Ecological Significance of Marine Microzooplankton

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Introduction

Microzooplankton are defined as heterotrophic organisms with body dimensions between 20 and 200µm in size. These taxonomically diverse communities constitute a significant component of the plankton community in many marine environments (Revelante et al., 1985; Burkill et al., 1987; Pierce and Turner, 1994). By virtue of their small body size, these organisms can exploit small food particles unavailable to most meso- and macrozooplankton, and thus act as trophic intermediaries between pico-and nanoplankton and meso- and macro-carnivores (Stoecker and Capuzzo, 1990; Gifford, 1991, 1993; Roman and Gauzens, 1997; Klein Breteler et al., 1999). In recent years, there has been an upsurge of interest in research on microzooplankton in the marine ecosystem owing to their higher mass-specific physiological rates compared with larger zooplankton.

Microzooplankton are important phytoplankton grazers (Landry et al., 1993, 1997, 1998; Verity et al., 1993, 2002; Kamiyama, 1994; Quevedo and Anadón, 2001; Liu et al., 2002; Landry and Calbet, 2004) and nutrient regenerators (Johansen, 1976; Harrison, 1980; Verity, 1985). Besides that, the nature of microbial food web (often referred to as the 'microbial loop') is diverse, complex and spatio-temporally varied. The microzooplankton community plays a central role in microbial systems and grazes a range of particle sizes.

Despite the increasing importance of microzooplankton as trophic intermediaries in the pelagic as well as marine food web, ocean energy flow and carbon cycling, ecological significance, population dynamics and trophodynamic roles of microzooplankton remains poorly investigated in tropical waters, particularly in Indian coastal marine and estuarine waters. This chapter is an attempt in putting together our understanding on population dynamics (abundance, biomass and production rate), food and feeding, and grazing activities of microzooplankton.

The pioneering and classical work on the qualitative and quantitative studies on microzooplankton was carried out by Lohmann (1901). From this study, the author underlined their ecological importance in the marine food web. Much later in 1988, under the NATO sponsorship, approximately 80 scientists from all over the world joined and worked together in Plymouth, U.K., for two weeks to evaluate the ecological role of protozoa in the sea. The outcome of their interactions has been brought out as a special volume, entitled 'Protozoa and their role in marine processes' (Reid et al., 1991). However, the diverse microzooplankton communities have recently received greater attention by planktologists because of their important role in the aquatic ecosystems/pelagic food web by providing a link between pico- and nanoplankton and higher trophic levels of meso- and macrozooplankton and fish larvae.

Researchers have identified that microzooplankton often constitute a significant component of the marine plankton community in many marine coastal and estuarine systems (Revelante et al., 1985, Burkill et al., 1987; Pierce and Turner, 1992). Microzooplankton are the primary grazers of phytoplankton production/ biomass in many open ocean systems (Burkill et al., 1993a, 1993b; Verity et al., 1993, 2002; Landry et al., 1993, 1997, 1998; Kamiyama, 1994; Quevedo and Anadon, 2001; Liu et al., 2002; Landry and Calbet, 2004) and in Antarctica regions (Caron et al., 2000; Selph et al., 2001; Landry et al., 2002). They also have a larger potential to regenerate plant nutrients and higher growth rates than metazoan competitors (Heinbokel, 1978; Verity, 1985, 1986) and provide an important link between the microbial fraction and larger grazers (Laval-Peuto et al., 1986; Pierce and Turner, 1994). Furthermore, microzooplankton communities are the food of some fish larvae, hence they have lucrative values in shell and finfish culture, especially first feeding larval fishes (Stoecker and Capuzzo, 1990; Vander Meeren and Nass, 1993; Fukami et al., 1999). Interestingly, in Antarctic pelagic zone, food chain was traditionally believed to be simple starting with diatoms that are grazed by krill and consumed by carnivores (El-Sayed, 1971). However, in recent years, microbial community such as bacteria, microplankton, and protozoa thought that they play a key role in the food web dynamics of the Antarctic pelagial system (Hewes et al., 1985). Extensive studies have been undertaken on the taxonomy of microzooplankton rather than on the whole microzooplankton community in Indian waters (Damodara Naidu, 1977; Krishnamurthy and Santhanam, 1978; Srinivasan et al., 1988; Godhantaraman, 1994, 2001, 2002; Mangesh et al., 1996).

Extensive research have been conducted on the ecological significance of major plankton communities in marine coastal and aquatic ecosystems both tropical as well as temperate waters. Research on microzooplankton received less attention by researchers owing to their smaller size, lack of proper methodology for collection, preservation and difficulties in identification. Guidelines and manuals to study microzooplankton from different habitats of the world have now been produced. Work on the last 20 years has demonstrated the ecological importance of microzooplankton in energy/material transfer and structuring of food webs in many marine coastal and aquatic ecosystems. In subsequent developments, the planktonologists/ecologists have realized the importance of microzooplankton in nutrient regeneration and their link in the 'microbial loop' where they mediate crucial flows of energy and matter in the sea. Hence, after 1980s, many researchers have intensively studied diversity, abundance, biomass, production rates and grazing activities of microzooplankton in oceanic, marine coastal and estuarine systems (Godhantaraman, 2002; Godhantaraman and Uye, 2001, 2003; Dolan et al., 2002; Verity et al., 2002; Landry and Calbet, 2004; Thompson, 2004; Urrutxurtu, 2004).

Studies concerning microzooplankton in marine coastal, estuarine and brackish-water systems along tropical Indian waters are limited. Hence, in the following sections, I provide the results obtained by the research conducted in the tropical Vellar estuarine systems, southeast coast of India. This was one of the first comprehensive studies on microzooplankton in India. There are also comparative accounts of microzooplankton researches from my studies in Japanese coastal marine waters.

Microzooplankton abundance and type in Indian waters

Taxonomic composition, abundance, biomass, estimated production rate and feeding habits of microzooplankton communities were studied in the tropical Vellar estuarine systems, southeast coast of

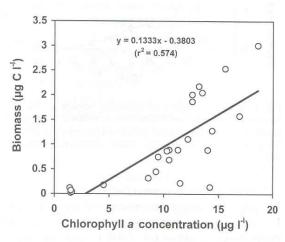


Fig.1. Relationship between biomass of tintinnids and chlorophyll *a* concentrations in the tropical estuarine system (from Godhantaraman, 2002)

India. It is one of the important tropical estuaries with complexity of environmental conditions, in Indian subcontinent.

A total of 81 species of microzooplankton were identified from this estuarine system and the total population was dominated by a single group i.e. tintinnid ciliates, both in terms of species diversity (mean 62%) and abundance (mean 65%). The remaining taxa included rotifers, copepod nauplii, naked ciliates (only 2 species) and some metazoan larval forms. Among tintinnids, Tintinnopsis was the most abundant genus in terms of number of species, followed by Codonellopsis, Stenosemella, Favella, Amphorellopsis, Tintinnidium, Dictyocysta, Coxliella, Dadayiella, Eutintinnus, Metacylis and Rhabdonella. Further, most of the tintinnid species found in these systems are cosmopolitan rather than endemic. Moreover, many microzooplankton, particularly tintinnids disappeared during rainy seasons and species composition and diversity also changed according to the exciting seasonal environmental factors. This kind of cyclic changes in the species composition of tintinnids was a special characteristic feature of the tropical Vellar estuarine systems.

The abundance of total microzooplankton exhibited clear seasonal variations: - being highest in summer and lowest in winter. The overall mean abundance (327 indiv. I⁻¹) was four-fold higher during summer which is attributable mainly to the combined effects of higher temperature, salinity as well as food supply reported as the most important factors affecting their abundance and growth rate (Verity, 1985; Taniguchi and Kawakami, 1983; Abbound-Abi-Saab, 1989). The maximum abundance estimated in other coastal marine systems such as Damariscotta Estuary, USA (Revelante and Gilmartin, 1987 - <44100 indiv. I⁻¹); Irish Sea (Edwards and Burkill, 1995- 60, 000 indiv. I⁻¹) and in the central and eastern Arabian Sea (Mangesh et al., 1996 - 5000 indiv. I⁻¹) are much higher

than the maximum abundance recorded from Vellar estuarine system. In the above studies counts of naked ciliates and heterotrophic dinoflagellates were included, but in my study, these groups were not included.

During the one year from January to December 1994, biomass of tintinnids ranged from 0.04 to 3.01 μg C I^{-1} and the maximum and minimum daily production 2.5 and 0.07 μg C I^{-1} day $^{-1}$ was estimated. Due to large thermal gradients (ranges 22.5 - 33.8°C), the overall mean biomass and production rate was highest in summer than during monsoon months. In essence, the seasonal changes in biomass of tintinnids in this tropical estuary could be related to the interactive effects of temperature and food availability. To augment this, a significantly positive relationship was obtained between the total biomass of tintinnids and chlorophyll a concentrations (p<0.05 - Fig.1).

Feeding and food web relationship

Herbivory among tintinnids and rotifers was investigated under laboratory conditions. Tintinnids were mainly fed on nannophytoplankton of cell width less than 30 mm in size, as their major diet. However, cyanobacterial species are the preferred diet for rotifers. In general, lorica diameter plays a decisive role in the selection of prey items. The ingestion rate of tintinnids increased when the previously size decreased. Thus as, Gifford, (1985) and Paranjape, (1990) suggested, the growth of many smaller sized phytoplankton is apparently 'controlled' by the grazing activity of tintinnids. Hence, it is evident from the experimental studies that the quality (i.e. size and shape) of prey is more important than the quantity of the prey species (Godhantaraman and Krishnamurthy, 1997).

The importance of microzooplankton in the planktonic food web was also examined by the gut content of the predator organisms (copepods, shell and finfishes). Based upon the gut content analysis of secondary consumers, the food item comprised of phyto-fragments (49.5%), microzooplankton (48.3%) and others (2.2%). In tertiary consumers, phytoplankton accounted for 27.6%, microzooplankton (31.5%), mesozooplankton (32.8%) and others (8.1%) for tropical estuarine and mangrove systems (Fig. 2).

The food web relationship closely followed the seasonal pattern of microzooplankton abundance. Tintinnids were noticed more (about 65%) in the gut contents of copepods, mesozooplankton and fishes during warmer months, however, in winter months rotifers, copepod nauplii and some euryhaline tintinnid species formed the main food types for the secondary

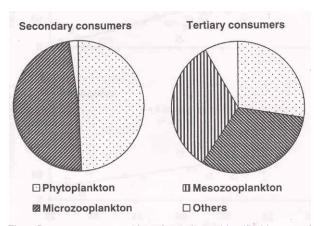


Fig.2. Percentage composition of prey items identified in guts of secondary and tertiary consumers (from Godhantaraman, 2001)

as well as higher trophic level organisms. Microzooplankton in general, and tintinnids in particular, are qualitatively important in planktonic food web because of their biochemical composition as rich source of protein and amino acids compared to phytoplankton and detritus (Stoecker and Capuzzo, 1990).

Trophodynamic roles of microzooplankton

The trophodynamic role of tintinnids, with reference to phytoplankton grazing, and the rate of daily removal of phytoplankton biomass was estimated in the tropical estuarine and mangrove waters (Fig.3).

The potential percentage of the initial phytoplankton biomass removed by grazing of tintinnids varied seasonally. It was estimated highest (1.24%) in summer and lowest (0.03%) in winter, and these results indicate that the seasonal environmental conditions not only affect the distribution and growth rate of tintinnids, but also changing their grazing activities. The grazing activities were higher in summer when there was more chlorophyll. The low grazing activities during monsoon might be due to scarcity of

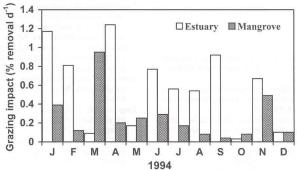


Fig.3. Seasonal variations in grazing impact of tintinnids as expressed by percent (%) removal of phytoplankton biomass per day in the tropical estuary and mangroves (from Godhantaraman, 2002)

food and high predation pressure from meso- and macrozooplankton. Hence, the abundance of food appears to have important effects on population abundance, survival and growth of tintinnids (Stoecker et al., 1984; Verity and Villareal, 1986).

Role of microzooplankton in subtropical Japanese waters

Hiroshima Bay is one of the most eutrophic embayment in the Inland Sea of Japan, since it receives large amounts of nutrients from the adjacent Ohta rivers (annual load of total nitrogen and phosphorous: 3700 and 290 t respectively; Yamamoto et al., 1996) and municipal sewage plants from densely populated cities like Hiroshima city. Therefore, remarkable eutrophic to oligotrophic gradient is formed from Hiroshima Bay, the Inland Sea of Japan to the Pacific Ocean. Taxonomic composition, abundance and biomass

In Hiroshima Bay, a total of 42 species of tintinnids and 2 species of naked ciliates were identified. Besides that, copepod nauplii were also identified. Among tintinnids and naked ciliates, genus Tintinnopsis from the former and Strombidium from the later were dominant. Over the study period, ciliated protozoans (naked ciliates and tintinnids) were numerically overwhelming (81 and 83%, respectively), followed by copepod nauplii. There was a remarkable seasonal and geographical variation in taxonomic composition, abundance, biomass and production rate of microzooplankton. The overall mean abundance and biomass of total microzooplankton was higher 2.1 and 2.3 fold respectively in summer than in winter, such seasonal variations being high in summer and low in winter have also been demonstrated in many temperate coastal waters (Burkill et al., 1987; Dolan and Coats, 1990; Leakey et al., 1992; Edwards and Burkill, 1995). Similarly, the average production rate of microzooplankton was also higher (3.8 fold) in summer than in winter, and majority (>83%) of the production was accounted by ciliated protozoans. The higher abundance of microzooplankton in springsummer was often explained by the increase of temperature and their food supply, and hence positive relationship was discernible between the abundance of microzooplankton and chlorophyll a concentrations. In these eutrophic waters, ciliated protozoans were numerically dominant (>80%), and copepod nauplii were minor components. However, in terms of biomass, due to the heavier individual body weight, copepod nauplii were dominant (>47%). Among microzooplankton communities, there was a shift of numerical dominance depending on the season, especially in summer and winter. These variations are

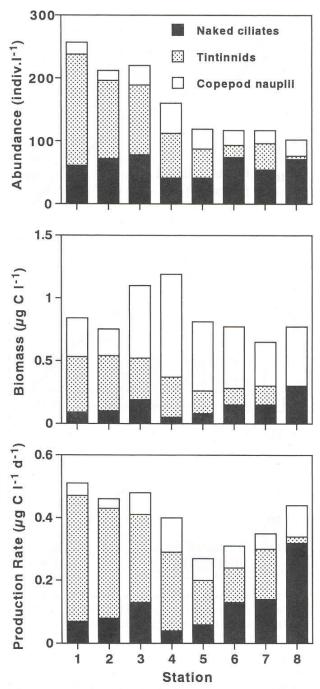


Fig.4 Geographical variations in abundance, biomass and estimated production rate of microzooplankton across the inshore-offshore gradient in the Inland Sea of Japan and adjacent Pacific Ocean. Values are depth-weighted water-column averages (from Godhantaraman & Uye, 2001)

useful to indicate that the reproductive response of these groups to the seasonal shifts in environmental factors may not be the same.

In both seasons, there were marked decreases in abundance, biomass and production rate from inshore eutrophic to offshore oligotrophic stations (fig.4).

A similar inshore-high and offshore-low gradient of microzooplankton abundance was classified along a eutrophic and oligotrophic transect drawn in the Hiroshima Bay and the eastern part of the Inland Sea of Japan through the Kii Channel (Kamiyama, 1994; Uye et al., 1996, 1998). Based upon the geographical distribution of microzooplankton in the Inland Sea of Japan and adjacent waters can be roughly summarized as follows: - 'They are always most abundant in heavily eutrophic embayments like Osaka Bay and Hiroshima Bay and gradually decrease towards the Pacific Ocean through Kii Channel and Bungo Channel'.

Trophodynamic roles

As discussed in the previous section, the trophodynamic role of microzooplankton was assessed across the inshore and offshore trophic gradient. The potential percentage of the initial phytoplankton biomass removed by grazing of microzooplankton was relatively constant over the transects studied. It varied from 4.1 to 9.6% in summer

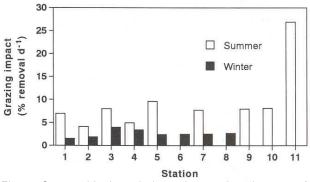


Fig.5. Geographical variations in grazing impact of microzooplankton as expressed by percent (%) removal of phytoplankton biomass per day across the inshore-offshore gradient in the Inland Sea of Japan and adjacent Pacific Ocean during summer and winter (from Godhantaraman, & Uye, 2001)

and from 1.5 to 3.9% in winter with mean values of 7.2% and 2.6% in summer and winter, respectively (Fig.5).

Hence, over the extended study area (except station 11), microzooplankton might play a relatively minor role as phytoplankton grazers in spite of a remarkable trophic gradient. However, the more removal rate at the oligotrophic waters suggested that the trophodynamic roles of microzooplankton might be more important in the offshore regions, where the food resources are limited.

Role of microzooplankton in biological production of brackishwater lagoonal system

In the first ever qualitative and quantitative study on microzooplankton in highly productive brackish-water lagoonal systems, namely Lake Shinji-Ohashi River-Lake Nakaumi, Japan. It was observed that naked ciliates numerically dominated the microzooplankton community (annual mean 39.6%), followed, in order, by tintinnids (30.3%), copepod nauplii (24.6%) and rotifers (5.5%). Owing to large thermal gradients and salinity variations, seasonality among tintinnids and spatial differences among copepod nauplii were evidenced. A total of 49 species of tintinnids from 9 genera were identified. Among them, Tintinnopsis was the most dominant in terms of number species (29), followed by *Eutintinnus* (4 species), *Codonelloppsis* (3), Favella (3), Helicostomella (3), Leprotintinnus (3), Stenosemella (2), Amphorellopsis and Tintinnidium (1 species respectively each). Among them, 15 species attained concentrations >500 indiv. I-1. Moreover, majority of tintinnid species was confined to certain months or locations, and closely associated with species-specific temperature and salinity preference and/or tolerance. According to their environmental preference, they were classified into 6 types, such as 1. Wide temperature and wide salinity species, 2. High temperature and wide salinity species, 3. High temperature and high salinity species, 4. Intermediate temperature and wide salinity species, 5. Intermediate temperature and high salinity species, 6. Low temperature and wide salinity species.

Because of high nutrient input from adjacent land sources, the chlorophyll a concentration was extremely high (over the entire area-annual mean: 31.6 µg I-1). However, the average biomass of microzooplankton (mean range 0.19 – 18.7µg C I⁻¹; and annual mean 21.0 µg C I⁻¹) in this brackish-water lagoonal system are comparable to or lower than the ranges reported in other temperate coastal and estuarine systems (Table 1). As per the available of food sources (high chlorophyll a concentration), the population growth of microzooplankton must be higher in this eutrophic brackish-water system. However, the low microzooplankton biomass might be by the predation loss of meso- and macrozooplankton, since this area sustains high meso-zooplankton biomass (annual average and maximum of 43.9 and 292 mg C m⁻³, respectively (Uye et al., 2000). From this, it was confirmed that microzooplankton play an important role as a trophic link between pico- and nanoplankton and meso- and macro-metazoan predators in this eutrophic brackish - water system.

Table I: Comparison of microzooplankton biomass among various temperate coastal and estuarine systems (from Godhantaraman and Uye, 2003)

Location	Biomass (μg C L ⁻¹)	References
Suo Nada, Japan	0.31-1.29	Aizawa (1985)
Osaka Bay, Japan	0.81-26.4	Aizawa (1987)
Hiroshima Bay, Japan	0.39-4.24	Godhantaraman and Uye 2001)
Inland Sea of Japan	0.53-28.3	Uye et al., (1996)
Dokai Inlet, Japan	2.92-22.42	Uye et al., (1998)
Lake Shinji & Lake Nakaumi, Japan	0.19-18.7	Godhantaraman and Uye 2003
Chesapeake Bay, USA	5.0-12.0 ^a	Dolan and Coasts (1990)
Chesapeake Bay, USA	7.5-12.5	Dolan (1991)
Damariscotta Estuary, USA	0.4-33.0 ^b	Revelante and Gilmartin 987)
Gulf of Marine, USA	<1-5.7	Montagnes et al., (1988)
Solent, UK	0.6-6.1ª	Burkill (1982)
English Channel	1.2-29.7	Linley et al., (1983)
Southampton Waters, UK	1.4-219.0°	Leakey et al., (1992)
Northern Adriatic Sea	3.0-16.0	Revelante and Gilmartin (1983)
Po River region, Adriatic Sea	4.1-123.6	Revelante et al., (1985)
Kiel Blight, Germany	1.0-56.0 ^a	Smetacek (1981)

^a for ciliated protozoans, ^b for tintinnids

Perspective of research on microzooplankton in the future

Currently the knowledge of microzooplankton is increasing rapidly due to the recognition of their dynamic role in marine coastal systems. Hence studies on microzooplankton have been well recognized and included as an important component in the Global Ocean Ecosystem Dynamics (GLOBEC) and Joint Global Ocean Flux Study (JGOFS) programmes where they have been shown to be the major movers of energy, carbon cycling and remineralization of nutrients in the oceans.

A comprehensive understanding of microzooplankton population dynamics is a prerequisite to fully understand and to quantitatively model carbon cycling pathways and other biogenic elements on a global scale. Therefore, more information is needed, both in coastal and open ocean regions, to judge the relative contributions of these communities to global production. Estimates should be made based on longterm annual studies, so that the influences of various parameters on community structure across latitudes can be understood. Therefore, we need to develop improved methodologies for preservation, identification, and counting observing microzooplankton in natural aquatic assemblages. Also we have to develop better techniques to measure the physiological activities such as respiration, excretion, growth and grazing rate of planktonic microzooplankton, especially *in situ*. Further research on the microbial food web is essential to determine, how environment variables influence the functioning of the microbial loop, in particular the balance between the 'sink' or 'link' nutrient flux/cycling needs further study.

Besides that, researchers need better knowledge of the transfer routes of various pollutants to shell and finfishes via microzooplankton to fully understand of their ecological role. By taking into account, the functions and activities of microzooplankton, researchers have to identify priority research areas for the future. To estimate the contribution of microzooplankton to carbon flow in the trophic tier, to better understand their dynamic role, fill gaps in knowledge and apply these results to ecosystem management and greater emphasis should be placed on microzooplankton research. In my opinion, research on microzooplankton will emerge as one of the important thrust areas in biological oceanography, especially in studies on the microbial food web, where microzooplankton is acting as a central link between the bacterial population and metazoan consumers and larval fish consumers. Further, biotechnological applications can be incorporated in the study of microbial food web and also to estimate the magnitude of the carbon cycling pathways at different trophic levels. Besides, molecular tools may be used in future to study the physiological activities, evolution and species characterization of microzooplankton.

Summary and conclusion

Work described here has demonstrated wide seasonal as well as regional variations in the taxonomic composition, occurrence and grazing activities of microzooplankton in a range of marine environments. For example, in tropical waters, tintinnid ciliates are the dominant taxonomic group, however, in temperate waters, naked ciliates are most abundant. There are many factors that determine distribution patterns and control physiological, growth and grazing activities. Thus the ecological and trophodynamic roles of microzooplankton many not be the same in all systems and tend to show variations in abundance according to bathymetry and environmental conditions.

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