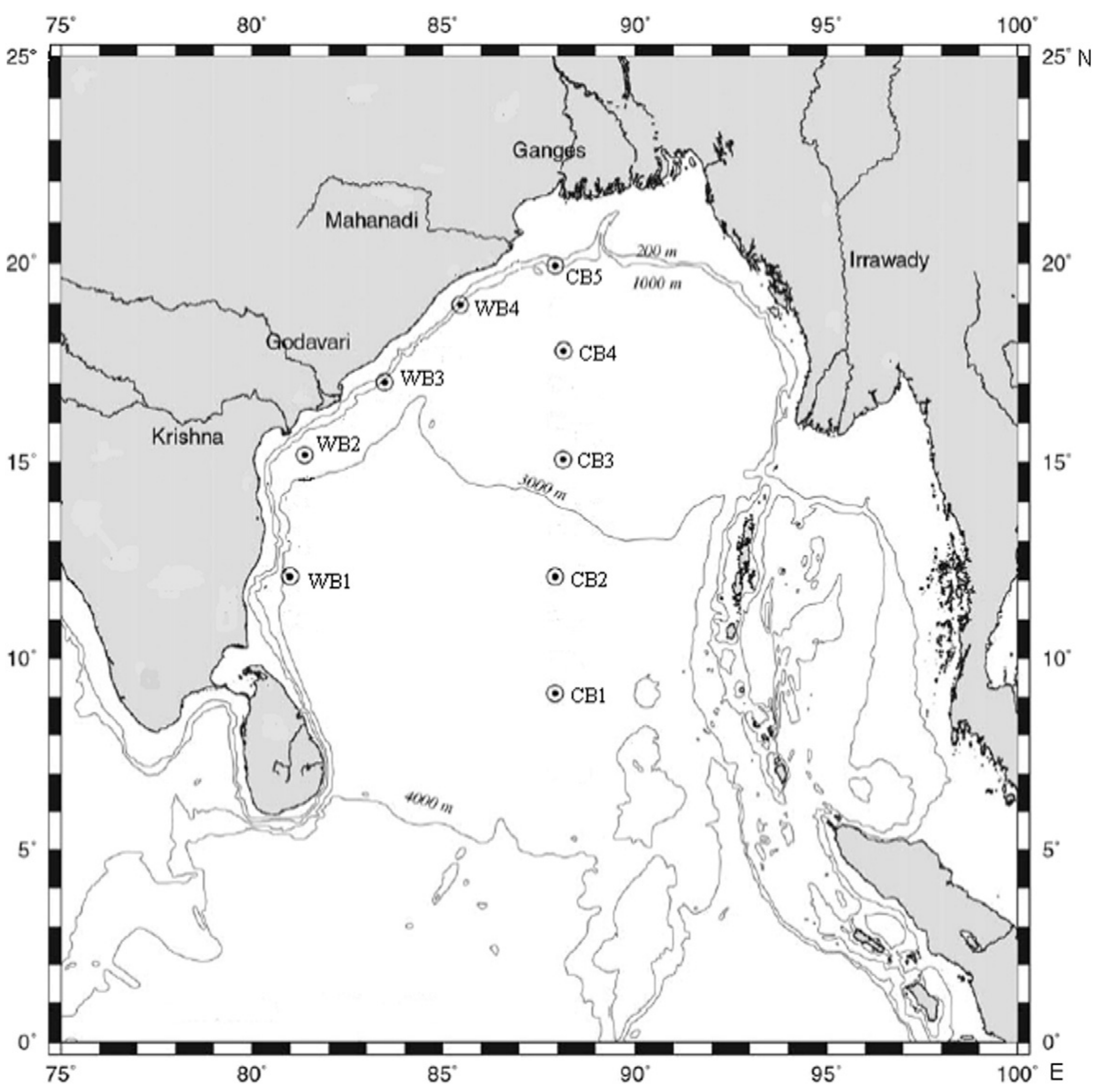

Fig. 1. Study area with sampling locations for mesozooplankton and other physico-chemical parameters. Stations CB1 to CB5 are along the central transect (88°E) and WB1 to WB4 are in the western Bay of Bengal.