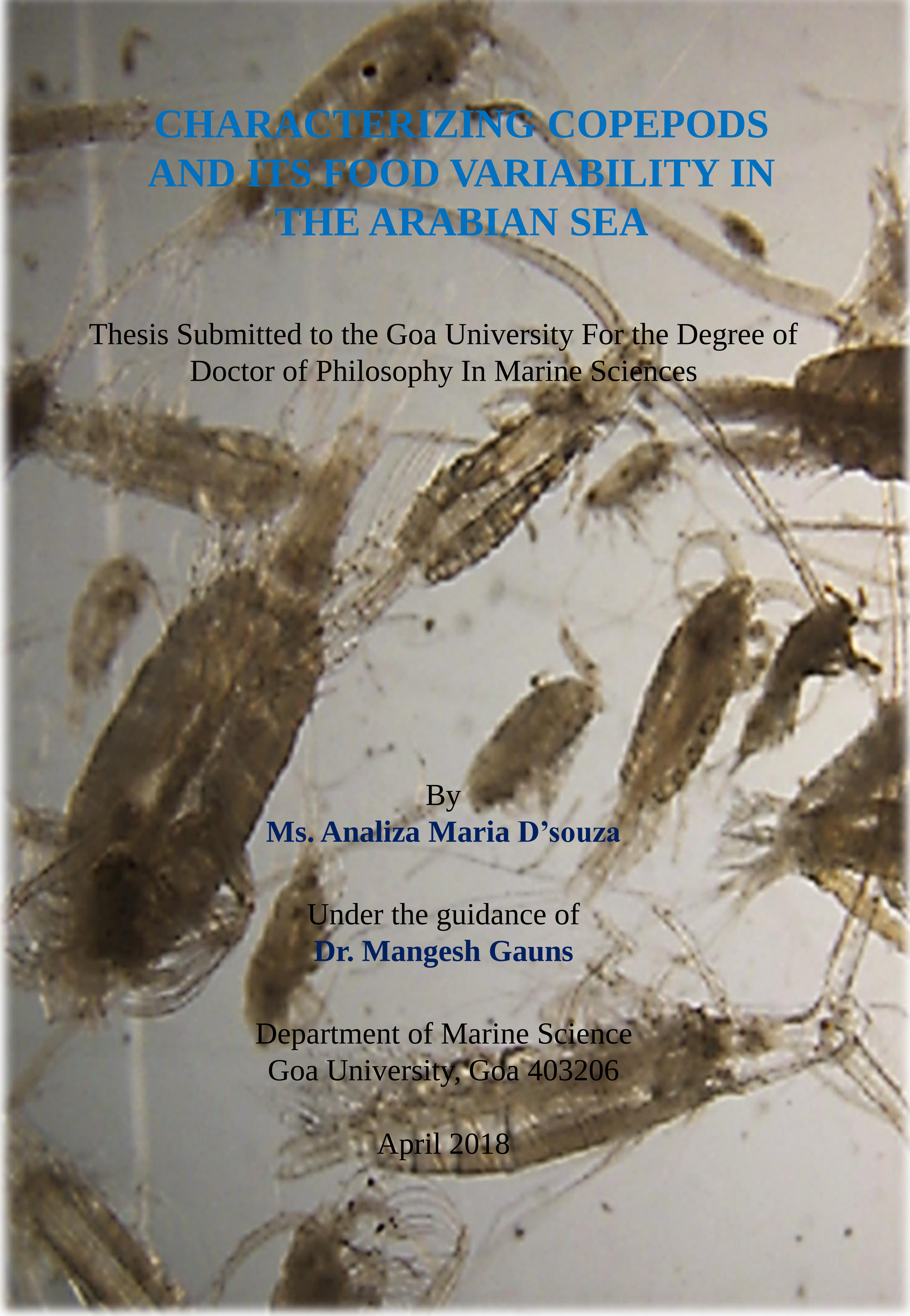

CHARACTERIZING COPEPODS AND ITS FOOD VARIABILITY IN THE ARABIAN SEA

Thesis Submitted to the Goa University For the Degree of
Doctor of Philosophy In Marine Sciences

By
Ms. Analiza Maria D’souza

Under the guidance of
Dr. Mangesh Gauns

Department of Marine Science
Goa University, Goa 403206

April 2018

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APRIL 2018

Dedicated to Saint Francis and to my beloved family

Dedicated to Saint Francis and to my beloved family

सी एस आई आर - राष्ट्रीय समुद्र विज्ञान संस्थान
(वैज्ञानिक एवं औद्योगिक अनुसंधान परिषद)
दोना पौला 403 004 गोवा, भारत
CSIR-NIO
CSIR - National Institute of Oceanography
(Council of Scientific & Industrial Research)
Dona Paula 403 004 Goa, India

CERTIFICATE

This is to certify that the thesis entitled "Characterizing copepods and its food variability in the Arabian Sea", submitted by Ms. Analiza Maria D'souza, for the award of the degree of Doctor of Philosophy in Marine Sciences is based on original studies carried out by her under my supervision.

The thesis or any part thereof has not been previously submitted for any degree or diploma in any Universities or Institutions.

Place: Dona Paula

Dr. Mangesh Gauns
(Research Guide)
Principal Scientist
CSIR-National Institute of Oceanography
Dona Paula – 403 004, Goa

DECLARATION

As required under the university ordinance OB9.9, I state that the present thesis entitled "Characterizing copepods and its food variability in the Arabian Sea" is my original contribution and the same has not been submitted on any previous occasion. To the best of my knowledge the present study is the first comprehensive work of its kind from the area mentioned.

The literature related to the problem of investigation has been cited. Due acknowledgements have been made wherever facilities and suggestions have been availed of.

Place:

Date:

(**Analiza Maria D'souza**)

STATEMENT

I hereby state that all necessary corrections/modifications as advised by the examiners for my Ph.D thesis entitled "Characterizing copepods and its food variability in the Arabian Sea" are incorporated.

Analiza D'souza

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“*Sing the praises of the LORD, you His faithful people, praise his holy name (Psalms 30:4)*.”

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Chapter 1

INTRODUCTION

1.1 GENERAL INTRODUCTION

The ocean is the cradle of life, wherein tiny plankton, bacteria, microflora, microfauna and macrofauna swing in harmony. The term "plankton" was coined by Victor Hensen (1887) for all those organisms drifting in the water that were unable to move against the currents. The animal constituent of the plankton community is known as zooplankton and employ herbivorous, carnivorous, detritivorous, omnivorous (Metz and Schnack-Schiel 1995), mixotrophic (Tittel et al. 2003) and coprophagous feeding habit (Noji et al. 1991; Gonzales et al. 1994; Goes et al. 1999).

1.1.1 Zooplankton

Marine zooplankton comprises of a variety of organisms ranging from tiny flagellates of micrometers to 2 m in diameter the giant jellyfish. The pioneer work of classification of zooplankton was carried out by Schutt (1892). Later, Sieburth et al. (1978) organized these organisms into nano– (2–20 tm), micro– (20–200 gm), meso– (200 gm –2 cm), macro– (2–20 cm) and mega–plankton (20–200 cm). Marine zooplankton is approximated of 36000 species (Harris 2000) and its diversity is characterized by having representatives of almost every taxon of the animal kingdom. Mostly, the species diversity is governed by temperature, thus, the highest diversity is found in the tropics with warm oceanic waters (Rutherford et al. 1999). Vaguely, the doubling time of zooplankton varies between 2 to 12 days (Sheldon et al. 1972; Steele 1977).

Zooplankton are either holoplankton, spending their entire life as plankton or meroplankton, drifting as plankton only for a part of their life before settling as benthos or nekton (Martin et al. 1996; 1997). Foraminifers, radiolarians, siphonophores, ctenophores, heteropods, pteropods, ostracods, copepods with few exceptions, hyperiids, euphausiids, most chaetognaths, appendicularians, cladoceran and salps are holoplankton. While, most of the larval stages of cephalopods and fish that grow as nekton when adult or polychaetes, mollusks, echinoderms, barnacles and decapods which spend their adult stage as benthos are meroplankton (Raymont 1983). However, hydrozoans and scyphozoans alternate between the planktic medusae during summer and benthic polyp stage during winter (Hartwick 1991).

1.1.2 Mesozooplankton

Mesozooplankton is the component of zooplankton that is comprised of 0.2–20 mm in body sizes (Raymont 1983). These organisms help in regulating algal and microbial productivity through grazing (Dejen et al. 2004). Thus, process the photosynthetically fixed carbon in the oceans by transferring the energy to other trophic levels (Ingrid et al. 1996; Turner et al. 2001). Besides, they play crucial role in bentho-pelagic coupling of the fixed organic carbon by vertical migration thereby, structuring pelagic food webs and mediating biogeochemical cycles.

Mainly, mesozooplankton are composed of copepods (Timonin 1971), tunicates, ostracods, chaetognaths (Madhupratap et. al. 2001), polychaete larvae (Peter 1969a), fish larvae (Peter 1969b), euthecosome molluscs (Sakthivel 1969), cephalopod juveniles (Aravindakshan and Sakthivel 1973), amphipods (Nair et al. 1973), and euphausiids (Brinton and Gopalakrishnan 1973; Gopalakrishnan and Brinton 1969). Due to the connections between the Pacific and Indian oceans through the Straits of Malacca and Indonesia similarity of plankton within these oceans is observed as compared to the Atlantic Ocean plankton (Fleminger and Hulsemann 1973; Rao and Madhupratap 1986). The chaetognath species recorded from the Arabian Sea belong to the typical Indo–Pacific species complex, while the species of planktonic ostracods are cosmopolitan (Nair and Madhupratap 1984). Despite differences in the physical regimes between the Arabian Sea and the Bay of Bengal, particularly with regard to salinity (Madhupratap et al. 2003), no major differences in plankton composition have been detected (Rao and Madhupratap 1986). The seasonal monsoon cycles also causes changes in zooplankton abundance (Smith 1982; Banse 1991; Smith et al. 1998; Wishner et al. 1998).

In the marine milieu, mesozooplankton support sustained fishery (Madhupratap et al. 2001b). The linking between mesozooplankton and potentials of pelagic fishes, crustaceans, mollusks and marine mammals has been well documented (Arai 1988; Ates 1988; Harbison 1993; Plounevez and Champalbert 2000; Dalpadado et al. 2003; Sabates et al. 2007). Commonly, krill forms the principal diet of baleen whales, seabirds and pinnipeds in the Antarctic (Croxall et al. 1985). Also, the productive regions for the world's fisheries occur in the coastal areas with dense plankton populations (O'Driscoll et al. 2011; Madhupratap et al. 2001b). Thus, mesozooplankton are considered as the chief index of the secondary production by virtue of sheer abundance and intermediary role between phytoplankton and fish (Hays et al. 2005). Also, globigerina ooze and radiolarian ooze occurring at the sea floor formed by shell or tests of protozoan plankton like foraminifers, radiolarians and gastropod is of great economic value (Jones 1973). For instance, the radiolarian ooze is utilized as a filler and extender in paint, paper, rubber and in plastics as an anti-caking agent; thermal insulating material; catalyst carrier; as support in chromatographic columns and polish, abrasive and pesticide extender (Kadey 1983). Certain mesozooplankton species are important indicators of water masses (Webber et al.

1992), like *Thysanoessa* sp., *Aglantha* sp., *Meganyctiphanes* sp. and *Clione limacina* are the indicator species of Atlantic cold water mass and *Agalma elegans* and *Sagitta serratodentata* are associated with the warmer Gulf Stream (Russel 1935; Russel and Yonge 1936). Similarly, *Doliolum* is known as an indicator of the North Atlantic warm water current. Mesopelagic chaetognaths namely *Sagitta lyra, S. planctonis, S. decipiens* and *Eukrohnia hamata* were recorded in connection with upwelling events off Chile (Alvarino 1965; 1992; Ulloa et al. 2004) and on the west coast of India (Srinivasan 1976).

1.1.3 Ecological adaptation of mesozooplankton

Typically, the tropical mesozooplankton are diverse, grow faster, live shorter and reproduce often (Briggs 1995; Hirst et al. 2003). These mesozooplankton are of smaller body size and favor omnivorous feeding habit (Barton et al. 2013). Their distribution is affected by the physical factors such as light, food, oxygen, temperature and salinity (Breitburg 1997; Nybakken 2003; Kimmel et al. 2006). Thus, it is needed to undergo certain adaptations in order to adjust in such a dynamic ecosystem. The most common adaption observed in these tiny creatures is the diel vertical migration wherein the organisms feed at surface water column during the night, and migrate deeper during the day, forming the 'deep scattering layer' (Kinzer 1969). Possibly, such diel vertical migrations are caused to escape the predators (De Robertis 2002) and could save energy by the reduced metabolic rate in colder deeper water (Enright 1977). Another adaptation is of camouflaging with the environment, the copepod, *Labidocera* are particularly blue to purple in color due to the presence of carotenoid proteins and is a significant member of the neustonic community in the warmer seas (Herring 1967; 1977). Likewise, transparency of tissues provides camouflage with no surfaces to match or hide behind in the open sea.

It is a requirement for the mesozooplankton to be present in the euphotic zone, where phytoplankton thrive as their crucial predators. Many mesozooplankton are incapable of active movement, consequently, buoyancy is achieved by means of morphological adaptations which modulates the frictional resistance (Power 1989). The increase in surface body area due to feather–like projections, development of long spines, extreme flattening or due to infection of the organisms helps the mesozooplankton to float passively (Belmonte et al. 1997). Commonly, medusae, siphonophores, ctenophores, tunicates and fish larvae achieve flotation by the inclusion of more fluids and oil droplets in the body to reduce the specific gravity. Certain gelatinous organisms increase buoyancy by eliminating heavy ions and replacing them with chloride or ammonium ions (Bone et al. 1991). Particularly, buoyancy in jellyfishes is maintained due to the presence of pneumatophores. While, planktonic gastropod secrete foamy mucous substance to facilitates its floatation. Other members like salps, tunicates, and echinoderm larvae have specialized ciliary structures to propel through the water.

1.1.4 Copepods

Copepods are well-documented to be the numerically most abundant member of mesozooplankton community in both the coastal as well as oceanic waters of the eastern Arabian Sea and other parts of the world oceans (Padmavati et al. 1998; Paffenhofer and Mazzocchi 2003; Kurten et al. 2016; D’souza and Gauns 2018). Their life stages include six naupliar and five copepodid stages that moult into a complete adult copepod (Landry 1975). Interestingly, size-wise, male copepods are generally smaller and less abundant than that of their female counterpart (Buskey 1998; Paffenhofer and Mazzochi 2003). Mate finding could have been challenging for the pelagic copepods, however, they have evolved mechanisms like amassing of ready-to-mate adults at particular location (Hayward 1981; Tsuda and Miller 1998) and capability of males to remotely trace receptive females using distance-pheromones (Katona 1973; Griffiths and Frost 1976) and contact-pheromones (Snell and Morris 1993; Snell and Carmona 1994) to enhance mate encounter rates. Also, the abundance of males and females (Kiorboe 2006) and the female biased sex-ratio (Lee and McAlice 1979) play an important role in population dynamics.

Factors like temperature, body-size of females and nourishment affect copepod reproduction (Marshall and On 1955; McLaren 1978; Durbin et al. 1983). After copulation, egg-sacks are formed in females that hold the eggs usually embedded into a mass of secretions. In some copepods, there is a single egg sac or a loose egg mass (Kimmerer et al. 1994); while in others, the eggs are released directly in water (Runge 1984). Copepod females that produce egg-sacks, nurture the eggs for few days and egg sack is cast off to form larvae. Insufficient feed may produce the non-hatching eggs (Ban et al. 1997; Miralto et al. 1999), or resting eggs (Castellani and Lucas 2003) or at times the eggs may be unfertilized (Ianora et al. 1989) and the virgin copepod females may produce sterile eggs (Parrish and Wilson 1978; Uchima 1985).

<u>1.1.5 Significance of copepods in marine ecosystems</u>

Planktonic copepods play important role in marine milieu; on one hand, they graze on diatoms (Metz 1998) and on other hand, secondary consumers graze on them (Madhupratap et al. 2001a). Also, copepods generate carbon rich fecal pellets that add greatly to the marine snow and therefore accelerate the downward flux of organic matter from surface waters. In addition, via the extensive diel and seasonal vertical migrations, copepods transfer organic matter from the euphotic layer to deeper layers (Bathmann et al. 1987;

Longhurst and Williams 1992). Collectively, copepods greatly influence the transfer of energy and carbon compound to the different trophic level throughout the marine food web. Remarkably, this group constitutes the biggest source of protein in the oceans (Masuda et al. 2006). Apart, the carotenoids solely produced by autotrophs (Lotocka and Styczynska-Jurewicz 2001; Nieuwerburg et al. 2005), are grazed upon by copepods and processed into astaxanthin and canthaxanthin via metabolic pathway (Kleppel et al. 1985; Nieuwerburg et al. 2005). The exploitation of precursors and successive synthesis of astaxanthin by herbivorous zooplankton thus represents a vital entry point of astaxanthin into marine food webs (D’souza and Gauns 2016). The sheer abundance of this most diverse group in marine plankton secures them a vital role in the marine economy. Most of the commercially harvested fishes and even the whales in the northern hemisphere directly feed on them.

1.2 REVIEW OF LITERATURE

Copepods the most significant mesozooplankton have grabbed the considerable attention of scientific community from many decades. The research papers on copepod distribution, taxonomy and its ecological role have increased tremendously from the polar, tropical and temperate region. Amongst, the most fundamental study is regarding copepod feeding ecology as it tends to vary depending upon the locale (D’souza and Gauns 2016).

1.2.1 Copepods taxonomy and distribution

Taxonomy and distribution of copepods being the most pertinent to ecological studies, a lot of emphasis has been laid on this aspect from various habitats.

Systematic studies on copepods have been extensively carried out from different regions of the world. Early research on copepods mostly concentrated on taxonomy and distribution from different habitats. The distant and obscure oceanic regions revealed copepods as the dominant mesozooplankton, to name few regions like in North Atlantic (Hulsemann and Grice 1963; Deevey 1964; Morales et al. 1991; Hays et al. 1997; Berasategui et al. 2005), tropical Pacific (Grice 1961; Longhurst 1967; 1985; Vinogradov and Shushkina 1976; Dessier and Donguy 1985; Sameoto 1986; Roman et al. 1995), Subarctic Pacific (Miller 1993; Mackas et al. 1993; Shih and Chiu 1998;Yamaguchi et al. 2002), North Pacific gyre (Hayward and McGowan 1979), off Jamaica (Webber and Roff 1995), southwestern Atlantic (Berasategui et al. 2005), mid Atlantic ridge (Gaard et al. 2008) and the Sargasso Sea (Deevey and Brooks 1971; 1977; Roman et al. 1993). Noticeably, the copepod abundance and distribution vary on the seasonal scale in the North Eastern Pacific Ocean (Davis 1949), Buzzards and Capecod Bay (Anraku 1964), Osashio and Kuroshio region of South Japan and California (Furuhashi 1966; Fleminger 1967). Another fascinating observation of reduced zooplankton abundance with depth was reported in the Pacific Ocean (Longhurst 1967). More emphasis was laid on zooplankton with reference to upwelling by Santander (1981) from Peruvian region. The study highlighted that feed, both qualitatively as well as quantitatively, was regulating the zooplankton composition. The knowledge on mesozooplankton community was enhanced by Heron et al. (1984) from the Arctic Ocean and Smith and Vidal (1986) from the Georgia River. Great Barrier Reef harbored different copepod assemblages than the Southern Gulf of Maine (McKinnon and Thorold 1993). Additionally, zooplankton that were unable to adapt to low oxygen seemed to exclude oxygen minimum zone as evidenced from the reduction of biomass and density in this zone of the equatorial Pacific (Saltzman and Wishner 1997).

Mesozooplankton communities were examined from Chesapeake Bay (Dolan and Gallegos 2001), North Atlantic and North Sea (Beaugrand 2003), Atlantic (Clark et al. 2001) and Kenyan Seagrass bed (De Troch et al. 2001). Similarly, zooplankton studies were carried out from Kenyan waters revealed copepod to be the dominant mesozooplankton and higher diversity was observed in open waters by (Osore et al. 2003; Mwaluma et al. 2003). Nilssen et al. (2003) studied the variation of pelagic copepods from the boreal region. Kazmi (2004) reported detailed encounter of copepod community in Pakistani waters. Lo et al. (2004) investigated copepod assemblages in relation to hydrological conditions in the southeastern Taiwan Strait. Islam et al. (2005) reported the spatial variations and trophic ecology of copepods in a highly embayed estuarine system in Ariake Sea. Cornilis et al. (2005) studied the distribution pattern, taxonomic composition and community structure of mesozooplankton between the Gulf of Aqaba and the northern Red Sea. Magalhaes et al. (2006) noticed the spatio-temporal variation in abundance of *Pseudodiaptomus* species. Hwang et al. (2007) observed higher copepod species richness in lower latitudes of the northern South China Sea. Zervoudaki et al. (2007) revealed the important contribution of small–bodied copepods in the frontal zone of Aegean Sea. Tseng et al. (2008) scrutinized the succession of copepod assemblages governed by the monsoon in coastal waters of Taiwan. Chang et al. (2010) examined the copepod community in an embayment of Taiwan during the transition of monsoon. Mazzocchi et al. (2011) provided a detailed description on zooplankton associations in the Mediterranean Sea. Valois et al. (2011) studied the recovery of zooplankton in a multiple stressor environment in lakes of Sudbury. Escribano et al. (2012) studied zooplankton variation with special emphasis on copepod community during upwelling in the coastal waters off Chile. Mackas et al. (2012) reported seasonal variations in Marine zooplankton within the upper-ocean environment in North Atlantic, North Pacific and Mediterranean region. Ward et al. (2012) investigated seasonal variations in mesozooplankton assemblage from the Scotia Sea. Inter–annual and regional differences in mesozooplankton of the western North Pacific Ocean was studied using Continuous Plankton Recorder (Yoshiki et al. 2013). Jackson and Smith (2016) reported the vertical distribution of Eucalanoids from the Costa Rica Dome, Eastern Tropical Pacific. Pierson et al. (2016) examined the impacts of temperature on *Eurytemora carolleeae* within the Upper Chesapeake Bay. Overall, studies on copepod diversity reveled higher species richness in the tropics is strongly coupled to temperature (Rutherford et al. 1999).

Till date, published papers on zooplankton from Indian waters mostly deals with the interaction between zooplankton and the environment (Pillai et al. 2000; Jagadeesan et al. 2013; Gauns et al. 2015), species composition (Nair et al. 1981; Rakesh et al. 2006; Srichandan et al. 2015), diel vertical migration (Mitra and Patra 1990; Santhakumari and Peter 1993; Goswami et al. 2000), and zooplankton relative to fish stock (Chidambaram and Menon 1945; Dalal and Parulekar 1991; Goswami et al. 1992) or hydrographic variability (D’souza and Gauns 2018). Numerically abundant mesozooplankton, the copepods, were mostly studied with respect to a taxonomy and spatial distribution in both the coastal as well as oceanic waters of the Arabian Sea and Bay of Bengal. Particularly, the seasonal and spatial occurrence of zooplankton groups along both the coasts of India received ample importance. Pioneering research work on zooplankton of the coastal waters of India was carried out by Hornell and Nayudu (1923), Menon (1931), Chidambaram and

Menon (1945) and Prasad (1954). The fundamental work on coastal and open waters mesozooplankton from Indian waters was extensively carried out from the John Murray Expedition (1933–1934), the International Indian Ocean Expedition (IIOE; 1959–1965) and the Indian Ocean Experiment (1979). Important contribution were laid by the IIOE and the Joint Global Ocean Flux Studies (JGOFS) programs that led the most detailed investigation on the quantitative and qualitative distribution of zooplankton in the Indian Ocean. Similarly, surveys by the Netherlands (Netherlands Indian Ocean Program, 1992–1993), the United Kingdom (Arabesque, 1994), Germany (German–JGOFS, 1995–1997), Pakistan (North Arabian Sea Environmental and Ecological Research; 1992–1995), India (Indian–JGOFS, 1994–1997) and the United States (US–JGOFS, 1994–1996) expanded the understanding on biogeochemistry of Indian waters (Smith and Madhupratap 2005).

The John Murray Expedition mostly covered the Arabian Sea and concentrated on copepods (Sewell 1948). The IIOE collected zooplankton samples throughout the Indian Ocean, but sampling was restricted to upper 200 m of the water column using nets of 330 µm mesh (Banse 1963). The mesozooplankton taxa studied during IIOE showed high abundance of polychaete larvae (Peter 1969a), fish larvae (Peter 1969b), euthecosome molluscs (Sakthivel 1969), young ones of cephalopod (Aravindakshan and Sakthivel 1973), amphipods (Nair et al. 1973), and euphausiids (Brinton and Gopalakrishnan 1973; Gopalakrishnan and Brinton 1969) during southwest monsoon. Investigations by JGOFS-Netherlands (Baars 1994), the United Kingdom (Arabesque 1994; Burkill 1999), Pakistan (Kidwai and Amjad 2000), India (Krishnaswami and Nair 1996) and the United States (Smith et al. 1998) expanded the zooplankton facts of this region.

It is noteworthy to mention the Indian oceanographic research vessels namely RV Gaveshani, ORV Sagar Kanya and FORV Sagar Sampada, which were significant in sample collections from various regions of the Arabian Sea to understand the biochemistry (Bhattathiri et al. 1980; Qasim 1982; Naqvi et al. 1987; Mathew 1990; Unnikrishnan and Antony 1992; Madhupratap and Parulekar 1993; Sarma et al. 1996; Gunderson et al. 1998; Padmavati et al. 1998; Nair et al. 1999; Madhupratap et al. 2001a; Prasannakumar et al. 2004; Madhu 2004; Naqvi et al. 2006; Parab et al. 2006; Prasannakumar et al. 2010; Naqvi et al. 2010).

Early zooplankton works concentrated on spatial and temporal variations and taxonomy of zooplankton (Madhupratap et al. 1979; Achuthankutty et al. 1980; Nair and Peter 1980; Nair et al. 1981; Kumar and Sarma 1988). Subbaraju and Krishnamurthy (1972) studied the plankton production off Porto Novo, Bay of Bengal and documented copepod dominance that varied with a change in salinity and rainfall. Menon et al. (1977), Kumar (1984) and Katti et al. (2002) studied spatio-temporal variations in the zooplankton on the quantitative and qualitative aspects in relation to hydrology in the coastal waters of Mangalore. Goswami et al. (1977) investigated zooplankton production off Vengurla and Karwar revealed high biomass at subsurface depth as compared to surface waters. Later, the secondary production and zooplankton abundance in the coastal waters from Vengurla to Malpe, west coast of India was investigated by Goswami (1985). Stephen and Iyer (1979) reported monthly variations in species composition and coexistence of calanoids in shelf waters off Cochin. Similarly, Madhupratap et al. (1979) presented the distribution, community structure and species succession of copepods from Cochin Backwaters. Peter (1977) recorded dominance of copepods and decapods along the southwest coast of India.

Nair and Peter (1980) studied zooplankton from shelf waters off the west coast of India. Kumar and Sarma (1988) carried out zooplankton studies in Vishakapatnam harbor and near shore waters off the East Coast of India. Likewise, Neelam and Nair (1997) studied distribution and abundance of copepods of Bombay harbor. Also, Gajbhiye et al. (1991) investigated on copepods of the near shore waters of Mumbai. Ecological studies on copepods in the Mandaramani creeks of West Bengal showed no diel pattern in distribution or migration of zooplankton (Mitra and Patra 1990). Maruthanayagam and Subramanian (1999) studied the variation in zooplankton in relation to hydrological condition in Palk Bay and Gulf of Mannar. Recently, D'costa and Pai (2013; 2015) studied zooplankton from Malvan waters and reported their community structure and concluded that salinity and turbidity as important factors responsible for their distribution.

There have been more attempts to characterize the zonation of zooplankton in the northern Arabian Sea (Madhupratap et al. 1990; Paulinose et al. 1992; Bottger- Schnack 1996; Madhupratap et al. 1996b; Padmavati et al. 1998; Wishner et al. 1998; Madhupratap et. al. 2001; Smith and Madhupratap 2005; Wishner et al. 2008), Bay of Bengal (Rakesh et al. 2006; Fernandes and Ramaiah 2009; 2013) and Indian Ocean (Kasturirangan et al. 1973; Saraswathy 1973; Haridas and Rao 1981; Tsujimoto et al. 2006; Jayasiri and Priyadarshani 2007). To elaborate, Madhupratap and Haridas (1990) reported detailed study on calanoid copepods from the upper 1000 m of southeast Arabian Sea. Goswami and Shrivastava (1996) studied zooplankton abundance and diversity of northern Arabian Sea including coastal, shelf, slope and Open Ocean. Madhupratap et al. (2001) reported mesozooplankton biomass, composition and distribution in relation to oxygen gradient during the fall inter-monsoon in the Arabian Sea. Distribution of zooplankton and selected hydrographical parameters in the Arabian Sea was investigated by Katti et al. (2003). Study on bacterial and zooplankton distribution in deep waters of the Arabian Sea was carried out by Koppelmann et al. (2003). Fabian et al. (2005) examined zooplankton composition in deep western and central Arabian Sea. Habeebrehman et al. (2008) studied the variability in biological response to different phases of southwest monsoon. Vimalkumar et al. (2008) reported the hydrographic condition of southeast Arabian Sea during southwest monsoon and spring inter–monsoon. Gauns et al. (2015) reported an interesting study on the ecology of *Pyrosoma spinosum* from the Central Arabian Sea that were associated with picophytoplankton dominated silicate depleted waters that prevailed during the southwest monsoon. Distribution of zooplankton biomass and its composition in the western Bay of Bengal during southwest monsoon was investigated by Achuthankutty et al. (1980). Further, Fernandes and Ramaiah (2009) noted that temperature, salinity, and food supply are some of the important factors that are known to cause spatial changes in zooplankton populations in the Bay of Bengal. These environmental parameters have an impact on the breeding and hence affect the density and composition of zooplankton. Later, Fernandes and Ramaiah (2013) described the copepod communities from upper 1000 m water column of western Bay of Bengal during fall inter–monsoon and suggested cold-core eddies provide nourishment to the less productive waters sustaining the zooplankton. Also, Fernandes and Ramaiah (2014) described the copepod communities in surface-layer of Bay of Bengal during winter monsoon and highlighted dense pockets of zooplankton biomass in the moderately productive bay. In addition, Srichandan et al. (2015) provided a detailed taxonomic study that revealed the 186 groups of holoplankton and 23 groups of meroplankton from coastal waters of Bay of Bengal. On a similar note, Rajthilak et al.

(2016) reported 23 species belonging to 7 families of calanoids along Tamil Nadu coast. Likewise, Kasturirangan et al. (1973), Saraswathy (1973), Haridas and Rao (1981), Tsujimoto et al. (2006) and Jayasiri and Priyadarshani (2007) reported mesozooplankton variations from the Indian Ocean. Stephen and Rao (1980) studied the distribution of bathypelagic family Arietellidae in the upper 200 m in the Indian Ocean. Recently, *Pseudodiaptomus serricaudatus*, a planktonic copepod with cosmopolitan distribution was reported for the first time in the open oceanic waters of the Equatorial Indian Ocean transported by offshore moving coastal currents (Rebello et al; 2013).

Temporal variability in mesozooplankton abundance can arise as a consequence of biological and physical processes. Biological variability can crop up on weeks durations depending upon the life cycle of the organisms, and on a diurnal time scale linked with vertical migration. Physical variations can be either seasonal or on a time scale of days as a resultant of onshore–offshore advection. Mesozooplankton responses to seasonal changes in the physical environment are yet to be understood fully in the Arabian Sea. Nevertheless, the northeast monsoon is characterized by increased abundances of *Oithona*, *Oncaea* and *Farranula*, when compared with the southwest monsoon (Smith 1988; Stephen 1988; Smith et al. 1998; Madhupratap et al. 1996a; Smith and Madhupratap 2005). Variations in food availability (Garrison et al. 2000), deepened and dynamic mixed layers (Madhupratap et al. 1996b; Weller et al. 2002: Dickey et al. 1998; Wiggert et al. 2000) in the northeast monsoon were the characteristics accountable for their seasonal variations. Smith (1995) and Prasannakumar et al. (2001) reported high biological productivity from the central Arabian Sea during the southwest monsoon. Whereas, during northeast monsoon sizably high biological productivity is attained through convective mixing (Banse et al. 1996;

Madhupratap et al. 1996; Prasanakumar et al. 2001). Moreover, Nair et al. (1999) and Prasannakumar et al. (2000) reported that the biological productivity of the Arabian Sea is tightly coupled with the physical forcing mediated through nutrient availability. Madhupratap et al. (1992) reported that high zooplankton standing stock during early southwest and northeast monsoon periods along the southwest coast of India. Likewise, Pillai and Nair (1973) reported the least productive of zooplankton abundance during southwest monsoon from the southwest coast of India. In contrast, Menon and George (1977) reported that the zooplankton abundance were low during January–April and high during July–September from the southwest coast of India. On the other hand, Nair and Neelam (1998) documented peak zooplankton production during post–monsoon dominated by omnivorous copepods in coastal waters of Bombay. Higher zooplankton biomass during northeast monsoon corresponding to lower water temperature and dissolved oxygen was reported along Karnataka coast (Santhakumari 1991). Also, copepod species revealed a marked distinction between the coastal and offshore communities (Madhupratap et al. 1990; 1992; Padmavati et al. 1998). Further, Gauns et al. (2005) reported that the biological productivity and carbon fluxes of planktonic organisms with respect to their spatial and temporal variations in the Arabian Sea and Bay Bengal. Bhat et al. (1993) reported that coastal region was more productive than the oceanic region in terms of zooplankton standing crop. While, Wishner et al. (1998) revealed the high mesozooplankton biomass both in coastal and Open Ocean waters of the Arabian Sea. Padmavati et al. (1998) and Wishner et al. (1998) observed the mesozooplankton biomass to be higher in the upper 1000 m in the Arabian Sea. Another common feature of west-coast waters of India is the dual peaks of plankton abundances. Pillai (1968) noticed dual peaks of zooplankton abundances, one in pre–monsoon and other in the post–monsoon off Bombay coast. Also, Suresh and Reddy (1975) reported dual peaks of zooplankton abundance during monsoon and pre-monsoon in coastal waters of Mangalore. a similar study by Patil (1976) also documented the dual peak abundance of zooplankton during the southwest monsoon and northeast monsoon off Saurastra coast. On a similar note, Goswami and Padmavati (1996) recorded bimodal zooplankton production in coastal waters of Goa, the first peak during September–October and second one during March–April. Theyopined that the occurrence and abundance were influenced by seasons, depth of water column and hydrographic condition. Certain studies linked the spatio-temporal variation of mesozooplankton to the phytoplankton blooms like swarming of *Noctiluca* (Prasad and Jayaraman 1954) and *Trichodesmium* bloom (Nair et al. 1981). Patil (1980) reported zooplankton abundance receding phytoplankton blooms along the Balasore coast. Likewise, Goswami (1983) recorded swarming of zooplankton, *Crises ocicula* in the coastal waters of Goa during October and found that the environmental conditions favored the blooming. Also, pollution and diel variation in zooplankton were reflected in the variation of zooplankton abundances. Gajbhiye and Desai (1981) investigated zooplankton variability in polluted and unpolluted waters off Bombay and reported that group diversity was high in unpolluted waters. A study on the diurnal variation on zooplankton carried out from off Versova (Bombay) showed that zooplankton biomass was associated with the flood or ebb (Gajbhiye et al; 1984).

Seasonal variations in mesozooplankton are mostly driven by changes in wind speed and direction, which affect currents, eddies and upwelling intensity. Polychaetes and other species release larvae seasonally (Peter 1969a, b). Such seasonal spawning in turn affects the seasonal variations of zooplankton. Intense upwelling in the Arabian Sea occurs during June–September that enhances the biological production (Naqvi and Jayakumar 2000; Wiggert et al. 2005; Habeebrehman et al. 2008), thus, support primary and secondary production. Madhupratap et al. (1990) indicated that zooplankton composition and abundance from coastal upwelling situation was distinct as compared to non upwelling and offshore waters. Also, Achuthankutty et al. (1998) recorded highest zooplankton production in the coastal waters of Goa during the upwelling period and they have attempted to group copepods into different categories based on salinity preference. The effect of semi-permanent eddies on the distribution of mesozooplankton was studied by Fernandes (2008) in the central Bay of Bengal. Jagadeesan et al. (2013) studied reversing monsoon currents structuring the mesozooplankton in the Gulf of Mannar and the Palk Bay and revealed salinity as governing factor for copepod distribution using multivariate analysis. Malik et al. (2015) reported the interactions of biotic and abiotic factors in trophic levels from upwelling and non-upwelling regions during the summer monsoon.

The paradox of the Arabian Sea mesozooplankton that biomasses remain rather constant throughout the year was documented by Madhupratap et al. (1992). The maintenance of relatively high mesozooplankton biomass during inter-monsoon despite of variation in phytoplankton biomass is elucidated through the microbial loop (Azam et al. 1983), that might persuade seasonality of mesozooplankton in the Arabian Sea (Banse 1984). Primer of the microbial loop emerges due to large organic carbon pool produced by senescent phytoplankton blooms. The bacterial community actively uses this carbon that reaches the mesozooplankton through microzooplankton (Madhupratap et al. 1996b). Re-evaluation on the paradox of mesozooplankton in the eastern Arabian Sea was carried out by

Jyothibabu et al. (2010) and concluded that mesozooplankton biomass was high in the northern Arabian Sea during the winter monsoon and spring inter monsoon periods and along the south west coast of India during the summer monsoon. However, Vidya et al. (2013) studied the interaction between physical and biological processes on the biogenic flux in the equatorial Indian Ocean and revealed microbial loop mediated faster re-mineralization of photosynthetically produced organic matter. However, there is limited information available on feeding habits of zooplankton from Indian waters. Godhantaraman and Krishnamurthy (1997) conducted ex-situ experiment on food habits of tropical zooplankton and revealed that size and shape of the prey as important factors for microzooplankton feeding. Additionally, Edwards et al. (1999) made an attempt to study zooplankton herbivory in the Arabian Sea during and after the southwest monsoon. Likewise, Madhupratap (1999) recorded distribution, abundance and general feeding habitats of free living copepods from the Arabian Sea. Roman et al. (2000) evaluated the mesozooplankton production and grazing in the Arabian Sea using different growth rate equation.

Specific works on copepod cultures mostly in feeding ecology have received importance recently. Santhanam and Perumal (2012) evaluated the copepod *Oithona rigida* as live feed in Aquaculture. Jasmine et al. (2016) reported hatching, maturation and survival of *Euterina acutifrons* culture using a different type of feed.

In the Eastern Arabian Sea, a subsurface oxygen minimum zone (Naqvi et al. 2006) has a profound impact on the distribution of pelagic fauna. The Arabian Sea harbor intense permanent oxygen minima in the oceanic realm and seasonal anoxia in coastal region (Naqvi et al. 2006). The depleted oxygen waters in Arabian Sea were a foremost finding of the John Murray Expedition in 1933–1934 (Rice 1986). The upper boundary of the oxygen minimum zone generally occurs between 100 and 150 m in the Arabian Sea. Beneath this gradient, waters are oxygen–depleted until approximately 1000 m depth, where oxygen concentrations begin to increase slowly with depth. In the Arabian Sea, the oxygen minimum zone is thicker (100–1000 m) compared to the Bay of Bengal (200–600 m). On the other hand, suboxic zone has higher oxygen concentrations (>5 to <10l M) in the Bay of Bengal as compared to Arabian Sea (Smith and Madhupratap 2005). First reference to the depleted oxygen waters and its link to zooplankton in the Arabian Sea was by Sewell and Fage (1948) followed by Vinogradov and Voronina (1961). Later on, many studies on mesozooplankton in relation to the dissolved oxygen dynamics from coastal as well as open-ocean waters characterizing vertical gradient of mesozooplankton were undertaken from the Arabian Sea (Sewell and Fage 1948; Vinogradov and Voronina 1961; Smith 1982; Madhupratap et al. 1990; Madhupratap et al. 1996; Padmavati et al. 1998; Wishner et al. 2008; Madhupratap et al. 2001a; Banse et al. 2014). Typically, the copepods that can thrive in the oxygen minimum zone belonged to the families particularly Eucalanidae, Metridinidae and Augapatilidae (Smith and Madhupratap 2005). These copepods along with some of the mesopelagic fishes seem to have evolved to tolerate the oxygen minimum zone (Smith et al. 1998). Reduction in mesozooplankton biomass at depths below the thermocline is more acute in the Arabian Sea because of the persistent, oceanic, mid-depth oxygen minimum zone (dissolved oxygen < 0.1 ml L^{-1}; Naqvi 2006) in the eastern region. Vertical profiles of mesozooplankton often showed a large decline within the depleted oxygen waters (Banse 1994; Vinogradov 1970; Wishner et al. 1998). The column mesozooplankton biomass (0–1000 m) in the Arabian Sea showed a consistently high biomass in the surface layer, markedly reduced in the range of low oxygen waters, and slightly increased again with increase in dissolved oxygen (Banse 1994; Wishner et al. 1998). Comparative studies with and without low oxygen in Arabian Sea revealed high mesozooplankton biomass in the oxic upper 100 m (Vinogradov and Voronina 1962). A bulky fraction of the Onceaidae was frequent in the bathypelagic zone below the low oxygen waters of the Arabian Sea, consequential of enhancement in numbers of species in this precinct (Bolttger- Schnack 1996). A variety of other taxa showed diverse distributional reaction to oxygen gradients within the low oxygen waters. Abundance peak of gelatinous taxa like the Tunicata was relatively trivial in the extremely low oxygen waters. Moreover, crustaceans and fish actually require more oxygen hence they showed higher abundance deeper waters where oxygen concentrations were slightly more (Madhupratap et al. 2001a). The decapods particularly *Gennadas sordidus, Sergia filictum* and *Eupasiphae gilesii* spend their lives wholly within the low oxygen waters (Mincks et al. 2000). However, their feed varied widely; *G. sordidus* favored detritus and marine snow, while *S. filictum* chose euphausiids and other shrimp and *E. gilesii* preferred copepods, fish and shrimp (Mincks et al. 2000).

The lower section of oxygen minimum zone harbor relatively high particulate organic carbon concentrations coupled with increased feeding rates of mesozooplankton (Wishner et al. 1998; Gowing et al. 2003). Ciliate showed appealingly high abundance in the suboxic layer as compared to oxic layers, signifying reduced predation pressure on microplankton in low oxygen waters (Gowing et al. 2003). The most remarkable species of Metridinidae is *Pleuromamma indica* (Saraswathy 1986) that is probably an endemic species to the Indian Ocean (Saraswathy and Iyer 1986). Ecological study on copepod, *Lucicutia grandis*

L. grandis thriving in low oxygen waters (3.15–6.75 mM; Wishner et al. 2000) revealed year-round reproducing behavior and showed detritivorous–omnivorous feeding habit (Gowing and Wishner 1998; Wishner et al. 2000).

Vertical distribution of copepods seems to be governed by their nutritional requirement and physiological conditions. Thus, the salinity and temperature of water column play a role in structuring the copepod community. A detailed study on the vertical distribution of copepod species in the Arabian Sea was conducted by Madhupratap and Haridas (1986) and Padmavati et al. (1998). Calanoid copepods belonging to the families Aetideidae, Phaennidae, Scolecitrichidae, Metridinidae, Lucicutiidae and Augaptilidae were generally found at mesopelagic depths with very small numbers in the upper layers (Madhupratap and Haridas 1986; Stephen and Rao 1980; Padmavati et al. 1998). Occasionally, these species tend to undergo diel migrations (Madhupratap and Haridas, 1990). In an investigation, Bolttger-Schnack (1996) reported small-bodied Poecilostomatoida dominace (90–95% of total numbers) all depths below 0–100 m and *Oncaea bathyalis* and *O. subtilis* within the low oxygen waters. An additional group of copepods, the seasonal migrants occupying the low oxygen waters were *Rhincalanus nasutus*, *Eucalanus attenuatus*, and *Lucicutia maxima* (Vinogradov and Voronina 1962). Similarly, the copepod *Calanoides carinatus*, is known to a portion of their sub–adult stage in the suboxic waters, mostly in non-feeding and diapausing phase. These species feed and reproduced in the surface waters in large numbers only during the southwest monsoon (Smith 2001). Consequently, the mesozooplankton resident in the core of the low oxygen waters remains exceptionally low. Even though organisms are known to occupy different parts of the suboxic zone, especially its boundaries differ depending upon the season.

Bio-monitoring the species and evaluating the diversity indices helps in understanding the community structure. Zooplankton composition and its diversity in the western Bay of Bengal were investigated by Nair et al. (1981). Zooplankton distribution in neutson and water column along the west coast of India from Goa to Gujarat was studied by Padmavati and Goswami (1996) and revealed that species richness and evenness were negatively associated to the zooplankton biomass. Maruthanayagam and Subramanian (2000) studied the diversity of copepods in Palk Bay and Gulf of Mannar along the east coast of India. Santhanam and Perumal (2003) indicated higher values of zooplankton density and diversity during summer and post–monsoon and were positively correlated with salinity and surface water temperature in Parangipettai coastal waters. Rakesh et al. (2006) recorded high zooplankton diversity indices in the open sea relative to coastal locations.

It is well known that zooplankton supports the fishery by being their feed. Few studies pointed out the zooplankton-fish importance along with their spatio-temporal variability. To elaborate, Chidambaram and Menon (1945) associated plankton and physicochemical parameters for locating potential fisheries off Malabar and South Kanara coast. Similarly, Ramamurthy (1965) studied plankton in relation to the fishery and mentioned that monsoon and early post–monsoon exhibit high plankton productivity off North Karnataka coast. Moreover, Dalal and Parulekar (1991) necessitated the revalidation of zooplankton production based exploitable fishery resources in the Indian Ocean due to unavailability of data from productive neritic waters. Further, Goswami et al. (1992) pointed out the importance of zooplankton in the neritic and oceanic Indian seas to estimate fishery resources.

1.2.2 Feeding habits of copepods

Efforts to comprehend the copepod feed and its significance in terms of secondary production have been prominent in the literature for many decades (Marshall and Orr 1955; Ryther 1969; Morey–Gaines 1980; Kleppel et al. 1991; Goes et al. 1999; Islam et al. 2005; Tseng et al. 2008; D'souza and Gauns 2016; Fernandes and Ramaiah 2016). Apparently, both quality and quantity of feed affect copepod production (Durbin et al. 1983; Roman 1984; Tiselius and Jonsson 1990) and consequently, the production at higher trophic levels (Ryther 1969; Smith and Eppley 1982). Feeding studies of herbivorous copepods are imperative in order to understand the carbon cycle in the marine ecosystem. There are literatures available that have emphasized the relationship between copepod feeding, anatomical structure and behavior (Anraku and Omori 1963; Timonin 1971; Turner 1978; Paffenhofer 1988). To elaborate, mouthpart studies on calanoid copepods, particularly, the mandibular cutting edges and maxillae provide clue of their feeding habits (Esterly 1916; Anraku and Omori 1963; Itoh 1970; Trancter and Abraham 1971; Turner 1978; Ohtsuka 1991; Ohtsuka and Onbe 1989; 1991; Scnnack 1989; Ohtsuka et al. 1996). Commonly, copepods with fine setules on the basis and endopod like *Acartia* (Rosenberg 1980; Ohtsuka et al. 1996), *Centopages* (Cowles and Strickler 1983; Ohtsuka et al. 1996), *Eucalanus* (Paffenhofer et al. 1982), *Epilabidocera longipedata*, and *Eurytemora herdmani* (Ohtsuka et al. 1996) employ suspension-feeding. However, Pontellidae exhibit difference mouthpart structures and feeding modes (Ohtsuka and Onbe 1991), *Epilabidocera* spp., for example, employs both suspension and raptorial feeding modes, preying on both zooplankters and particles (Park 1966; Ohtsuka et al. 1996). Normally, Acartiidae and Temoridae are known to be suspension-feeders (Ohtsuka et al. 1996). Nonetheless, few species show carnivorous feeding behavior (Davis 1977; Turner 1991; Ohtsuka 1991) and certain species switch their feeding strategies based on the availability of feed and seasons. On the other hand, feeding habit of Centropagidae is complex as certain species prey on copepodids and copepod nauplii and few feed on phytoplankters and microzooplankters (Ohtsuka et al. 1996). The family Tortanidae is known to be carnivore, feeding on variety of zooplankters such as copepodids, copepod nauplii, cladocerans, polychaete and tintinninds in in-situ and ex-situ environment (Mullin 1979; Robertson 1983; Ohtsuka et al. 1987). In addition, mandibular gnathobases are indicator of feeding habits in the calanoids (Anraku and Omori 1963; Ohtsuka et al. 1996). Vaguely, the ventral teeth on the gnathobase are sharp in raptorial predators as compared to the suspension feeders and lesser number of teeth indicates carnivorous feeding habit (Ohtsuka 1991). On the basis of gnathobases tooth, *Tortanus discaudatus* seemed to exhibit strong carnivory as compared to *Eurytemora herdmani* (Ohtsuka et al. 1996). Also, Ohtsuka et al. (1996) suggested that *T. discaudatus* employ raptorial feeding with the maxillae that act as "chopsticks" to arrest big–sized prey and the additional support is gained from the three terminal serrated setae on the elongate coxal endite.

The sophisticated technique of cinematography was applied on calanoid copepods revealed the importance of maxillae in feeding process (Koehl and Strickler 1981). Also, high speed cine camera or video (Alcaraz et al. 1980; Cowles and Strickler 1983) and micro-impedance technique were used to evaluate copepod feeding mechanisms via cephalic appendage activity (Yule and Crisp 1983; Gill and Poulet 1986; Gill 1987; Gill and Poulet 1988). The pros and cons of these methods have been discussed by Gill and Poulet (1986).

Techniques of cell capture have been described for the calanoid copepods *Eucalanus pileatus* and *Paracalanus parvus* using a frame motion analyzer to digitize the appendage movements (Grice 1961). Collectively, these studies revealed that the appendage movements produce a feeding current used for particle capture and rejection. Also, the behavior and feeding rate of copepods vary in response to the quality of particulate food (Price et al. 1983; Harris et al. 1986). Gill and Poulet (1988) investigated copepod foraging behavior and appendage movements of *Temora longicornis* in the presence of food and non-food stimuli, as recorded with a computerized micro-impedance system.

Feeding habits of *Oncaea venusta*, *O. mediterranea* and *O. conifera* belonging to the poecilostomatoid were scrutinized from the coastal waters of the Korean Peninsula showed that the females and males of *Oncaea* preferred Chaetognatha, Appendicularia and Thaliacea (Go et al. 1998). The experimental study on *Oncaea* females showed a preference for large, non-motile food particles mainly the *Phaeocystis* bloom that contained gelatinous colonies along with other flagellate species and diatoms (Metz 1998). Recently, Saiz et al. (2014) investigated feeding behavior of *Oithona davisae* in the laboratory. This experimental study revealed that *O. davisae* can feed on dinoflagellate, ciliate and calanoid nauplii. Further, Saiz et al. (2014) strongly supported that the nauplii and females of *O. davisae* feed on relatively larger prey using their ambush-feeding behavior.

In the Arabian Sea, mostly the traditional approach of anatomical structures was considered to understand the copepod feeding behavior (Timonin 1971; Madhupratap and Haridas 1986; Madhupratap et al. 2001a). However, the recent techniques like gut content examination, gut fluorescence, fecal pellet studies, and use of biochemical markers like fatty acid and stable isotopes to deduce the feed of the organisms was mostly not employed. Lately, the feeding ecology of the calanoid copepod, *Lucicutia* was carried out in the Arabian Sea at one station during spring inter–monsoon and southwest monsoon using transmission electron microscopy (TEM) of gut contents (Gowing and Wishner 1998). Gut fluorescence technique was employed on copepods to understand their feeding patterns by Goes et al. (1999). Also, *Spinocalanus antarcticus* gut content has also been studied by Wishner et al. (2008) using TEM. The study of feeding ecology is gaining importance recently and limited studies have been reported from the Arabian Sea.

1.2.3 Gut fluorescence

The gut fluorescence method has been widely used for feeding studies of copepods (Mackas and Bohrer 1976; Boyd et al. 1980; Tande and Bamstedt 1985; Dam 1986; Dam and Peterson 1988; Tiselius 1988; Durbin et al. 1990; Rodriguez and Durbin 1992; Tsuda and Sugisaki 1994; Saito and Taguchi 1996; Saito and Hattori 1996). The work on copepods and bulk zooplankton gut pigments is summarized in table 1.1. In brief, Dagg and Walser (1987) showed relationships between ingestion rate, gut content, gut passage time, and egestion rate in the copepod *Neocalanus plumchrus* using laboratory-based experiments with a wide range of feed. Likewise, Uchima (1988) examined two copepods namely *Acartia omori* and *Oithona davisae* from diatoms dominated Tokyo Bay, Japan. In this study, copepods were pretreated with concentrated nitric acid and hydrogen peroxide and then gut contents were qualitatively analyzed on a scanning electron microscope. Buffan–Dubau et al. (1996) investigated the in-situ feeding behavior of harpacticoid copepod, *Canuella perplexa* collected from the benthic environment of Arcachon Bay, France. This study focused on the role of phototrophic microorganisms like diatoms, purple phototrophic bacteria, cyanobacteria and green microalgae as food sources for benthic copepods. Similarly, Islam et al. (2005) provided information of copepod feeding using gut fluorescence. Lopez and Anadon (2008) studied copepod communities, their abundance, size structure, and grazing rates by gut fluorescence technique sampled from an Atlantic Meridional Transect. Tseng et al. (2008) used gut fluorescence method to estimate *in situ* ingestion rates and clearance rates over a size-fractionation approach, in 3 size categories (small, < 1 mm; medium, 1-2 mm; and large, > 2 mm). Results showed that gut pigment contents were higher for large-sized copepods and lower for small-sized ones. Estimates of the copepod grazing impact showed that < 1% of the total phytoplankton standing stock was grazed daily during the early summer monsoon period.

An experimental study conducted by Nisbe et al. (2010) examined the feeding rates and selectivity of the cyclopoid copepod *Oithona similis* on natural assemblages of microplankton during the spring bloom in the Oyashio region. The report revealed *O. similis* to feed on ciliates at higher rates (2.8–11.9 mL copepod^{-1} d^{-1}) than dinoflagellates (1.4 mL copepod^{-1} d^{-1}) with no detectable ingestion of diatoms.

1.2.4 Stable Isotope technique

Stable isotopes have been extensively used in trophic ecological studies to understand the energy flows through food webs in marine systems (Fry 1988; Post 2002). Basically, the stable nitrogen isotope (δ^{15}N) content can be used to define the trophic level and the stable carbon isotope (δ^{13}C) content to evaluate the sources of carbon (Miyake and Wada, 1967; Owens 1987). The studies of stable isotopes of carbon and nitrogen in copepods genders, species, orders and bulk zooplankton is recapitulated in table 1.2. Briefly, Fry (1986) studied the sources of carbon and sulfur nutrition for consumers in three meromictic lakes of New York using the stable isotopes analyses. Isotopic signatures of food-webs vary spatially based on the change from prey to predator during chemical reactions of metabolic processes due to different reacting rates of isotopes (Peterson and Fry 1987). In a study, Kling et al. (1992) reported isotope values of algae and individual zooplankton species in eight arctic lakes determining the planktonic food-web structure. Likewise, Wozniak et al. (20the 06) monitorthe ed food-web chanthe ges in a tide restored salt marshes using a carbon stable isotope approach. Further, El-Sabaawi et al. (2009) investigated variability in the diets and trophic positions of calanoids species from the Strait of Georgia (British Columbia, Canada) and Ocean Station P in the subarctic northeast Pacific. According to El-Sabaawi et al. (2009), *Neocalanus plumchrus* and *Calanus marshallae* exhibited primarily omnivorous feeding habit, unlike carnivory in *Euchaeta elongata* and herbivory in *Eucalanus bungii*. However, the stability of the trophic position with respect to variability in geography and time was recorded. Another study on calanoid copepod, *Temora longicornis* mentioned that this species exhibit a broad and opportunistic feeding behaviors in the waters off Helgoland island (Gentsch et al. 2009). To elaborate, Gentsch et al. (2009) emphasized preference of *Temora longicornis* on other zooplankton, protists and phytoplankton differing in sizes. On the basis of ^{15}N signatures, Gentsch et al. (2009) indicated that the trophic level of *T. longicornis* ranges from herbivory to omnivory with a large contribution of heterotrophic organisms. On the similar basis, Hannides et al. (2009) estimated the trophic position of zooplankton in the Pacific region employing stable nitrogen isotopes. Likewise, Kurten et al. (2016) investigated isotopic content in many copepod species from the Red Sea. This study provided detailed stable isotope content of nitrogen for many copepod species.

1.3 ZONATION IN THE MARINE WATER SYSTEM

Continental shelf (Fig. 1.1), a seafloor extension from the shoreline to the upper continental slope, is geologically part of the continental crust that is relatively of shallower depth as compared to Open Ocean. The shelf varies noticeably in width and some regions may have practically no shelf at all, mostly where the front edge of an oceanic plate sinks under continental crust in subduction zone like off Chile or Sumatra coast. Notably, Siberian Shelf is the largest shelf that is located in the Arctic Ocean which varies from few meters to 1,500 km in width. Likewise, South China Sea harbor extensive area of continental shelf, which connects Borneo, Sumatra, and Java to the Asian mainland. Other familiar water bodies that overlie continental shelves are the North Sea, the Arabian Sea and the Persian Gulf. Overall, the average width of continental shelves is about 80 km and depth of the shelf is approximated to 150 m. Although, the continental shelf is behaved as a physiographic province of the ocean, it is the flooded margins of the continent. The passive margins of Atlantic coasts have wide and shallow shelves that are composed of thick sedimentary wedges, eroded from neighboring continent. On the contrary, the active margins have narrow, relatively steep shelves, due to frequent earthquakes that move sediment to the deep sea. The point where continental shelf terminates and continental slope commences is termed as the shelf break. The sea floor beyond the shelf break is the continental slope. Beyond the continental slope is the continental rise that merges into the abyssal plain of the deep ocean floor. The continental shelf and the slope are part of the continental margin, each with their specific geomorphology and marine biology. The character of the shelf changes dramatically at the shelf break, where the continental slope begins. Commonly, the shelf break is stationed at a uniform depth of

140 m approximately. Thus, this is more likely a hallmark of previous ice ages, when sea level was lower than the present sea level. The continental shelves are covered by terrigenous sediments derived from continental erosion. Usually, sediments get fine away from the coast; sand is limited to shallow, wave-agitated waters, while silt and clays are deposited in quieter, deep water further offshore.

Continental slope (Fig. 1.1) is the seaward side of the continental shelf with a total length of approximately 300000 km and lies between the shelf break and ocean basins at depths of 100 to 3200 m. The continental slope is much steeper than the shelf. The gradient of the slope are steeper in Pacific than in Atlantic and comparatively flat in the Indian Ocean. The transition from continental crust to oceanic crust usually occurs below the continental slope and minor portion of the ocean floor is roofed by the continental slope-rise system. Further, than the shelf-slope break, the continental crust becomes less dense and the rise lies partly on the continental crust and partly on the oceanic crust in the deep sea. Also, the continental slope can approach vertical on carbonate margins, on faulted margins, or on tectonically active margins. The predominant sediment of continental slopes is mud with smaller amounts of sand or gravel. Slopes are sometimes scoured by ocean currents like the Florida Current that erode their surfaces.

The term “ocean” is derived from Greek word Okeanós is a saline water body that encompasses the majority of earth’s hydrosphere. An ocean covers almost 71% of earth’s surface and consists of the Pacific, Atlantic, Indian and Southern Oceans. World Oceans covers about 361.9 million km^2 area and holds approximately 1.335 billion km^3 of volume. The Indian Ocean being the third largest of the world's ocean holds approximately 20% of the water and is surrounded by Asia, Africa, Australia and the Southern Ocean. It is also recognized as Hind Mahasagar and its marginal seas includes Arabian Sea, Persian Gulf, Red Sea, Gulf of Oman, Gulf of Aden, Gulf of Kutch, Gulf of Khambat, Bay of Bengal, Andaman Sea, Malacca Strait, Mozambique Channel, Great Australian Bight, Gulf of Mannar and Laccadive Sea.

Oceanographers divide the ocean vertically into different zones based on physical and biological conditions (Fig. 1.1). Pelagic zone includes the surface layers of the water body, and can be subdivided into the neritic zone and the oceanic zone. Neritic zone envelopes the water mass above the continental shelves whereas the oceanic zone overlay the open water. Further, the pelagic zone can be divided further based on depth and light availability. The epipelagic zone includes the photic part of the oceans from the surface to a depth of 200 m. This region is important as photosynthesis occur here and is, therefore, the most diverse. Life found below the epipelagic zone mostly either relies on marine snow or undergo chemosynthesis. Accordingly, hydrothermal vents provide the primary source of energy in the aphotic zone that lie below 200 m depth. Beyond the epipelagic zone lies the mesopelagic zone that extends from 200 m to 1000 m and is sometimes referred to as the twilight zone. Most of the strange and bizarre bioluminescent creatures and fishes dwell in this zone. The consecutive layer is called the bathypelagic zone and sometimes referred to as the midnight zone or the dark zone that extends from 1000 m down to 4000 m. The water pressure in deeper depth is immense, and in spite of the pressure, a surprisingly large number of creatures can be found. Most of the creatures that live at these depths are black or red in color due to the lack of light. The next layer is the abyssopelagic zone derived from a Greek word meaning "no bottom", also known as the abyssal zone or abyss extends from 4000 m to 6000 m. The water temperature is near freezing, and there is no light at all and few creatures mostly invertebrates such as basket stars and tiny squids can be found at these depths. Beyond the abyssopelagic zone is the hadalpelagic zone that extends from 6000 m to the bottom of the deepest parts of the ocean. These areas are mostly found in deep water trenches and canyons and the deepest point in the ocean is located in the Mariana Trench at 10911 m. The temperature of the water is just above freezing, and the pressure is an incredible eight tons per square inch. In spite of the pressure and temperature, invertebrates like starfish and tube worms can survive (adopted from: http://www.seasky.org/deep-sea/ocean-layers.html).

Vertically, ocean can be further divided into three density zones: the mixed-layer zone, the thermocline, and the deep zone. The surface mixed layer zone refers to the uppermost density zone of the ocean, where temperature and salinity are relatively constant due to currents and wave action. These waters have contact with the atmosphere and lay within the photic zone. The surface zone has the least dense water of the oceans. The mixed-layer zone usually ranges between depths of 500 feet to 3,300 feet below ocean surface, but this can vary a great deal. Sometimes, the mixed-layer zone does not exist. Typically, the mixed-layer zone is thicker in the tropics than in higher latitude. The consecutive layer thermocline have steep decline in physical properties of seawater especially temperature. Further, thermocline efficiently splits the less dense mixed layer zone above from the below dense zone. Like mixed-layer zone, the tropical thermocline is characteristically deeper compared to higher latitudes. Conspicuously, the high latitude waters, which receive moderately less solar insulation, generally lack a thermocline as surface water are nearly as cold as bottom waters. The deep zone normally begins at depths below 3,300 feet in mid-latitudes and undergoes negligible changes in water density with depth and contains relatively colder and stable water (adopted from https://en.wikipedia.org/Indian_Ocean; http://www.britannica.com/continental-slope; https://en.wikipedia.org/Continental_shelf).

1.4 STUDY AREA

1.4.1 The eastern Arabian Sea

The Arabian Sea is situated to the northwest of the Indian Ocean bounded by the Arabian Peninsula and the Indian subcontinent that is approximated to be 8970 feet deep and spans a total area of 1491000 square miles (Prasannakumar and Prasad 1999). The periphery of Arabian Sea is linked to Somalia, Yemen and Oman in the west and to India and Pakistan in the east. Each sub-region has its own hydrography with respect to its water currents, physical and chemical characteristics, dominant species and biodiversity. The Arabian Sea is distinctive low latitude sea (Dwivedi and Choubey 1998) due to the permanent oxygen minimum zone and periodic monsoon cycle (Naqvi et al. 2010) that is characterized by Northeast Monsoon (December–March) and Southwest Monsoon (June–September) punctuated by inter-monsoon periods (Wiggert et al. 2005). Surface layer thermodynamics of the Arabian Sea can be related to Ekman drifts and annual monsoonal cycle of air–sea momentum that influence the hydrography and consequently the biological processes (Madhupratap et al. 2001b). Also, northern Arabian Sea experience prominent eddies formations (Prasannakumar et al. 2001). Overall, outcrop of the periodic monsoon reversals is noticed in seasonal variability in mesozooplankton abundance and in the sedimentation of carbon from euphotic to the sediments (Madhupratap et al. 2001b; Jagadeesan et al. 2013).

Complexity with eutrophic upwelling, downwelling and oligotrophic stratified environments in the oceanic basin of the Arabian Sea is a prominent feature along the study region (Burkill et al. 1993; Maya et al. 2011). In southwest monsoon, west coast of India apprehends nutrient rich upwelled waters that promotes phytoplankton and subsequently mesozooplankton production (Naqvi et al. 2010; Maya et al. 2011; Pratihary et al. 2014). Another peculiar phenomenon of the southwest monsoon over the Arabian Sea is the formation of a strong and steady surface wind jet formerly described by Findlater (1969). Consequential wind stress accessorized with this Findlater Jet trigger oceanic upwelling and downwelling towards northwest and southeast, respectively. In the north of 15°N, northward flowing current are reported to turn westwards off the coast of Saurashtra. Such environmental changes guide the seasonal change in phytoplankton community along the west coast of India (Jyothibabu et al. 2004; Matondkar et al. 2006). The cold–dry continental air fanning into the northern Arabian Sea during northeast monsoon results in cooling and downwelling (Maya et al. 2011). Consequently, it deepened the mixed layer depths (exceeding 100 m) despite weaker wind (Banse and McClain 1986; Madhupratap et al. 1996a, 2001a). Further, this cooler surface temperatures and increased nitrate favors the propagation of the *Noctuluca scintillans* bloom (Wiggert et al. 2000). Prior to and receding the southwest monsoon (April-May and October-November) in the Arabian Sea is characterized by a reduced wind stress over ocean surface and substantial thinning of the mixed-layer depth. However, understanding the oceanic ecosystems have been limited mostly due to unavailability of long-term, continuous and detailed measurements of ecological parameters like phytoplankton and zooplankton standing stocks and the factors influencing them.

1.4.2 Intensive study area

The study area of this investigation is shown in figure 1.2. The coastal site was located at 15°31.17N and 73°44.200E (G5) off Candolim, Goa, on the continental shelf of the central west coast of India with the depth of ~ 28 m. It is a highly productive ecosystem (Naqvi et al. 2006) that undergo seasonal upwelling (Maya et al. 2011; Pratihary et al. 2014), and a feeding ground for a variety of economically important fishes (Madhupratap et al. 2001b). Biological, chemical, and physical attributes show strongly seasonal variability at continental shelf G5 station. The sea surface temperatures (SST) in the region vary between ~ 22°C to ~ 31°C (Naqvi et al. 2006). During pre-monsoon (February-May) due to solar insolation, the SST attained is maximum and during monsoon (June-September) due to upwelling the waters are cooled. In post-monsoon (October-January), the region undergoes downwelling and the water column remains well mixed with SST in the range of 26–27 °C. Surface circulation in the present study region is dominated by the monsoonal regime (Pratihary et al. 2014). In the present study region, water circulation remains less energetic and comparatively poorly organized during the south-west monsoon. Coastal upwelling induced by off-shore Ekman drift occurring in the south-west monsoon season enriches the near-surface waters with nutrients over the inner and mid-shelf regions (Banse 1968). A northeast monsoon hold low nutrient in the water column, but coastal upwelling during south-west monsoon enriches the water column with nutrients and gets depleted later on due to denitrification (Pratihary et al. 2014). The West India Coastal Current (WICC) begins to flow equatorwards in March, becomes strongest by July and collapses by October (Cutler and Swallow 1984; Shetye and Shenoi 1988).This northward flowing WICC was reported to induce downwelling that leads to the non-stratified water column, which is responsible for 35–35.1 ranges of surface salinity during post-monsoon (Pratihary et al. 2014). However, high evaporation in the pre-monsoon season increases the salinity to 35.8–36.0. During the monsoon, the salinity is conspicuously lower due to the freshening of water caused by intense rainfall in the coastal zone and larger land runoff, beneath the low saline cap lies the high- salinity upwelled water (Naqvi et al. 2006).

Phytoplankton biomass production in the Arabian Sea is seasonal, with peak chlorophyll concentrations usually occurring in monsoon (Maya et al. 2011; D'souza and Gauns 2016). Also, blooms of centric, chain-forming diatoms (e.g. *Skeletonema costatum*, *Thalassiosira* spp., *Chaetoceros* spp.) as well as large flagellates and ciliates are observed in this region (Harrison et al. 1983; Parab et al. 2006). Toward the early summer, chlorophyll concentrations decrease and *Trichodesmium* spp. blooms are known to occur when the water column becomes nitrate limited (Chidambaram and Unny 1944; Devassy and Bhattathiri 1974; Chellam and Alagarswami 1978; Devassy et al. 1978; Parab et al. 2006; Royet al. 2011). The *Trichodesmium* population deminishes later during the pre-monsoon due to turbulence and diatoms dominate the algal community utilizing regenerated nutrients. Once upwelling enriches the water column, the biological production is seemed to be greatly enhanced. However, the upwelled water is overlain by a fresher-water lens and thus deepens the productivity and chlorophyll maxima few meters below the surface (Naqvi et al. 2003). Occasionally, harmful algal blooms are also observed in the coastal waters of eastern Arabian Sea (Naqvi et al. 1998; Matondkar et al. 2004; Ramaiah et al. 2005; Sahayak et al. 2005; Iyer et al. 2008; Padmakumar et al. 2008; Madhu et al. 2011).

The farthest oceanic station, Arabian Sea time series (ASTS) station is located at $17^{o}0.03$N and $68^{o}0.002$E with total station depth of 3000 m (Fig. 1.2) and the other stations of transect study lies between G5 and ASTS on the continental shelf and slope. Annual estimate of primary production in the Arabian Sea seem to be as high as that in the spring blooms in the Atlantic Ocean (Barber et al. 2001). This high productivity consequently consumes more oxygen for organic matter oxidation and meager aeration along with higher microbial respiration in intermediate layers leads to oxygen minimum zones (Wyrtki 1962; Morrison et al. 1999). Such major oxygen minimum zones are found in the intermediate depths of eastern tropical North Pacific (Wyrtki 1966), eastern tropical South Pacific (Wyrtki 1966), eastern Arabian Sea (Wyrtki 1973; Madhupartap et al. 1996; Naqvi and Jayakumar 2000) and eastern South Atlantic (Teuber et al. 2013). It is interesting to note that within the oxygen minimum zone, anaerobic processing (denitrification and anaerobic ammonia oxidation) of nitrogenous compounds lose fixed nitrogen to the atmosphere (Naqvi 1994; Stramma et al. 2008). Thus, the processes controlling the nutrient cycling and biological production are complex and this complexity, in turn, is likely to affect the copepods and its feeding behavior at the shallow coastal site (G5), continental slope and oceanic station (ASTS), which is investigated in the present study.

1.5 OBJECTIVES

The study region is very dynamic and show seasonal variability in the ambient biology and chemistry that is persuaded by the monsoon. Consequently, the mesozooplankton community is subjected to spatial and temporal variations in the Arabian Sea. An extensive review of the literature suggests comprehensive work on spatial and temporal changes in copepods and other mesozooplankton from this region. However, work on feeding studies of copepods received less attention. These feeding studies on copepods are imperative in order to understand the carbon cycle in the marine ecosystem. Qualitative estimations of feeding impact of copepods on the autotrophic biomass are necessary in understanding the trophic dynamics of the ecosystem. The length of food-chain plays important role in foraging the energy transfer to the higher trophic level. Scrutiny of the literature showed few studies based on feeding behavior of copepods in the eastern Arabian Sea.

Thus, comprehensive study of copepod variability in the Arabian Sea on continental shelf, slope and in open waters during pre-monsoon, monsoon and post-monsoon is needed. The present study provides a characterization of copepods from the continental shelf, slope and the oceanic Arabian Sea on a seasonal scale. Also, an attempt is made to understand the seasonal variation of the feeding behavior of copepods from this region. Precisely, complementary techniques of gut fluorescence and stable isotopes of carbon and nitrogen have been used to study the feeding behavior of copepods. The stable isotope analyses provide information on actual feed assimilated over the time in the organism. In contrast, the gut content analysis provides information on recent food ingested by the organism. Blending both, stable isotopes and gut fluorescence techniques is attractive because these are relatively inexpensive and easy to measure. Feeding of copepod population at gender–, species– and order–level might show variations as they are morphologically different. Understanding the feeding behavior of copepod community in the Arabian Sea will enhance the knowledge of energy transfer to higher trophic level. Therefore, the following objectives were selected to fill the research gaps:

1. To investigate trophic segregation between sexes of dominant larger copepods using a stable isotope technique.
2. To investigate spatial and temporal variation in the dietary composition of copepod species using a stable isotope technique.

3. To characterize seasonal variability in the diet of copepod orders using stable isotope analysis.
4. To assess the gut content in copepod orders using gut fluorescence method
5. To investigate spatio-temporal distribution and taxonomy of copepods.

Table 1.1 Summary of gut fluorescence studies on copepods from different parts of world

Copepod species	**Gut content (ng/copepod)**	**Region**	**Author**
Acartia clausi	2–11.49	France	Tireli and Mayzaud 1953
Species of Calanoida	Diel periodicity	Nova Scotia	Mackas and Broher 1976
Temora longicornis	1.4–4.0	Nova Scotia	Wang and Conover 1986
Neocalanus plumchrus	1.52±0.63	Pacific Ocean	Dagg and Walser 1987
Temora longicornis	Gut clearence rate	New York	Dam and Peterson 1988
Acartia tonsa	3.6–4.2	South California	Kleppel et al. 1988a
Acartia tonsa	0.1–0.4	California	Kleppel et al. 1988b
Calanus pacificus	2.41±1.54	Dabob Bay	Dagg et al. 1989
Metridia lucens	8.35±3.31	Wasington	
Acartia tonsa	0.31–6.97		Durbin et al. 1990
200–350 µm	0.1–0.6	English	Bauptista
350–710 µm	0.2–0.8	Channel	and Harris 1992
>710 µm	0.3–3		
Acartia spp.	Gut Clearence		Irigoien 1998
Temora longicornis	rate constant		
Eurytemora affinis	Ingestion and	Baltic Sea	Engstrom et al. 2000
Acartia bifilosa	clearence rate		
200–500 µm	0.01–0.05	Atlantic Ocean	Huskin et al. 2001
500–1000 µm	0.1–1		
>1000 µm	0.5–6		
Neocalanus cristatus		Gulf of Alaska	Liu et al. 2005
Sinocalanus sinensis	0.08–0.548	Chickugo,	Islam et al. 2005
Acartia omorii	0.016–0.266	Estuary	

Continued …

Oithona davisae	0.012–0.284	Ariake Sea Japan	
Paracalanus parvus	0.054–0.099		
<1mm	0.5±0.5	South China Sea	Tseng et al. 2009
1–2mm	0.9±0.5		
>2mm	1.9±1.7		
Eucalanus bungi	10.0–40.0	Oyashio region	Kobari et al. 2011
Neocalanus flemingeri	10.0–50.0		
Metridia pacifica	1.0–25.0		
Metridia okhotensis	5.0–80.0		
Gaetanus spp.	5.0–50.0		
Pleuromamma sp.	5.0–75.0		
Calanoida	0.27–5.93	Arabian Sea	D'souza and Gauns 2016
Poecilostomatoida	0.12-2.01		
Cyclopoida	0.20–2.75		
Harpacticoida	0.17–2.41		
Copepods	1.8–5.2	Bay of Bengal	Fernandes and Ramaiah 2016

Table 1.2 Summary of δ^{13}C and δ^{15}N values for copepods and bulk zooplankton from different part of the world

Species	δ^{13}C (‰)	δ^{15}N(‰)	Area of study	Reference
Copepod	−20.8±0.5	7.0±1.9	Georges Bank, Atlantic	Fry 1988
Zooplankton	−30.1–−16.5		Gautami Godavari estuary	Bouillon et al.2000
Mixed zooplankton	−31–−26	7 – 17	Loch Ness, Scotland	Grey and Jones 2001
Calanus glacialis	−23–−21	7 – 9	Spitbergen, Artic	Sato et al. 2002
Calanus finmarchicus				
Metridia longa				
Calanoida	−22.7–−19.1	5.4–10.4	Coastal lagoon	Vizzini and Mazzola
Harpacticoida	−21.1–−14.9	7–9.6	Italy	2003
Mixed zooplankton	−22–−17	2 –10	Spain	Bode and Alvarez-Ossorio 2004
Centropages hamatus		6.5–8.5	Mesocosm expt	Sommer et al. 2005
Pseudocalanus elogatus		7.5–9.0	Lagoon, Norway	
Temora longicornis	no carbon	6.5–8.0		
Cyclops vicinus			Germany, Lake	Santer et al. 2006
C. abyssorum				
Calanus spp.	−23.3 ± 0.2	7.3 ± 0.2	European Artic	Soreide et al. 2006
<20		4.9	Atlantic shelf	Bode et al.2007
20-40		5.7		
40-80		5.5		
80-200	no carbon	5.8		
200-500		5.9		
500-1000		6.7		
1000-2000		7.1		
Macrosetella gracilis		3.06±2.29	North Pacific Gyre	Eberl and Carpenter

Continued …

Miracia efferata	no carbon	1.83±0.88		2007
calanoid copepod		2.7±1.95		
Ctenocalanus vanus	−22.0–−21.2	0.7–5.3	Red Sea	Cornils et al. 2007
Clausocalanus farrani	−23.0–−20.6	1.35–3.63		
Clausocalanus furcatus	−23.4–−20.7	0.1–3.5		
Sinocalanus sinensis	−26.6±1.5	11.0±0.9	Chikugo, River Japan	Suzuki et al. 2008
Acartia omorii	−23.3±2.6	11.9±1.3		
Calanus finmarchicus	−20.3	3.5	Reykjanes Ridge	Petursdottir et al 2008
Calanus hyperboreus	−21.3	7.8	Svalbard, Artic	Soreide et al. 2008
Calanus glacialis	−19.7	7.6		
Calanus finmarchicus	−20.5	7.1		
Neocalanus cristatus	−17–−21	8.5–9.5	Gulf of Alaska	Kline 2009
Neocalanus flemingeri	−16.5–−19	8–10.0		
Neocalanus plumchrus	−19.5–−20	10		
bulk zooplankton	−22–−18	2 –12	Mediterranean	Koppelmann et al 2009
Temora longicornis		14–16	Germany	Gentsch et al. 2009
Calanoida		0.01-6.8	Northern Red Sea	Aberle et al. 2010
Poecilostomatoida		>1%		
Cyclopoida		>1%		
Harpacticoida	No carbon	2.2		
Neocalanus spp.	−23.5–−19.5	6.5–13.5	Gulf of Alaska	Kline 2010
Calanus spp	−25.5–−20.8	5 –19	Arctic Ocean	Forest et al. 2010
Metridia longa				
Candacia armata	−23.4±0.2	7.9±0.3	North Sea	Kurten et al 2011
Calanus finmarchicus	−22.3±0.3	7±0.5		
Calanus helgolandicus	−22.1±0.3	6.9±0.3		
Centropages typicus	−23.4±0.3	5.9±0.4		
Metridia longa	−20.9±0.2	11±0.4		
Pseudocalanus elongatus	−22±0.8	7±0.2		
Temora longicornis	−19.6±0.6	7.9±1.2		
Paracalanus elongatus	−21.9	6.6		

Continued …

Calanus finmarchicus	−22.1+-0.1	6.3–9.7	Arctic	Hansen et al.2012
200-500	−19.7 ±0.2	2.0±0.2	Canary Island	Mompean et al. 2013
500-1000	−20.02±0.2	2.3±0.2	Florida	
1000-2000	−19.4±0.4	2.4±0.2		
>2000	−19.5±0.5	3.2±0.3		
Euchaeta media	−19.0 ± 0.3	6.4 ± 0.4	Sagami Bay	Sano et al. 2013
Pleuromamma gracilis	−19.1 ± 0.2	6.4 ± 0.4		
Oncaea spp.	−20.2 ± 0.3	4.5 ± 0.4		
Scottocalanus securifrons	−18.8 ± 0.5	7.4 ± 0.8		
Calanus hyperboreus	−24.00±0.7	8.1±0.8	Canadian Shelf	Connelly et al. 2014
Euchaeta marina	−21.3±0.3	7.3±0.4	Tropical	Teuber et al. 2014
Pleuromamma abdominalis	20.1	5.6	Atlantic	
Pleuromamma quadrungulata	−18.7±0.7	9.9±1.6	Ocean	
*Pleuromamma robusta*_f	−19.6±0.6	10.0±0.4		
*Pleuromamma robusta*_m	−19.8±0.2	11.1±0.3		
*Pleuromamma xiphias*_f	−21.6±0.3	6.9±1.1		
*Pleuromamma xiphias*_m	−21.8±0.5	6.9±0.4		
Lucicutia sp._female	21.8	9.4		
Lucicutia sp._male	22.3	10.2		
Mesozooplankton	−20.1±0.4	1.5±0.8	Northeast Aezean	Hannides et al. 2015
Mesozooplankton	−19.9±0.8	3.4±0.6	Sea	
Mesocalanus tenuicornis	−24.90±0.30	7.81±0.17		Im et al.2015
Metridia pacifica	−23.90±0.07	8.34±0.14		
Calanus sinicus	−23.99±0.23	8.26±0.17		
Copepods	−21.07±0.89	10.28±1.70	Eastern English	Kopp et al. 2015
	−21.43±0.77	9.68±1.51	Channel	
	−20.64±0.90	11.00±1.78		
Candacia sp.	−22.1–−20.8	3.4–8.3	Red Sea	Kurten et al. 2016
Corycaeus sp.	−21.6–−20.3	2.7–9.3		
Eucalanus sp.	−21.9–−20.2	4.3–8.2		
Euchaeta sp.	−21.4–−19.7	4.8–10.5		

Continued ...

Nannocalanus sp.	−21.2–−19.9	3.1–8.5
Pleuromamma sp.	−21.4–−19.8	3.3–8.5
Pontellina sp.	−21.1–−20.2	3.5–4.2
Macrosetella sp.	−21.2–−19.1	2.0–4.4
Rhincalanus sp.	−22.5–−19.6	2.0–9.6
Copilia sp.	−21.9–−20.6	2.7–6.5

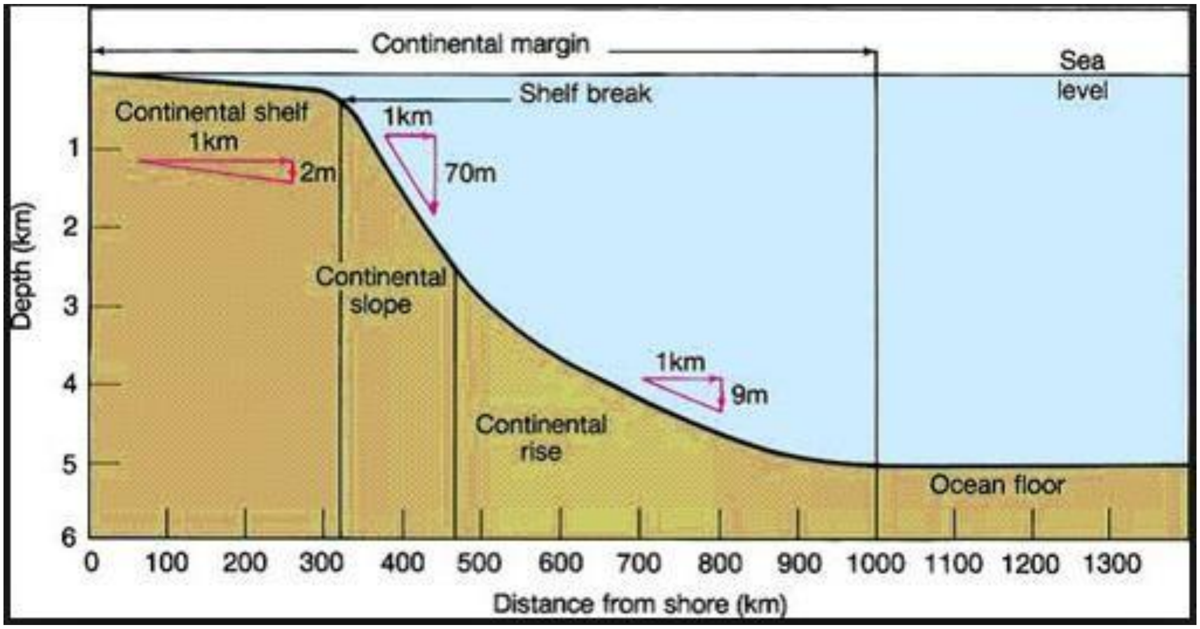


Fig. 1.1 Location of continental shelf, slope and open waters (adopted from http://geology.uprm.edu/MorelockSite/morelockonline/1_image/duxburyseafl.htm)

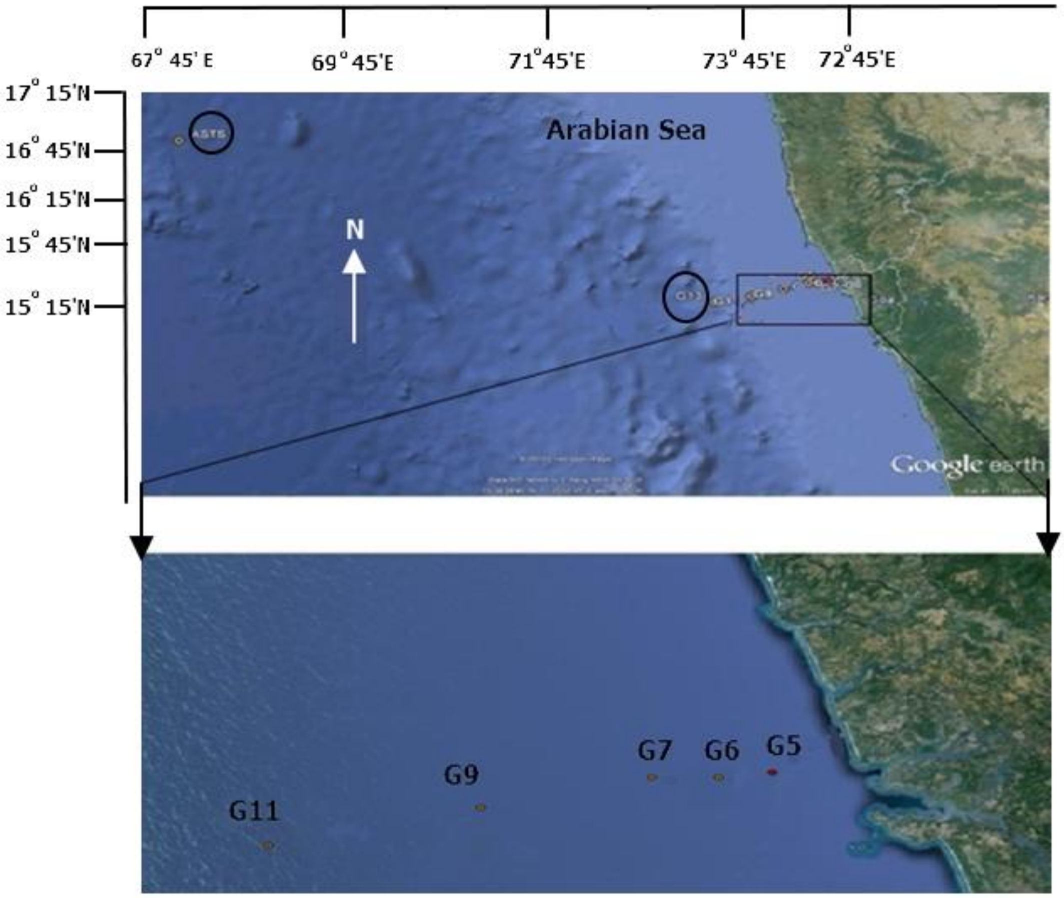


Fig. 1.2 Location of monthly sampled (G5), seasonal transect and open water station (ASTS) in the eastern Arabian Sea

Chapter 2

SPATIAL AND TEMPORAL VARIATIONS OF COPEPODS IN THE ARABIAN SEA

2.1 INTRODUCTION

Copepods the copious crustaceans, forming the bulk of the mesozooplankton (Hardy 1970; Gopalakrishnan 1984; Turner 2004) in aquatic ecosystems and thus, referred as the insects of the sea (Schiminke 2007). The Taxonomic classification of copepods covers 10 orders, namely Calanoida, Cyclopoida, Gelyelloida, Harpacticoida, Misophrioida, Monstrilloida, Mormonilloida, Platycopioida, Poecilostomatoida and Siphonostomatoida (Boxshall and Hasley 2004). They may be free-living, symbiotic, or internal or external parasites on aquatic fauna. A substantiated range of habitats from freshwater to marine conditions, from subterranean caves to hydrothermal vents (Tsurumi and Tunnicliffe 2003), from the highest mountains (Loffler 1968) to the deepest ocean trenches (Wolff 1960) and from streams, rivers, and lakes to the benthic layer in the open ocean are harbored by these creatures.

Morphologically, the copepod body is divided into prosome and urosome. The prosome further divided as cephalosome and metasome and bears a central naupliar eye, a pair of antennules, maxillipeds, mandibles and five pairs of biramous swimming legs. Moreover, the fifth leg is frequently modified, by the loss or fusion of the endopod or is absent in some species. The urosome consists of the genital apparatus, the abdomen and anal somite that bears terminally paired caudal rami with setae (Huys and Boxshall 1991). Typically, the copepod body length is usually between 0.5 and 5.0 mm, although the full range is from about 0.2 mm (some species of *Oncaea* Philippi) to about 28 mm (a species of *Valdiviella* Steuer; Huys and Boxshall 1991). Exceptionally, the smallest copepod, *Sphaeronellopsis monothrix,* a parasite attains a length of 0.11 mm (Bowman and Kornicker 1967) and the largest copepod, *Pennella balaenopterae,* an ectoparasite, measures 28±3 cm (Cicek et al. 2007). These tiny creatures (1–2 mm length) attains a speed of up to 90 m/hr with the movement by mouth appendages that provides the propulsion and swimming legs are used for faster movements (Alcaraz and Strickler 1998).

Copepod grazing is a vital source of phytoplankton mortality in the frontal zone of river plumes (Fielding et al. 2007), productive coastal waters (D'souza and Gauns 2016) and cyclonic cold-core eddies (Fernandes and Ramaiah 2016). Calanoida are typical particle feeders (Gauld 1966) that use maxillae to suck the food particles trapped between the bristles of the maxillae. Many harpacticoids feeds on microphytobenthos and microbes found in the benthic habitat. Certainly, predatory copepods can be found in the Calanoida and Cyclopoida (Gauld 1966). Some of the cyclopoids are able to tear pieces out of the body of their prey with their strong mandibles.

The greater part of investigations on Indian copepods were carried out during the John Murray expedition of the Arabian Sea (Sewell 1912). The copepods collected during the IIOE throws light on the copepod fauna of the epipelagic waters. A number of papers with new species were reported from the west coast of India (Haridas and Madhupratap 1978; Madhupratap and Haridas 1978; Madhupratap and Haridas 1989; Madhupratap and Haridas 1992; Haridas et al. 1994; Madhupratap and Haridas 1994; Kesarkar and Anil 2010). Copepods above and below thermocline from the Arabian Sea were characterized by Madhupratap et al. (2001). Moreover, studies on the copepods of the west coast of India have significantly improved our understanding (Padmavati et al. 1998; Madhupratap et al. 2001a; Jagadeeshan et al. 2014). Comprehensive work on copepods from the Arabian Sea was conducted in Indian–JGOFS program (1993–1997) and Bay of Bengal by BOBPS (Bay of Bengal Process Studies) investigation. However, long-term time series studies to understand the zooplankton dynamics is required. In this view, a small step to achieve the target has been the motivation of the present study. The primary aim of this research was to widen the knowledge of the copepod composition and their temporal distribution from the continental shelf, slope and oceanic realm in the Arabian Sea. Also, it was aimed to understand the seasonal variability in copepod species diversity.

2.2 METHODOLOGY

The study area includes stations on the continental shelf, slope and open ocean sites. The map with study locations (fig. 1.2) and details of sampling locations are presented in section 1.42 of chapter 1.

2.2.1 Sample collection and analysis

Mesozooplankton samples were collected from the G5 on a monthly basis from December 2010 to October 2013. However, depending on the weather and logistic conditions, a few months precisely, January’11, April’12, June–July’12 and June’13 were not sampled. Mostly, the sample collections at G5 were carried out by fishing trawlers and occasionally on research vessels. The seasonal sample collections across the study transect and at the oceanic site were conducted on research vessels and details of sample collections have been represented in the table (table 2.1; fig. 1.2). It covered monsoon (June–September), post-monsoon (October–January) and pre-monsoon (February–May) seasons. The stratum was selected based on mixed layer zone in the epipelagic zone.

The Vertical haul was conducted with the zooplankton net (mesh size of 200 µm and mouth area of 0.25 m^2) equipped with a calibrated digital flow meter (Hydrobios). The flowmeter observations were recorded to derive the volume of seawater filtered in the towing process of the sample collection. Samples, thus obtained in the cod end bucket of the net were stored in 500 mL plastic sample bottles.

The mesozooplankton samples were concentrated through a 200 μm nylon mesh and split using a Folsom splitter to get a sub-sample (50%) containing around 300 individuals. These sub-samples were preserved in 4% buffered (sodium borate) formalin in seawater for further analyses (Goswami 2004). The other sub-samples were preserved at −20°C for stable isotopes and gut pigment estimation.

In the laboratory, an individual sample (preserved in formalin) was placed in Bogorow's chamber (Hydrobios) and enumeration and morphological identification were done under a stereoscopic microscope (Olympus SZX 09). The sample was sorted to the group level, and the abundance of each group was calculated following standard procedure (Goswami, 2004). All the samples were identified as broad taxonomic groups (ICES 2000; Conway et al. 2003). Only copepods were identified till generic level and wherever possible till species level, using identification keys (Kasturirangan 1963; Bradford-Grieve 1994; Conway et al. 2003; http://copepodes.obsbanyuls. fr/en). Identification of the occasionally occurring calanoid species was confirmed by 5th leg dissection.

Water column temperature and water chlorophyll *a* content were recorded on a continental shelf (G5). The water column temperature was noted from the reversible thermometer attached to the Niskins sampler and chlorophyll a was measured using JGOFS protocol (UNESCO 1994), the detailed procedure is mentioned in chapter 5. The data on salinity were acquired from Naqvi et al. (2006). The hydrographic parameters for transect study during May 2011 were used from D'souza and Gauns (2018) and from Cowie et al. (2014). Likewise, the data on hydrographic parameters at the oceanic station (ASTS) during June 2012, September 2012 and February 2013 were obtained from published work of Jain et al. (2014).

2.2.2 Statistical analysis

To examine the significant variation in copepod abundance spatially, analysis of variance (ANOVA) was used. ANOVA followed by Tukey's Post Hoc test to reveal the significant difference between the stations. Values were considered significant at the 95 % level of confidence (Statastica 6.0, Statsoft, OK, USA).

The species diversity indices were estimated using PRIMER 6. The species diversity indices, particularly Margalef's species richness (*d*), Shannon–Wiener diversity (*H'*) and Peilou's evenness (*J'*) were calculated on copepods species abundance. Species diversity (*H'*) was calculated using the following equation:

$$H' = -\sum (P_i \log_2 (P_i)),$$

where $P_i = ni/n$ (proportion of the sample belonging to i^{th} species). *S* is the number of species and *N* is the total number of individuals of all the species in a sample as given by Shannon and Weaver (1963).

The square root transformation was performed on copepod abundance data to obtain a nearly normal distribution prior to non-multidimensional scaling (nMDS) and Bray–Curtis cluster analyses. nMDS analysis was performed on the clusters and the species having the peak contribution was recognized using SIMPER (PRIMER 6).

2.3 RESULTS

Among the sampling stations represented in figure 1.2, the stations G5, G6 and G7 lie on the continental shelf while, G9, G11, and G13 are on the continental slope and ASTS lies in open oceanic waters.

2.3.1 Hydrographic conditions

The water temperature was ranged between 23.5–29.4 °C and the concentration of surface water chlorophyll *a* ranged between 0.69 and 4.29 ng/mL at G5. Further, the salinity ranged between 34.8 and 36.0 (Naqvi et al. 2006). Monthly variations of temperature, salinity and chlorophyll *a* at the continental shelf location (G5) are elaborated in Chapter 5.

The published results on dissolved oxygen (DO) from pre-monsoon (May 2011) are described from Cowie et al. (2014), where the DO values were averaged for the entire water column. Thus, chlorophyll concentrations, temperature and salinity are described as the water column average for the same stations. Also, sea-surface temperature (SST) and sea-surface salinity (SSS) are reported from the stations during pre-monsoon. In the pre-monsoon (May 2011), the SST ranged between 28.56–28.98°C and SSS from 35.41–35.60 and averaged column chlorophyll ranged from 0.39–2.00 ng/mL at the continental shelf stations (G5, G6 and G7). Also, the shelf waters were reported to be well oxygenated (DO: 85.40–90.20 µM) during the study. Away from the coast on the continental slope, the hydrography varied widely with high values of SST (29.88–30.07 °C) as compared to a shelf. Also, SSS ranged between 35.07 and 35.36 and with low column averaged chlorophyll (0.12–0.16 ng/mL). In addition, the DO values in the epipelagic water column at slope ranged between 10–70 µM. The DO concentrations below the epipelagic zones were comparatively low (< 5.00 µM) due to the influence of permanent OMZ.

The vertical distribution of temperature, salinity and DO during three seasons at the oceanic station (ASTS) reported a general trend of high values in surface followed by gradual decline till thermocline. The surface temperature, salinity and DO concentration were

30.20°C, 36.32 and 200.00 μM L^{-1}, respectively in June 2012. During September 2012, the surface temperature was reported to get reduced to 27.74°C that decreased further in February 2013 (25.88°C). However, salinity and DO concentration in September 2012 (36.52; 205.98 μM L^{-1}) and February 2013 (36.65; 206.63 μM L^{-1}) did not show much variation. Further, the waters were well oxygenated in deep chlorophyll maxima, where the DO concentration was 203.76 μM L^{-1} in June 2012, 149.31 μM L^{-1} in September 2012 and 202.65 μM L^{-1} in February 2013. However, very low concentrations of DO at 250 m were reported, that apprehended for 11.79 μM L^{-1} in June 2012, 3.47 μM L^{-1} in September 2012 and 1.40 μM L^{-1}in February 2013.

2.3.2 Mesozooplankton and copepod abundance

The continental shelf station (G5) sampled on a monthly basis (December 2010 to October 2013) covered monsoon (June–September), post-monsoon (October–January) and pre-monsoon (February–May) seasons and showed a temporal pattern in mesozooplankton abundance (mean ± standard deviation) (Fig. 2.1) that ranged between 35 and 22199 individuals/m^3 (2050±4025 individuals/m^3). Copepods, the most dominant mesozooplankton, ranged between 29 and 22198 individuals/m^3 (1708±3961 individuals/m^3). The other abundant mesozooplankton groups were decapods, ostracods, chaetognaths, appendicularia and polychaetes. Seasonally, post-monsoon showed a higher abundance of copepods (29–22198 individuals/m^3) than pre-monsoon (71–2978 individuals/m^3) and monsoon (341–1312 individuals/m^3).

Likewise, seasonal variation in mesozooplankton abundance was noticed at the continental margin (studied transect). Mesozooplankton showing discrete spatial pattern along the transect is given in fig. 2.2; their abundance, ranged between 189 and 49314 individuals/m^3 (7844±13796 individuals/m^3) in pre-monsoon (February 2011 and May 2011). The highest counts were observed at G9 (in May 2011) and lowest at G13 (during February 2011). Copepods, the most dominant taxon of mesozooplankton, mirrored the mesozooplankton abundance with highest counts of 40752 individuals/m^3 and lowest of 160 individuals/m^3. Comparatively, continental shelf stations (G5, G6 and G7) showed a higher abundance of copepods than the slope region (G11 and G13). Overall, highest copepod and mesozooplankton abundance as compared to other seasons were recorded in pre-monsoon season.

Mesozooplankton and copepod abundance displayed identical spatial pattern along a transect in monsoon (June 2012 and September 2012; Fig. 2.3). Mesozooplankton abundance ranged between 187 and 2317 individuals/m^3 (977±801 individuals/m^3) and copepods ranged from 154 to 1338 individuals/m^3 (684±515 individuals /m^3). The highest counts of mesozooplankton and copepods were observed at G9 in September 2012 and lowest at the G7 in June 2012. Comparatively, the intermediate range of copepod abundance was recorded during monsoon.

During post-monsoon (December 2011 and January 2012), lowest counts of mesozooplankton as compared to monsoon and pre-monsoon were recorded (Fig. 2.4). In detail, mesozooplankton abundance ranged between 40 and 529 individuals/m^3 (181±154 individuals/m^3). The highest counts were observed at G5 in December 2011 and the lowest at G11 in January 2012. Concomitant to the mesozooplankton, the abundance of copepod showed similar spatial variability. The copepod abundance ranged from 25 to 480 individuals/ m^3 (152 ±140 individuals /m^3).

At the open ocean station (ASTS) as well, mesozooplankton displayed temporal variability wherein their abundance, ranged between 5 and 7697 individuals/m^3 (1181±2204 individuals/m^3; Fig. 2.5). Sample collection was done at day and/ night time, thus, temporal and diurnal variation was observed in mesozooplankton and copepod counts. The highest counts were observed at night in the 0–40 m stratum during October 2013 and lower during daytime in the 20–100 m stratum during June 2012. At this location as well, copepods displayed a similar pattern of variation resembling the mesozooplankton abundance. The copepod abundance ranged from 4 to 6141 individuals/m^3 (985±1755 individuals/m^3).

<u>2.3.3 Distribution of copepods</u>

2.3.3.1 At the continental shelf (G5)

Four copepod orders, namely Calanoida, Poecilostomatoida, Cyclopoida and Harpacticoida represented the continental shelf station (G5), which was sampled on a monthly basis (Fig. 2.6). Pre-monsoon was characterized by the dominance of Poecilostomatoida (40.54–53.88 %) followed by Calanoida (35.16–37.29 %) and least contribution was by Cyclopoida (3.14–4.69 %). Distinctly, Harpacticoida contributed in a high percentage (6.25–17.74 %) during this season as compared to other seasons. In monsoon, Calanoida dominated the copepod assemblage (39.50– 76. 43 %) followed by Cyclopoida (4.12–30.13 %) and Poecilostomatoida (10.93–26.24 %). Unlike pre-monsoon, Harpacticoida contributed the least percentage (4.11–8.51 %) during the monsoon. In the post-monsoon as well, Calanoida (35.28– 50.58 %) dominated the copepods followed by Poecilostomatoida (34.00–45.53 %), Cyclopoida (8.98–23.76 %) and Harpacticoida (2.01–9.01 %).

In total, 48 copepod species belonging to 22 families of Calanoida, Poecilostomatoida, Cyclopoida and Harpacticoida were identified from the studied region. The copepod families specifically Oncaeidae, Paracalanidae, Oithonidae, Centropagidae, Temoridae, Clausocalanidae, Euchaetidae, Euterpinidae and Acartiidae were dominant and present throughout the study period. The dominant species were *Oncaea* spp., *Acrocalanus* spp., *Euterpina acutifrons*, and *Corycaeus* spp. in the pre-monsoon, whereas, *Oithona* spp., *Oncaea* spp., *Acrocalanus* spp., *Acrocalanus gibber* and *Acrocalanus gracilis* were the dominant species in monsoon and *Oithona* spp., *Oncaea* spp., *Acrocalanus* spp., and *Oithona plumifera* were found in overwhelmed numbers during post-monsoon. Consistently, *Acartia erythraea*, *Temora discaudata*, *Pseudodiaptomus serricaudatus*, *Centropages furcatus*, *Canthocalanus pauper* and *Paracalanus aculeatus* were found in low numbers.

Bray–Curtis analysis performed on copepod abundances collected on a monthly basis clustered into the three groups (Fig. 2.7A). Further, nMDS plot showed an analogous pattern of clustering of the months (Fig. 2.7B). Results of SIMPER analysis (Table 2.5) exhibited that the group I was formed by April’13, May’13 and October’13 typically due to the absence of *Euterpina acutifrons* (Fig. 2.7C). Distinctly, the dominance of *Centropages furcatus* was responsible for clustering the months December 2010 and October 2011 and its dissimilarity with other groups (Fig. 2.7D). Markedly, *Temora turbinata* (Fig. 2.7E) and *Pseudodiaptomus serricaudatus* (Fig. 2.7F) accounted for the dissimilarity of group III formed by a majority of sampling months.

2.3.3.2 Along the transect during pre-monsoon

During Pre-monsoon (February and May 2011), the dominance of Poecilostomatoida at G6, G7, G9 and G13 (sampled in February 2011) and Calanoida at other stations were noticeable in shelf and slope region of the study area (fig. 2.8). The variation in percent composition of copepod orders in the region can be arranged as Calanoida (27.70–56.78 %) followed by Poecilostomatoida (23.62–49.66 %), Cyclopoida (4.71–23.85 %) and Harpacticoida (0.5–17.95 %).

Altogether, 56 copepod species belonging to 26 families and 4 orders, Calanoida (17), Poecilostomatoida (3), Cyclopoida (1) Harpacticoida (4) and Mormonilloida (1) were identified in the study. The copepod families could be ranked in descending order of the abundance as Oncaeidae, Paracalanidae, Oithonidae, Centropagidae, Temoridae, Clausocalanidae, Euchaetidae and Acartiidae. Calanoid copepods were abundant at the continental shelf in comparison to the continental slope. Among the calanoids, *Acartia* spp., *Acrocalanus* spp., *Centropages tenuiremis*, *Centropages* spp., *Subeucalanus pileatus* and *Temora turbinata* dominated the continental shelf and *Pleuromamma indica*, *Metridia* spp., *Euchaeta* spp. and *Calocalanus* spp. dominated the continental slope. The non-calanoids, *Oithona* spp., *Oncaea* spp., *Farranula* spp., *Euterpina acutifrons* and *Microsetella* sp. were high at the continental shelf and *Oithona plumifera*, *Macrosetella* spp., *Copilia mirabilis* and *Sapphrina* spp. were in high numbers at the slope region.

The Bray–Curtis analysis and nMDS plot performed on the copepod abundances and stations clearly demarcated the two groups based on the sampling months (Fig. 2.9 A and B). The stations G5, G6, G7, G9, G11 and G13 sampled in May 2011 showed 52 %

similarity (group I), while same stations sampled in February 2011 showed 50 % similarity (group II). Therefore, each sampling month was further subjected to Bray–Curtis analysis and nMDS to get a clear picture.

In February 2011, Bray–Curtis similarity coefficient specified that the observations consist of three clusters (Fig. 2.10 A). The stations G5, G6 and G7 associated to form a cluster at 58 % similarity (group I). In addition, stations G9 and G11 clustered together at 62 % similarity (group II). It was very distinct that the station G13 did not merge with other stations and shared only 22 % similarity with other clusters (group III). The nMDS plot (Fig. 2.10 B) and SIMPER analysis demonstrated that the varying dominance of *Oithona* spp. (Fig. 2.10 C), *Acartia erythrea* (Fig. 2.10 D) and *Microsetella*s pp. (Fig. 2.10 E) were responsible for the formation of the group I and II clusters. Noticeably, the absence of *Acartia erythrea* and *Microsetella* spp. were accountable for the distinction of the group III cluster.

Similarly, in May 2011, the Bray–Curtis similarity coefficient as well pointed out three clusters based on copepod abundances (Fig. 2.11 A). The stations G6, G11 and G13 associated to form a cluster at 50 % similarity (group I). It was very distinct that the station G9 did not amalgamate with other stations (group II). However, another group was formed by continental shelf stations (G5 and G7) at 62 % similarity (group III). Further, nMDS plot showed a related pattern of clustering of the stations with sampling periods (Fig. 2.11 B). The results of SIMPER analysis (Table 2.6) demonstrated that the first cluster differed from the other two clusters by the dominance of *Oncaea* sp. (Fig. 2.11 C), *the* second cluster due to *Pleuromamma indica* (Fig. 2.11 D) and third cluster by the dominance of *Microsetella* spp. (Fig. 2.11 E).

2.3.3.3 Along the transect during monsoon

During monsoon (June and September 2012), copepods belonging to the order Calanoida (30.21 – 62.69 %) were more dominant (fig. 2.12). The other copepod orders encountered were Poecilostomatoida (22. 39– 54.55 %), Cyclopoida (1.01–27.08 %), Harpacticoida (0–9.34 %) and Mormonilloida (0–7. 46 %).

The existence of 53 copepod species of 24 families of order Calanoida (16 species), Poecilostomatoida (2), Cyclopoida (1), Harpacticoida (4) and Mormonilloida (1) were recorded during the monsoon season. The dominant copepod families could be organized by a descending order of their abundance as Oncaeidae, Paracalanidae, Oithonidae, Corycaeidae, Temoridae, Euterpinadea and Clausocalanidae during this season. The calanoids, *Acrocalanus* spp., *Acartia* spp., *Paracalanus* spp., *Subeucalanus* spp. and *Temora turbinata* were dominant at the shelf, while the slope was marked by the dominance of *Euchaeta* spp. and *Calocalanus* sp. Distinctly, Metridinidae and Lucicutiidae, mostly their juveniles dominated the continental slope (G13). Among non-calanoid; *Oithona* spp., *Oncaea* spp. and *Farranula* spp. marked dominance across the transect, specifically *Oithona plumifera* and *Euterpina acutifrons* showed higher counts at the continental shelf and *Oithona spinirostris* and *O. rigida* at the slope. The study reveals that the calanoid copepods thickly populated the shelf region in comparison to the slope.

As per the Bray–Curtis (Fig. 2.13 A) and nMDS (Fig. 2.13 B) analysis, the stations in reference to the sampling time (months) and copepod abundance can be categorized into three groups during monsoon. The station G13 (June 2013) did not reciprocate with other stations and thus forms group I. The continental shelf station G7 forms group II by 40%

similarity on the basis of June and September 2012 sampling. The group III was formed by G5 (September 2012), G9 (June and September 2012) and G11 (June 2012) with 40% similarity like group II. Results of SIMPER analysis revealed that the group I was distinct from others by the dominance of *Pleuromamma indica* (Fig. 2.13 C) and absence of *Lucicutia flavicornis* at G13 (Fig. 2.13 D). The variable dominance of *Corycaeus* spp. (Fig. 2.13 E) and *Oithona* spp. (Fig. 2.13 F) were accounted for the formation of group II and III.

2.3.3.4 Along the transect during post-monsoon

In the post-monsoon, the stations G5, G7, G9 and G13 (January 2012) showed the dominance of Calanoida and the other stations revealed the dominance of Poecilostomatoida (fig. 2.14). The Calanoida (18.68– 64.15 %), Poecilostomatoida (28.79–62.39 %), Cyclopoida (1–32.41 %) and Harpacticoida (0–3.79 %) was the order of dominance by virtue of their respective percent abundances in this season.

The systematic study revealed 50 copepod species belonging to 26 families of Calanoida (17 species), Poecilostomatoida (3), Cyclopoida (1) and Harpacticoida (5) during post-monsoon. Among calanoids, Paracalanidae, Centropagidae, Temoridae and Clausocalanidae were the dominant copepod families. While, *Acrocalanus* spp., *Acartia* spp., *Centropages tenuiremis*, *Centropages* spp., *Subeucalanus pileatus* and *Temora turbinata* were the dominant calanoids species at the continental shelf. Concurrently, *Euchaeta* spp. and juveniles of Eucalanidae were abundant at the continental slope.

Oncaeidae and Oithonidae were the dominant non-calanoid families. The copepod belonging to *Oithona* spp., *Oncaea* spp., *Farranula* spp. *Euterpina acutifrons* and

Microsetella spp were dominant throughout the study. Spatially, *Oithona plumifera*, was abundant on the continental slope. Presence of *Metis* spp. (Harpacticoida) at a continental shelf station (G7) during December 2011 was remarkable. However, the reason for occurrence is not very well understood. Consistently, copepods community showed a high abundance of calanoids over the continental shelf than the continental slope.

It is noteworthy that the clustered formed by Bray–Curtis similarities did not show similarity based on the continental shelf and slope demarcations like that of pre-monsoon (Fig. 2.15 A). The stations G7 (December 2011 and January 2012) and G11 (January 2012) together formed the group I at 50 % similarity. It was very distinct that the station G11 (December 2011) did not amalgamate with other stations at 48 % similarity and formed group II. However, group III was formed by stations G5 (December 2011 and January 2012), G9 (December 2011 and January 2012) and G13 (January 2012) at 56% similarity. The nMDS plot (Fig. 2.15 B) showed grouping similar to Bray–Curtis clusters. Results of SIMPER analyses (Table 2.8) demonstrated that the first and third cluster differed from the each other by the varying abundance of *Acrocalanus* spp. (Fig. 2.15 C) and *Oncaea* spp. (Fig. 2.15 D). The reason for the uniqueness of group II was the absence of *Oithona* spp. (Fig. 2.15 E) and dominance of *Lucicutia flavicornis* at G11 (December 2011) (Fig. 2.15 F).

2.3.3.5 At the Open Ocean site

Study of copepod orders at the open ocean station, ASTS revealed the dominance of Poecilostomatoida (32.85–56.72 %) followed by Calanoida (13.87–54.55 %), Cyclopoida (2.27–34.78 %), Harpacticoida (0–4.47 %) and Mormonilloida (0–1.61 %; fig. 2.16).

However, Calanoida dominated the copepod community in terms of species richness. A total of 49 calanoid species (belonging to 14 families) were identified from the study region. Among them, the dominant ones were *Acrocalanus* spp., *Acartia* spp., *Lucicutia flavicornis*, *Euchaeta* spp., *Subeucalanus* spp., *Paracandacia* spp., *Pleuromamma indica*, *Metridia* spp., *Scaphocalanus* spp. and *Calocalanus* sp. A rare species *Euchirella amoena* was noticed at sub-surface stratum (40-140 m) of this station during September 2012 at the night time.

Eight copepod families (Oncaeidae, Corycaeidae, Sapphirinidae, Oithonidae, Euterpinidae, Clytemnestridae, Miraciidae and Mormonillidae) with 17 species belonged to the non-calanoid orders (Poecilostomatoida, Cyclopoida, Harpacticoida and Mormonilloida) at this site. *Oncaea* spp. and *Farranula* spp. were the most abundant poecilostomatoids, *Euterpina acutifrons* and *Macrosetella* sp. represented the harpacticoids and *Oithona* spp., *Oithona brevicornis*, *Oithona plumifera* and *Oithona spinirostris* were the predominant cyclopoids. In Mormonilloida, the species *Mormonilla phasma* and *Neomormonilla minor* were observed only in night-time sampling.

In Bray–Curtis analyses, dendograms based on the copepod abundances and sampling months (also depths and time of sampling) showed a clear separation into three groups (Fig. 2.17 A). It was noteworthy that samples collected in October 2013 (0–40 m stratum, during the night) clustered together with only 10 % similarity with other groups and is addressed as group I. The group II was formed with samples collected in the month June 2012 (0–20 and 20–100 m strata sampled during daytime) at 61 % similarity. The group III was formed at 42 % similarity that clustered the sample collected during the months September 2012 (0–40 and 40–140 m strata sampled during day and night), October 2013

(40–160 m sampled at night), February 2013 (0–200 m stratum sampled at night) and June 2012 (0–20 and 20–100 m strata collected at night). The nMDS plot showed an analogous pattern of clustering of the stations (Fig. 2.17 B). Results of SIMPER analysis (Table 2.9) exhibited the distinction of the first cluster based on the dominance of *Pleuromamma robusta* and *Mormonilla phasma* (Fig. 2.17 C and D). The absence of *Euchaeta concinna* was responsible for clustering the group II (Fig. 2.17 E) and the presence of Harpacticoid copepod, *Macrosetella* spp. accounted for the formation of group III (Fig. 2.17 F).

2.3.4 Diversity of copepods

Monthly, seasonal and inter-annual variations in the copepod species diversity, richness and evenness at the continental shelf station G5 (Fig. 2.18) showed overall species diversity indices (H') in the range from 1.90 (March'11) to 3.71 (Nov'12), species richness (d) 0.57 (October'13) to 2.43 (April'13) and evenness (J) 0.54 (March'11) to 0.89 (Oct'13 October'13). Pre-monsoon was accounted for comparatively low copepod species diversity index (averaged 2.81±0.11), whereas the species richness (1.54±0.12) and evenness (0.67±0.02) were moderate. The dominance of *Acrocalanus* spp., *Centropages furcatus* and *Paracalanus* spp. could be marked as one of the factors for lowest evenness observed in March 2011 (0.54). The monsoon season was peculiar with low species richness (1.24 to 1.39), probably due to the overall low copepod abundance during this season. Further, moderate species diversity (2.89 and 3.30) and the evenly distributed species (J: 0.72–0.86) were observed in monsoon. The arithmetic mean for the diversity indices, specifically H', J and d were 3.10±0.29, 0.78±0.10 and 1.32±0.10, respectively in monsoon. Receding of upwelling effect marked a steep rise in copepod species diversity and species richness and gentle rise in evenness during post-monsoon. The H', J and d arithmetic mean were

3.18±0.29, 0.76±0.03 and 1.63±0.29, respectively. The year 2012 observed the highest species diversity (3.37±0.28) and richness (1.89±0.37).

The overall spatial, inter-annual and seasonal variations in the copepods diversity across the studied transect (Fig. 2.19) showed H' in the range from 3.56 (monsoon at G7) to 4.63 (pre-monsoon at G7), d from 2.03 (monsoon at G11) to 4.76 (Post-monsoon at G9) and J from 0.89 (pre-monsoon at G9) to 0.95 (pre-monsoon at G11). A high species richness of transect locations in comparison to the continental shelf (G5) and oceanic station (ASTS) is noteworthy. The Shannon diversity index was comparatively high in pre-monsoon (3.88 –4.63) as compared to monsoon (3.56 –4.59) and post-monsoon (3.89 –4.62). On the other hand, the high species richness was observed during post-monsoon (3.39 –4.77) than pre-monsoon (2.29–4.25) and monsoon (2.03 –3.78). However, species evenness showed minor variations during pre-monsoon (0.89 –0.95), monsoon (0.92– 0.95) and post-monsoon (0.92– 0.95) period.

Largely at the oceanic station, ASTS showed high species diversity and evenness indices in comparison to the continental shelf and slope. The variations in diversity indices on a seasonal scale were recorded as H' in the range of 2.48 (post-monsoon: Feb'13) to 3.93 (monsoon: June'12, 0–20 m at night), d from 0.92 (post-monsoon: Feb'13) to 3.46 (monsoon: June'12, 20–100 m at night) and J from 0.54 to 0.85, lowest and highest values were recorded during monsoon (June'12 in 20–100m stratum) at night and day, respectively (Fig. 2.20). On the seasonal scale, the copepod species diversity index (2.48), species evenness (0.76) and species richness (0.92) were comparatively low during the pre-monsoon season (February 2013) may probably be due to the invariably abundant amphipod counts, which might have reduced the values of diversity indices during the study. The species diversity (2.68– 3.93) and richness (1.93– 3.46) were high and species were evenly distributed (J: 0.59– 0.84) in monsoon (June’12 and September’12). The diversity pattern during monsoon was peculiar with the highest number of species (36; June’12, 20–100_N). During the post-monsoon, the species diversity indices were moderate, wherein species diversity ranged 3.30–3.34, species richness 1.12–1.74 and evenness (J) 0.77–0.80. Additionally, the upper 0–40 m stratum showed highest species diversity and the sub-surface 40–140 m stratum showed high species richness.

Table 2.1 Mesozooplankton sampling locations from different cruises

Shipping Vessel	Sampling period	Sampling stations
RV Sagar Paschimi	February 2011	G5, G6, G7, G9, G11, G13
	December 2011	G5, G7, G9, G11
RV Sindhu Sankalp	May 2011	G5, G6, G7, G9, G11, G13
	January 2012	G5, G7, G9, G11, G13
	September 2012	G5, G7, G9, ASTS
	February 2013	ASTS
	October 2013	ASTS
ORV Sagar Kanya	June 2012	G7, G9, G11, G13, ASTS

Table 2.2 Result of ANOVA comparing inter-annual and seasonal variations in copepod abundances at continental shelf (G5)

Effect	F	df	p
Inter-annual	1.00	2	0.40
Season	1.32	4	0.29
Inter-annual X Season	1.01	4	0.42

Table 2.3 Result of ANOVA comparing spatial and seasonal variations in copepod abundances

Effect	**F**	**df**	**p**
Sampling site	0.39	4	0.81
Season	1.05	4	0.41
Sampling site X Season	1.23	8	0.34

Table 2.4 Checklist of marine copepod species encountered during the present investigation

Orders	**Families**	**Species**
Calanoida	Acartiidae	*Acartia (Odontacartia) erythraea* Giesbrecht, 1889
	Aetideidae	*Acartia (Odontacartia) spinicauda* Giesbrecht, 1889
	Paracalanidae	*Acartia* spp.
	Calanidae	*Acrocalanus gibber* Giesbrecht, 1888
	Candaciidae	*Acrocalanus gracilis* Giesbrecht, 1888
	Calocalanidae	*Acrocalanus longicornis* Giesbrecht, 1888
	Centropagidae	*Acrocalanus* spp.
	Clausocalanidae	*Aetidius* spp.
	Eucalanidae	*Calocalanus* spp.
	Rhincalanidae	*Calanopia aurivili* Cleve, 1901
	Euchaetidae	*Calanopia elliptica* (Dana, 1849)
	Augaptilidae	*Calanopia minor* A. Scott, 1902
	Pontellidae	*Canthocalanus pauper* (Giesbrecht, 1888)
	Lucicutiidae	*Candacia ethiopica* (Dana, 1849)
	Metridinidae	*Candacia bradyi* A. Scott, 1902
	Pseudodiaptomidae	*Candacia discaudata* A. Scott, 1909
	Scolecitrichidae	*Candacia pachydactyla* Dana, 1849)
	Temoridae	*Candacia* spp.
		Centropages furcatus (Dana, 1849)
		Centropages gracilis (Dana, 1849)
		Centropages orsinii Giesbrecht, 1889
		Centropages tenuiremis Thompson & Scott, 1903

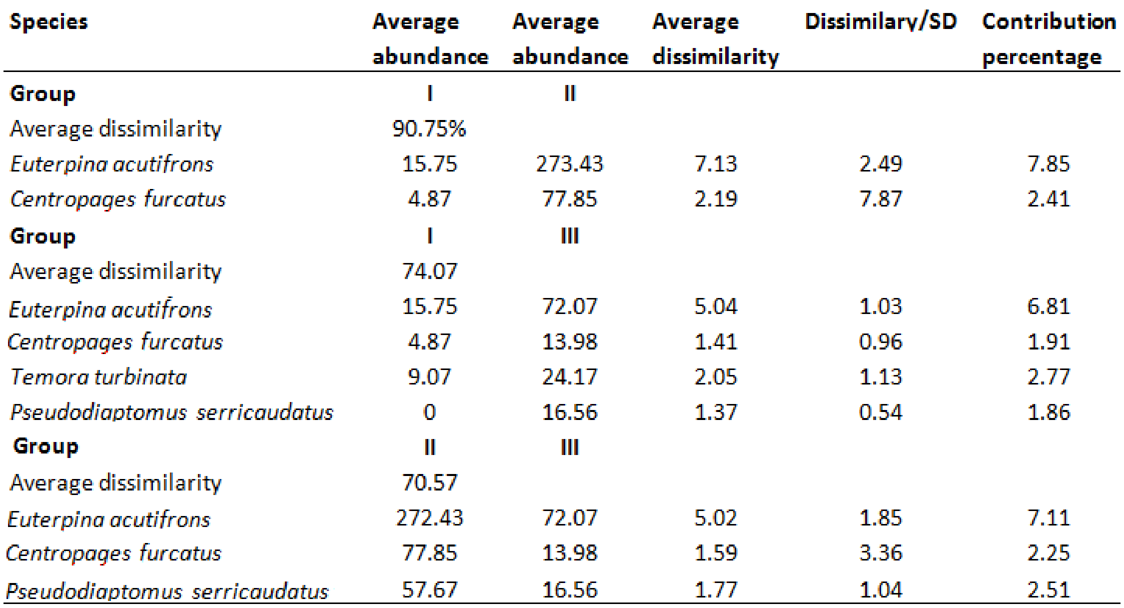
Continued …

Centropages trispinosus Sewell, 1914
Centropages spp.
Clausocalanus spp.
Cosmocalanus spp.
Pareucalanus attenuatus (Dana, 1849)
Subeucalanus crassus (Giesbrecht, 1888)
Subeucalanus monachus (Giesbrecht, 1888)
Eucalanus spp.
Euchaeta concinna Dana, 1849
Euchaeta longicornis Giesbrecht, 1888
Euchaeta marina (Prestandrea, 1833)
Euchaeta spp.
Euchirella amoena Giesbrecht, 1888
Euchirella spp.
Haloptilus spp.
Labidocera acuta (Dana, 1849)
Labidocera minuta Giesbrecht, 1889
Labidocera pectinata Thompson I.C. & Scott A., 1903
Labidocera spp.
Lucicutia flavicornis (Claus, 1863)
Lucicutia spp.
Mesocalanus tenuicornis (Dana, 1849)
Metridia spp.
Paracalanus aculeatus Giesbrecht, 1888
Paracalanus parvus (Claus, 1863)
Paracalanus spp.
Paracandacia spp.
Pleuromamma indica Wolfenden, 1905
Pleuromamma robusta (Dahl F., 1893)
Pleuromamma spp.
Pontella securifer Brady, 1883
Pontella spp.
Pontellina plumata (Dana, 1849)
Pseudodiaptomus serricaudatus (T. Scott, 1894)
Pseudodiaptomus bowmani Walter, 1984
Rhincalanus spp.
Scaphocalanus sp.
Subeucalanus subtenuis (Giesbrecht, 1888)

Continued …

		Subeucalanus subcrassus (Giesbrecht, 1888)
		Subeucalanus mucronatus (Giesbrecht, 1888)
		Subeucalanus pileatus (Giesbrecht, 1888)
		Subeucalanus spp.
		Scolicithricella spp.
		Temora turbinata (Dana, 1849)
		Temora discaudata Giesbrecht, 1889
		Undeuchaeta plumosa (Lubbock, 1856)
		Undeuchaeta spp.
		Undinula vulgaris (Dana, 1849)
Cyclopoida	Oithonidae	*Oithona brevicornis* Giesbrecht, 1891
		Oithona plumifera Baird, 1843
		Oithona setigera (Dana, 1849)
		Dioithona rigida (Giesbrecht, 1896)
		Oithona spp.
Harpacticoida	Euterpinidae	*Euterpina acutifrons* (Dana, 1847)
	Clytemnestridae	*Clytemnestra* spp.
	Miraciidae	*Macrosetella* spp.
	Metidae	*Metis* spp.
	Ectinosomatidae	*Microsetella* spp.
Poecilostomatoida	Oncaeidae	*Oncaea venusta* Philippi, 1843
	Corycaeidae	*Oncaea* spp.
	Sapphirinidae	*Corycaeus* (Onychocorycaeus) *catus* F. Dahl, 1894
		Corycaeus danae
		Corycaeus crassiusculus Dana, 1849
		Corycaeus speciosus Dana, 1849
		Coryaceaus spp.
		Farranula gibbula (Giesbrecht, 1891)
		Farranula spp.
		Copilia mirabilis Dana, 1849
		Sapphirina spp.
Mormonilloida	Mormonillidae	*Mormonilla phasma* Giesbrecht, 1891
		Neomormonilla minor (Giesbrecht, 1891)

Table 2.5 Result of SIMPER analysis based on group obtained from the cluster and MDS ordination showing the species that contributed to the differences among the groups at G5



Species	Average abundance	Average abundance	Average dissimilarity	Dissimilary/SD	Contribution percentage
Group	**I**	**II**			
Average dissimilarity	90.75%				
Euterpina acutifrons	15.75	273.43	7.13	2.49	7.85
Centropages furcatus	4.87	77.85	2.19	7.87	2.41
Group	**I**	**III**			
Average dissimilarity	74.07				
Euterpina acutifrons	15.75	72.07	5.04	1.03	6.81
Centropages furcatus	4.87	13.98	1.41	0.96	1.91
Temora turbinata	9.07	24.17	2.05	1.13	2.77
Pseudodiaptomus serricaudatus	0	16.56	1.37	0.54	1.86
Group	**II**	**III**			
Average dissimilarity	70.57				
Euterpina acutifrons	272.43	72.07	5.02	1.85	7.11
Centropages furcatus	77.85	13.98	1.59	3.36	2.25
Pseudodiaptomus serricaudatus	57.67	16.56	1.77	1.04	2.51

Table 2.6 Result of SIMPER analysis based on group obtained from the cluster and MDS ordination showing the species that contributed to the differences among the groups at studied transect during pre-monsoon

Species	**Average abundance**	**Average abundance**	**Average dissimilarity**	**Dissimilary/SD**	**Contribution percentage**
Pre-monsoon 1					
Group	**I**	**II**			
Average dissimilarity	54.77				
Oithona spp.	345.19	200.57	2.63	1.38	4.8
Acartia erythraea	186.53	11.28	3.28	3.23	5.99
Microsetella spp.	200.02	46.9	2.96	0.93	5.4
Group	**I**	**III**			
Average dissimilarity	84.07				
Oithona spp.	345.19	25.83	7.72	3.72	9.19
Acartia erythraea	186.53	0	4.49	3.5	5.34
Microsetella spp.	200.02	21.09	4.38	0.94	5.21
Group	**II**	**III**			
Average dissimilarity	67.66				
Oithona spp.	200.57	25.83	8.27	18.17	12.23
Microsetella spp.	46.9	21.09	1.23	4.27	1.82
Pre-monsoon 2					
Group	**I**	**II**			
Average dissimilarity	89.48				
Oncaea spp.	95.96	1230.25	13.1	36.17	14.64
Pleuromamma spp.	4.01	131.52	1.47	19.69	1.65
Group	**I**	**III**			
Average dissimilarity	69.63				
Oncaea spp.	95.96	296.01	6.45	6.36	9.26
Microsetella spp.	20.81	103.96	2.69	4.92	3.86
Group	**II**	**III**			
Average dissimilarity	66.67				
Oncaea spp.	1230.25	296.01	8.83	28.68	13.25
Pleuromamma spp.	131.52	0	1.24	254.48	1.86

Table 2.7 Result of SIMPER analysis based on group obtained from the cluster and MDS ordination showing the species that contributed to the differences among the groups at studied transect during monsoon

Species	**Average abundance**	**Average abundance**	**Average dissimilarity**	**Dissimilary/SD**	**Contribution percentage**
Group	**I**	**II**			
Average dissimilarity	63.12				
Pleuromamma indica	16	0	1.56	2.92	2.48
Corycaeus spp.	0	52.09	4.53	2.92	7.18
Oithona spp.	0	52.52	5.11	3.2	8.09
Group	**I**	**III**			
Average dissimilarity	80.04				
Pleuromamma indica	16	0	1.1	3.76	1.38
Corycaeus spp.	0	70.81	4.7	2.95	5.87
Oithona spp.	0	53.25	3.4	1.44	4.24
Group	**II**	**III**			
Average dissimilarity	57.56				
Lucicutia flavicornis	8.94	9.49	0.61	1.18	1.05
Corycaeus spp.	52.09	70.81	1.91	1.21	3.31
Oithona spp.	52.52	53.25	1.77	1.36	3.08

Table 2.8 Result of SIMPER analysis based on group obtained from the cluster and MDS ordination showing the species that contributed to the differences among the groups at studied transect during post-monsoon

Species	Average abundance	Average abundance	Average dissimilarity	Dissimilary/SD	Contribution percentage
Group	**I**	**II**			
Average dissimilarity	55.36				
Acrocalanus spp.	17.89	12.14	0.99	4.23	1.79
Oncaea spp.	58.88	38.42	3.54	1.64	6.4
Oithona spp.	0	17.37	2.79	1.71	5.04
Lucicutia flavicornis	15.49	0	2.65	6.6	4.78
Group	**I**	**III**			
Average dissimilarity	59.6				
Acrocalanus spp.	12.14	30.58	2.18	5.34	3.65
Oncaea spp.	38.42	84.28	5.16	2.27	8.67
Oithona spp.	17.37	24.22	1.44	1.43	2.41
Group	**II**	**III**			
Average dissimilarity	53.79				
Acrocalanus spp.	17.89	30.58	1.35	4.95	2.51
Oncaea spp.	58.88	84.28	2.63	1.47	4.89
Lucicutia flavicornis	15.49	0	1.67	6.36	3.11

Table 2.9 Result of SIMPER analysis based on group obtained from the cluster and MDS ordination showing the species that contributed to the differences among the groups at the oceanic station (ASTS)

Species	Average abundance	Average abundance	Average dissimilarity	Dissimilary/SD	Contribution percentage
Group	**I**	**II**			
Average dissimilarity	98.76				
Euchaeta concinna	170.93	0	2.33	233.09	2.36
Group	**I**	**III**			
Average dissimilarity	88.03				
Pleuromamma robusta	0	170.93	2.09	24.6	2.37
Mormonilla phasma	2.65	170.93	2.06	17.04	2.34
Group	**II**	**III**			
Average dissimilarity	86.01				
Euchaeta concinna	0	38.02	3.18	1.2	3.69
Macrosetella spp.	4.17	11.41	0.93	2.19	1.08

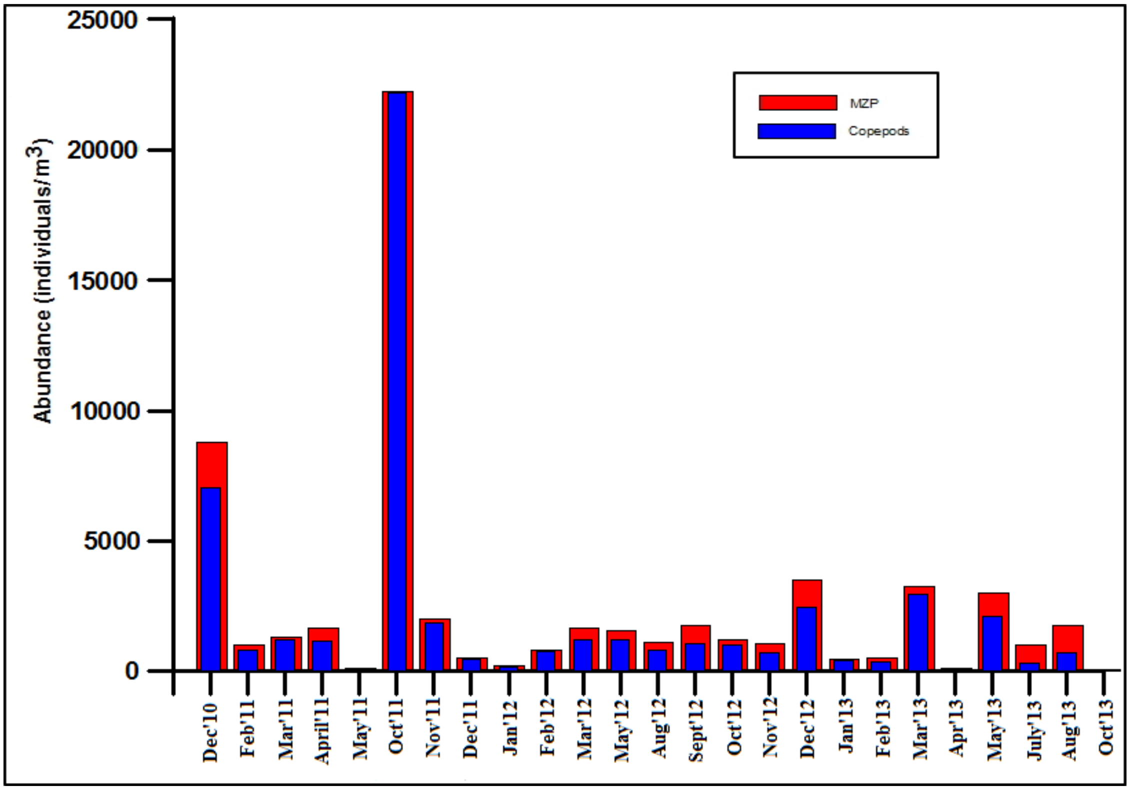


Fig. 2.1 Monthly variations in copepod and mesozooplankton (MZP) density registered at continental shelf (G5) in the Arabian Sea

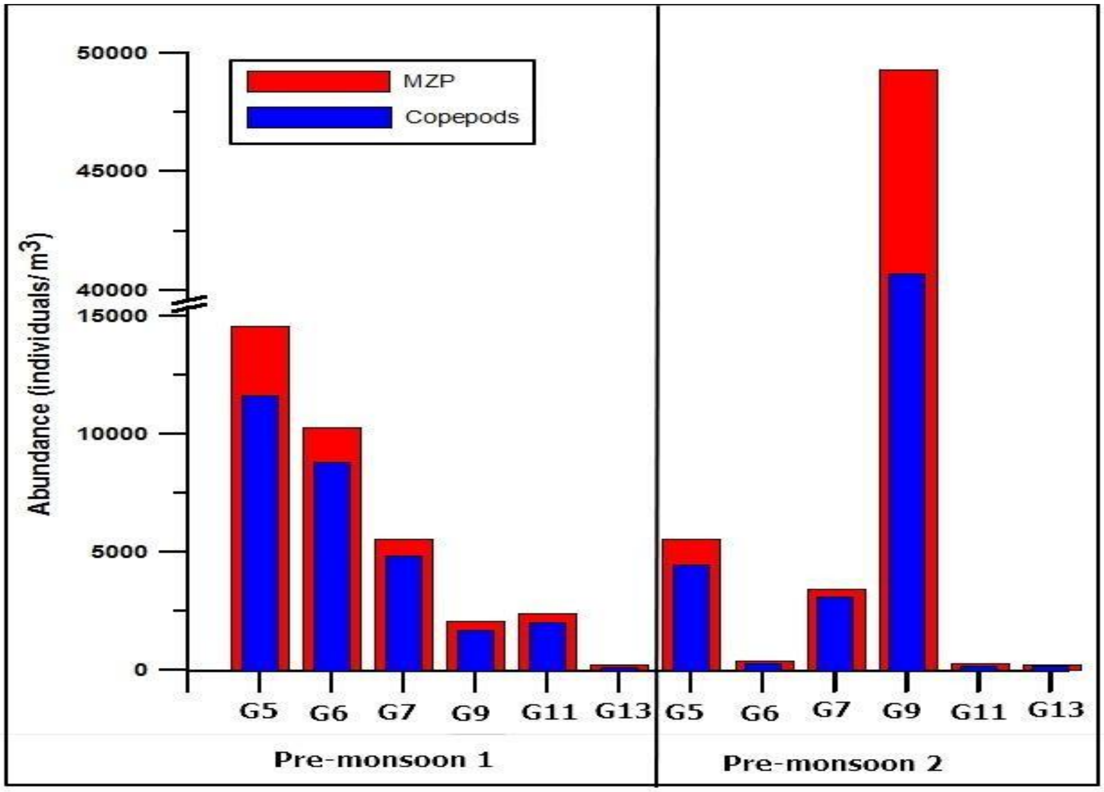


Fig. 2.2 Variations in copepod and mesozooplankton (MZP) density registered at continental shelf and slope regions in the Arabian Sea during pre-monsoon (1: February 2011 and 2: May 2011)

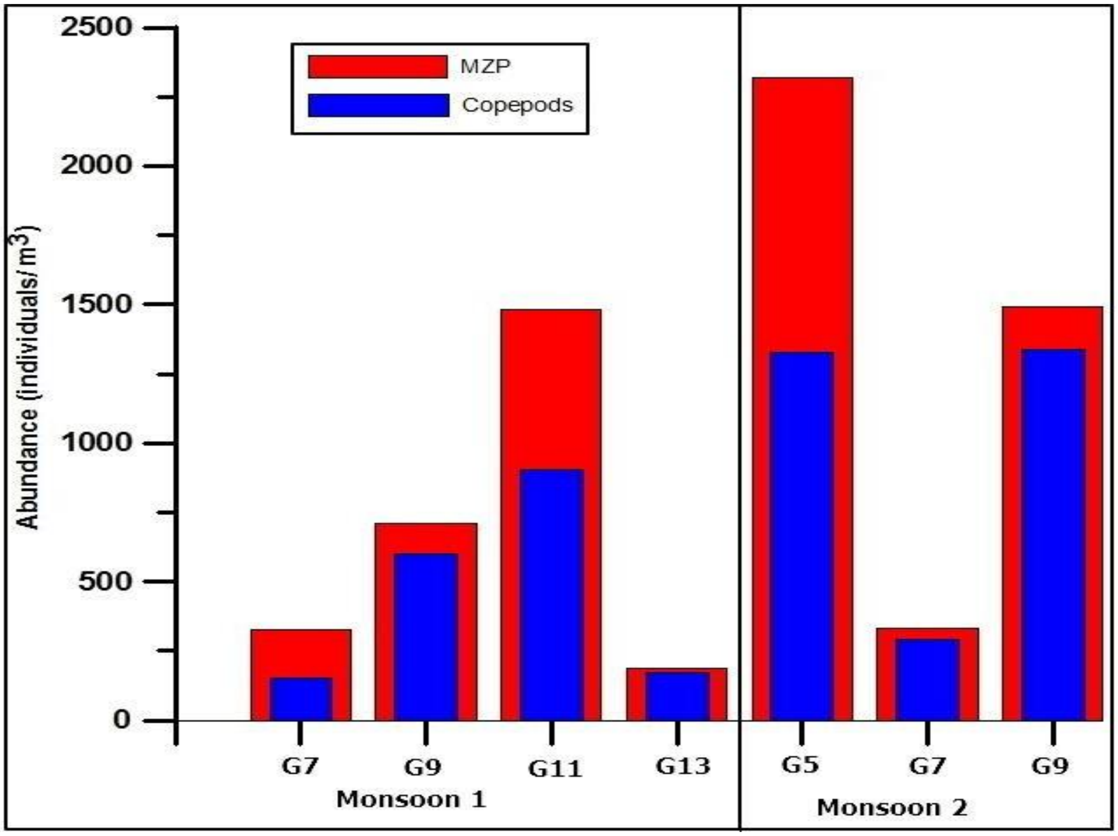


Fig. 2.3 Variations in copepod and mesozooplankton (MZP) density registered at continental shelf and slope regions in the Arabian Sea during monsoon (1: September 2012 and 2: June 2013)

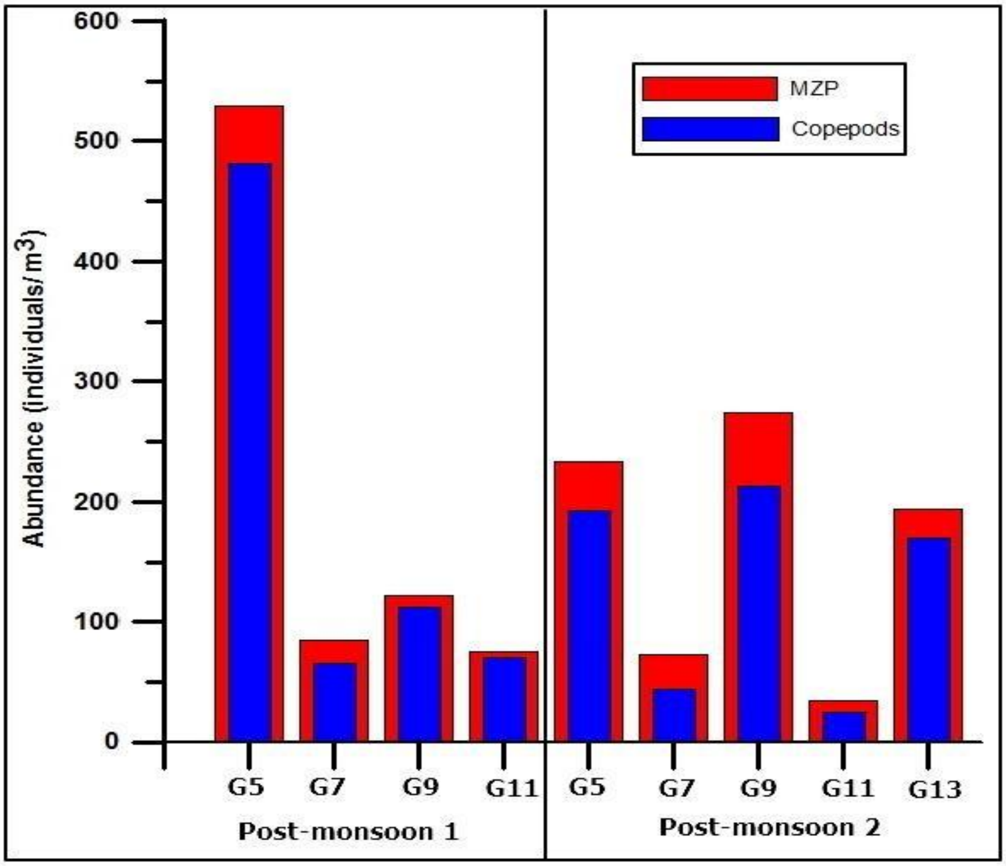


Fig. 2.4 Variations in copepod and mesozooplankton (MZP) density registered at continental shelf and slope regions in the Arabian Sea during post-monsoon (1: December 2011 and 2: January 2012)

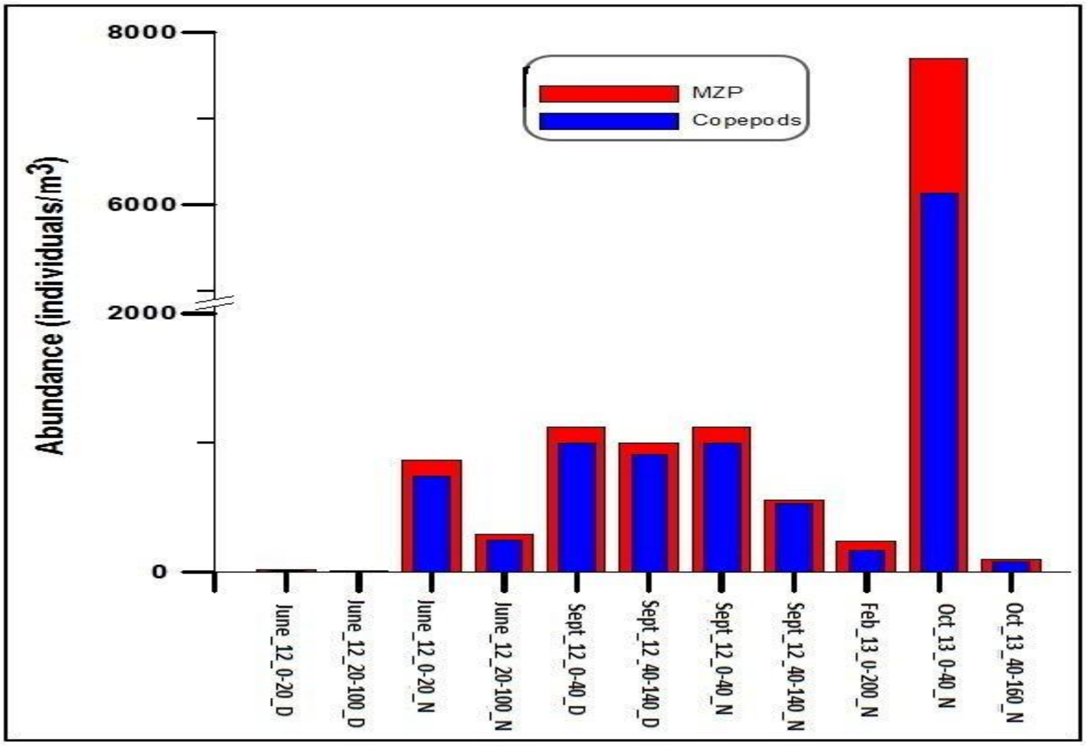


Fig.2.5 Seasonal variations in copepod and mesozooplankton (MZP) density registered at open waters (ASTS) of the Arabian Sea.

Legends read as *June_12_0-20_D* and *June_12_0-20_N:* sampled during day and night, respectively at 0-20 m stratum in June’12; *June_12_20-100_D* and *June_12_20-100_N*: sampled during day and night, respectively at 20-100 m stratum in June’12; *Sept_12_0-40_D* and *Sept_12_0-40_N* : sampled during day and night, respectively at 0-40 m stratum in September’12; *Sept_12_40-140_D* and *Sept _12_40-140_N*: sampled during day and night, respectively at 40-140 m stratum in September’12*Feb_13_0-200_N*: Sampled during night at 0-200 m stratum in February’13; *Oct_13_0-40_N* and *Oct_13_40-160_N* Sampled during night at 0-40 m a 40-140 m stratum in October’13

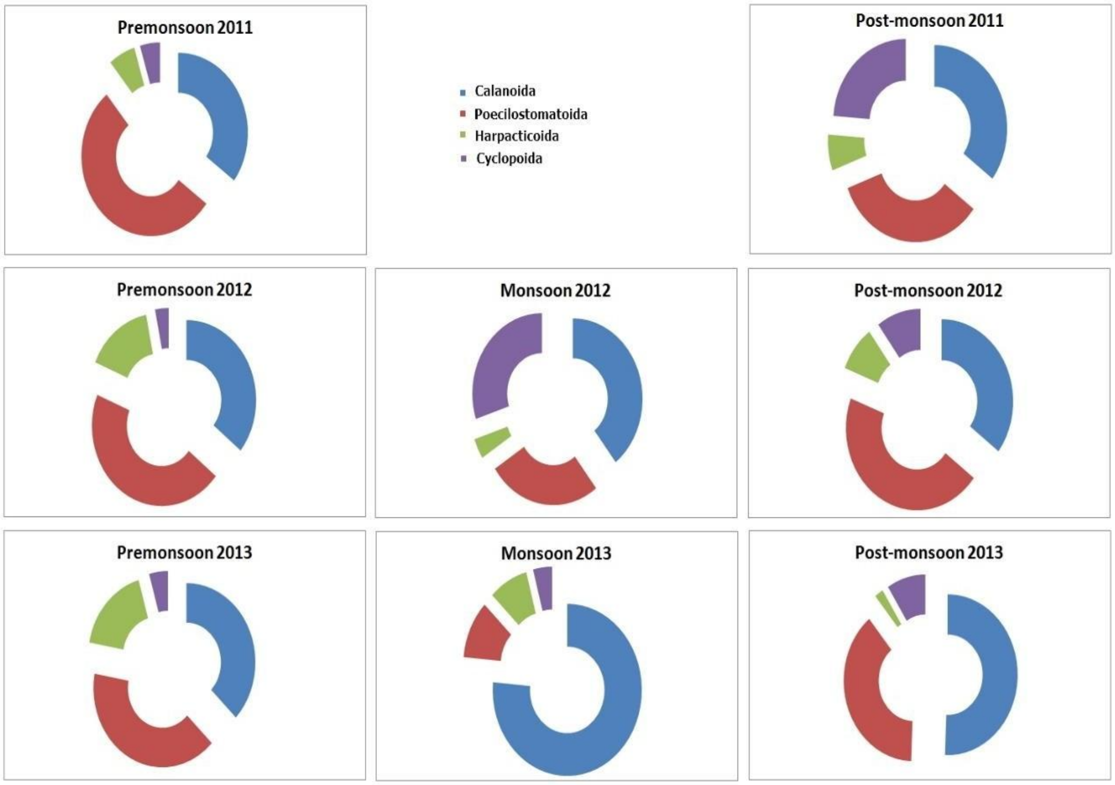


Fig. 2.6 Inter-annual and seasonal variations in copepod orders recorded at continental shelf (G5) in the Arabian Sea

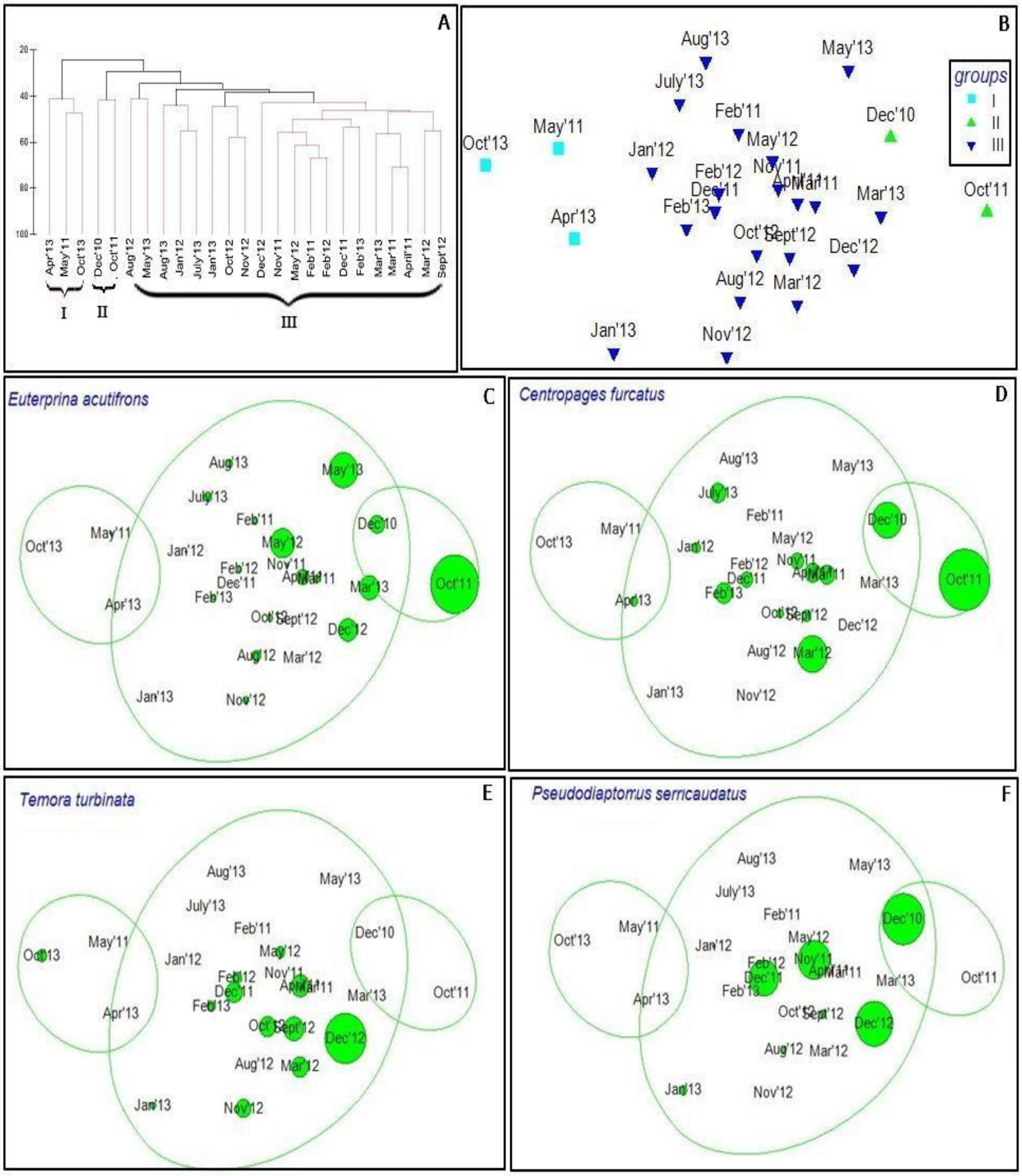


Fig. 2.7 Bray–Curtis similarity (A) based on clustering of months manifested through dendrogram and nMDS plot (B) based on copepod abundance. Bubble plot of distinct copepod species (C–F) at continental shelf (G5)

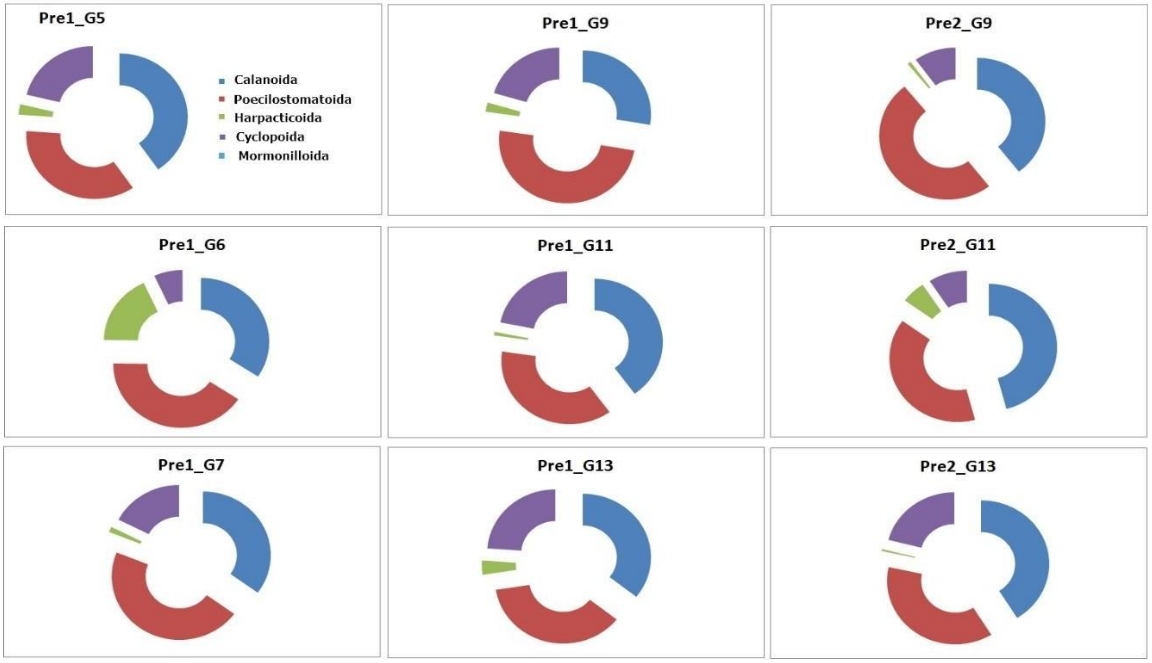


Fig. 2.8 Variations in relative abundance of copepod orders recorded at continental shelf and slope region in the Arabian Sea during pre-monsoon

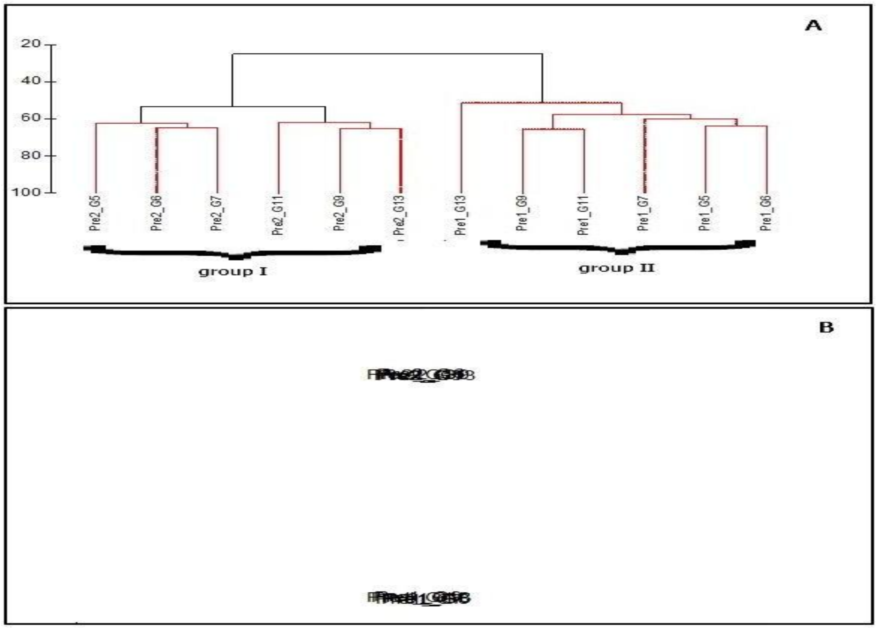


Fig. 2.9 (A) Bray–Curtis cluster and (B) nMDS plot based on copepod abundance in pre-monsoon.

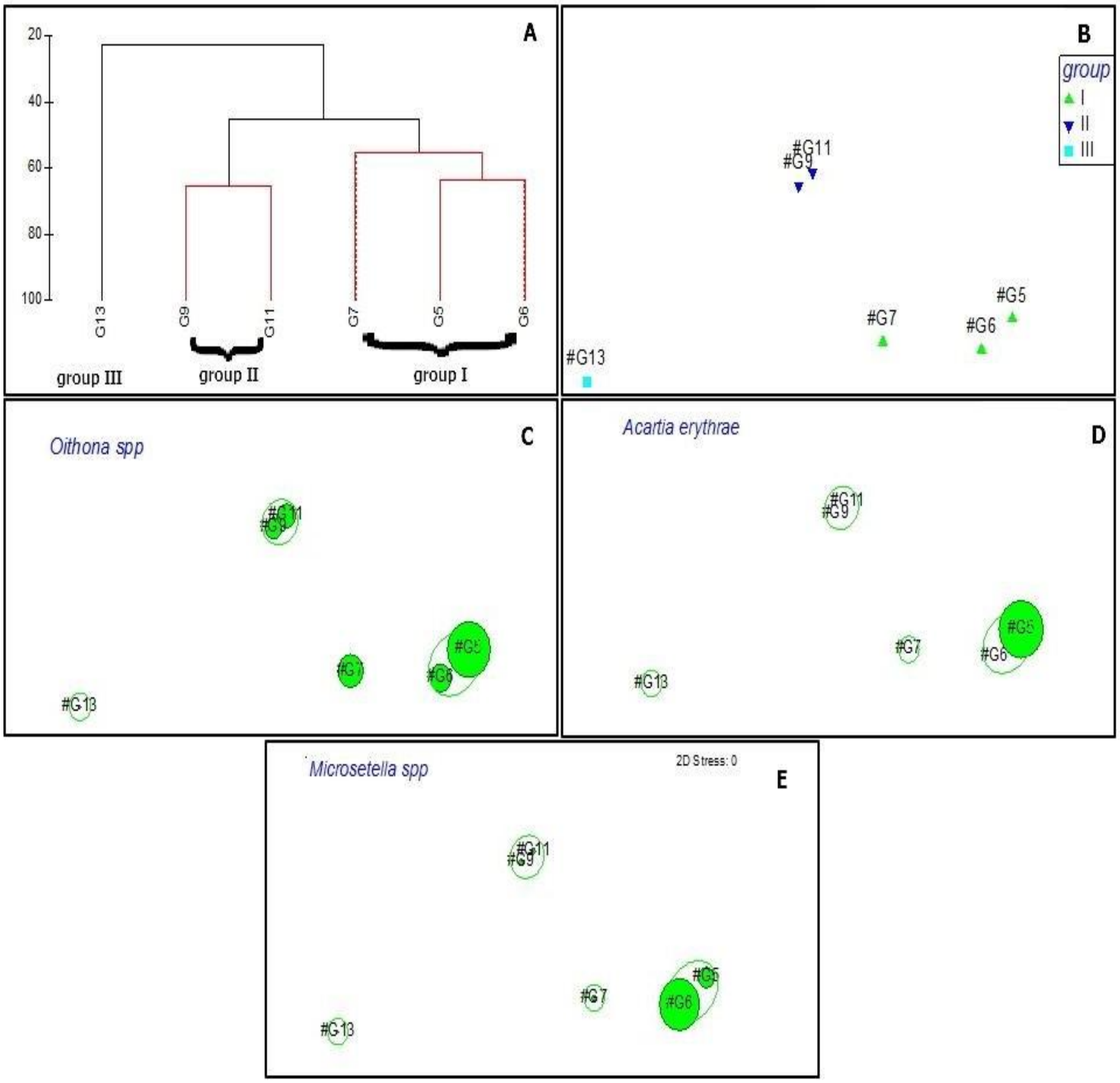


Fig. 2.10 (A) Bray–Curtis cluster and (B) nMDS plot based on copepod abundance in February 2011. Bubble plot of distinct copepod species (C–E)

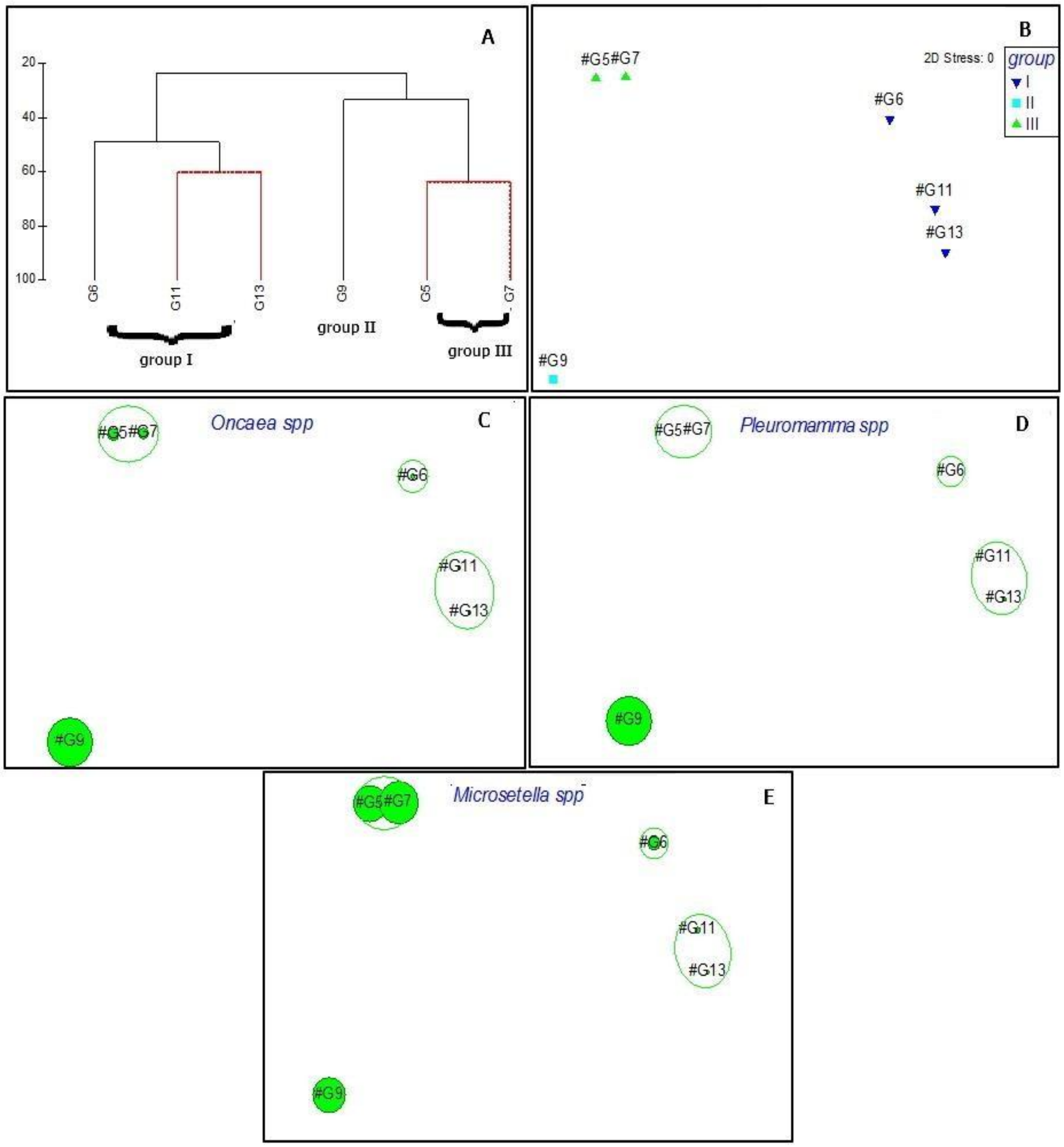


Fig. 2.11 (A) Bray–Curtis cluster and (B) nMDS plot based on copepod abundance in May 2011. Bubble plot of distinct copepod species (C–E)

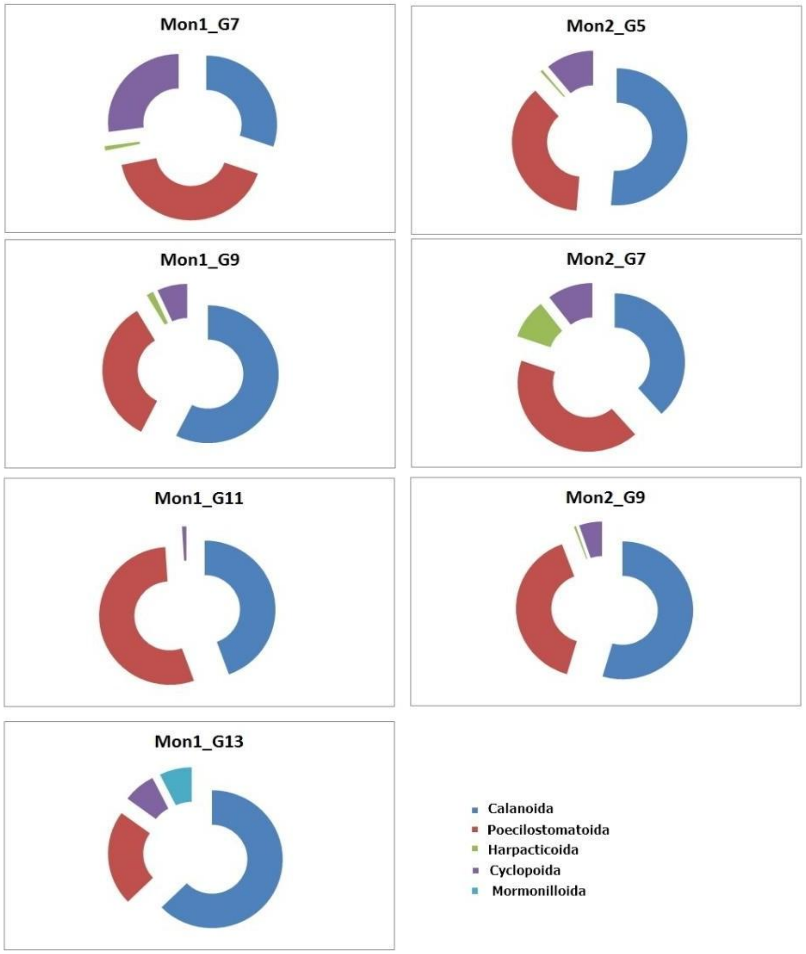


Fig. 2.12 Variations in relative abundance of copepod orders recorded in a monsoon at continental shelf and slope region in the Arabian Sea

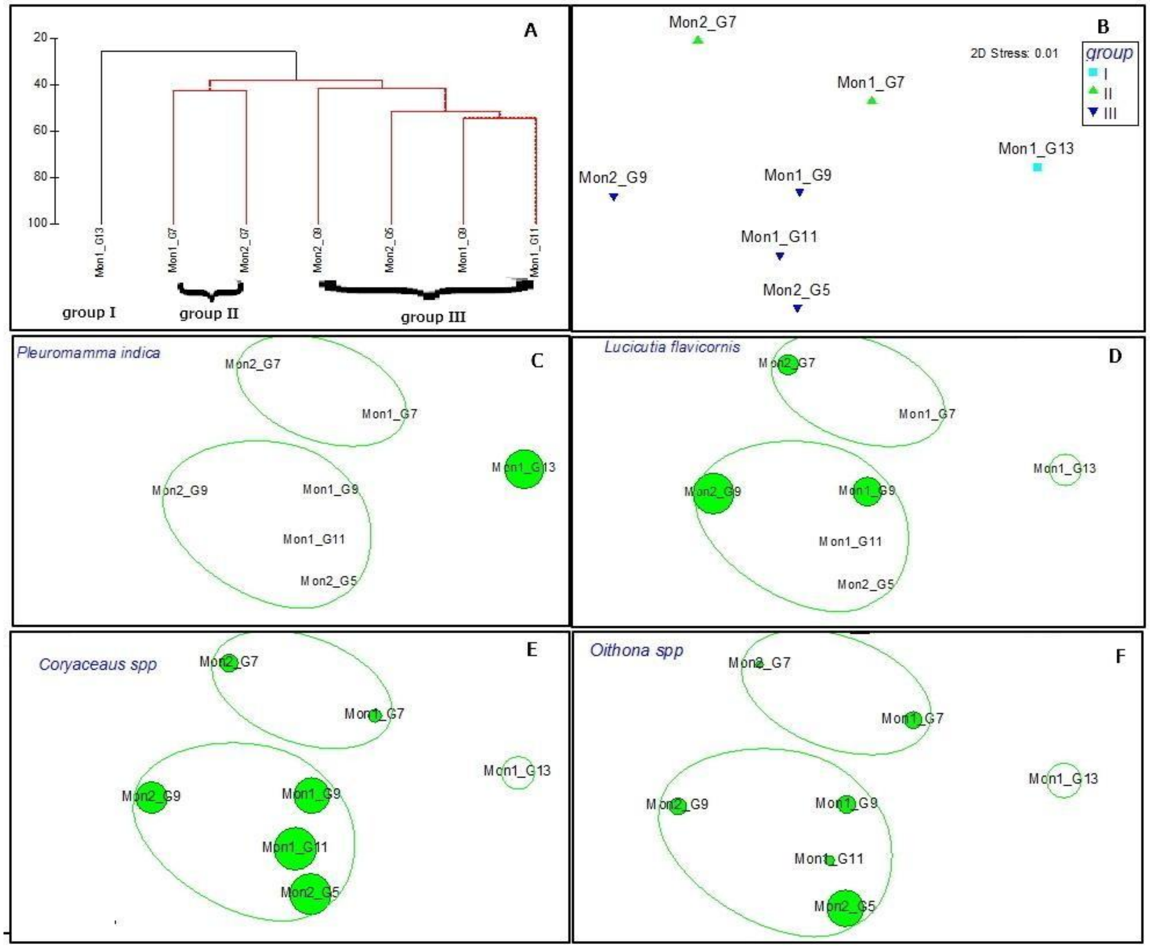


Fig. 2.13 (A) Bray–Curtis cluster and (B) nMDS plot based on copepod abundance in monsoon. Bubble plot of distinct copepod species (C–F)

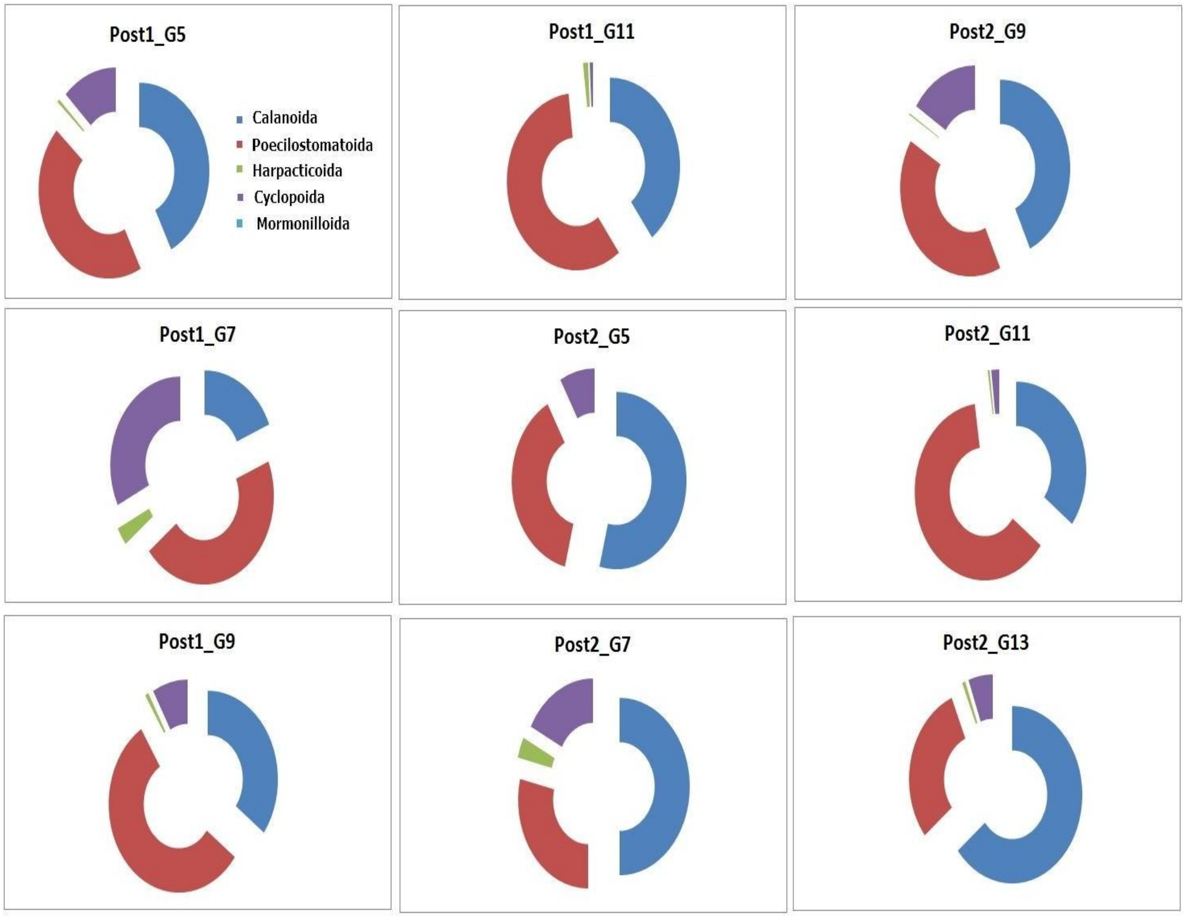


Fig.2.14 Variations in relative abundance of copepod orders recorded in post-monsoon in continental shelf and slope waters of the Arabian Sea

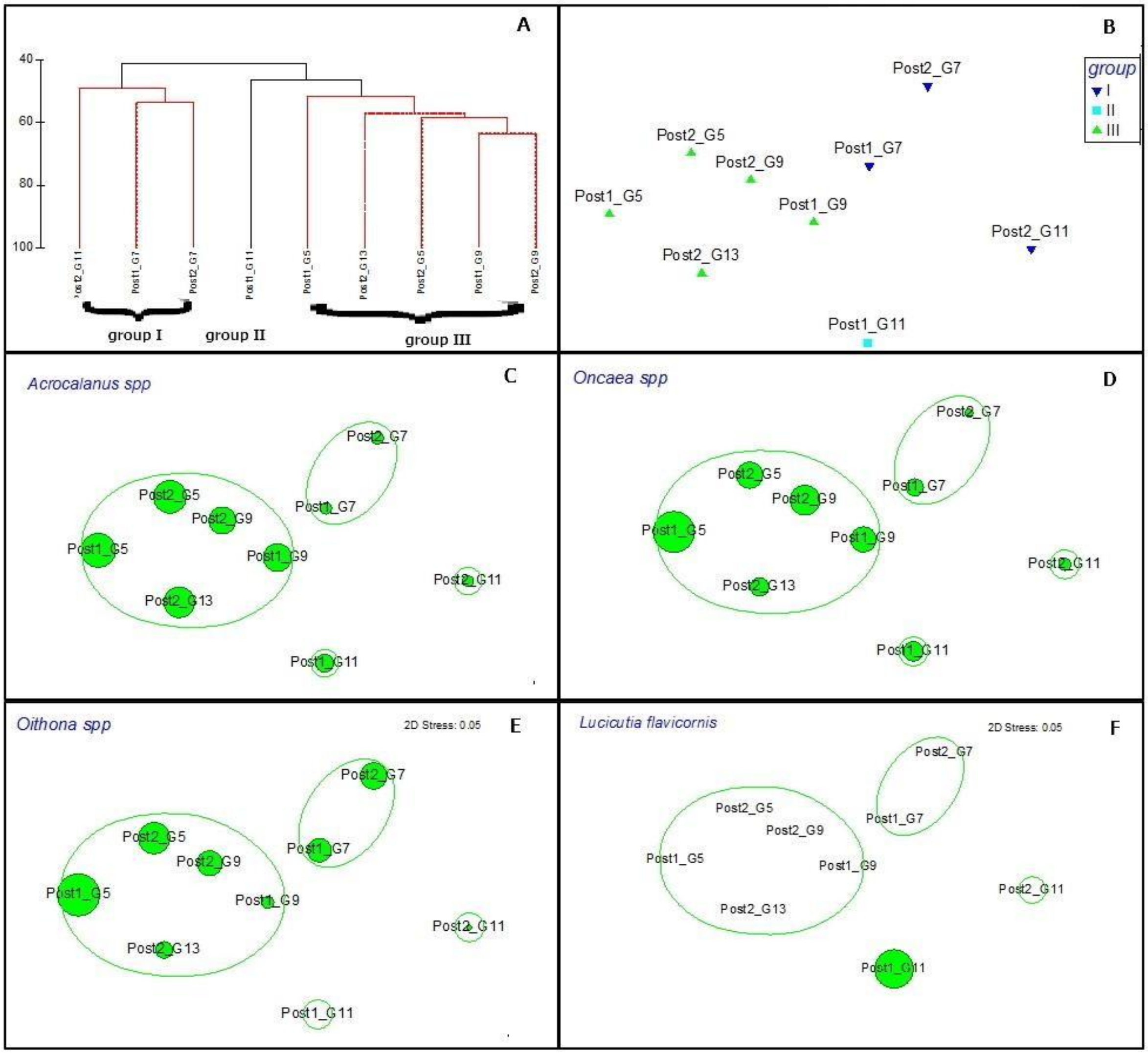


Fig. 2.15 (A) Bray–Curtis cluster and (B) nMDS plot based on copepod abundance in post-monsoon. Bubble plot of distinct copepod species (C–F)

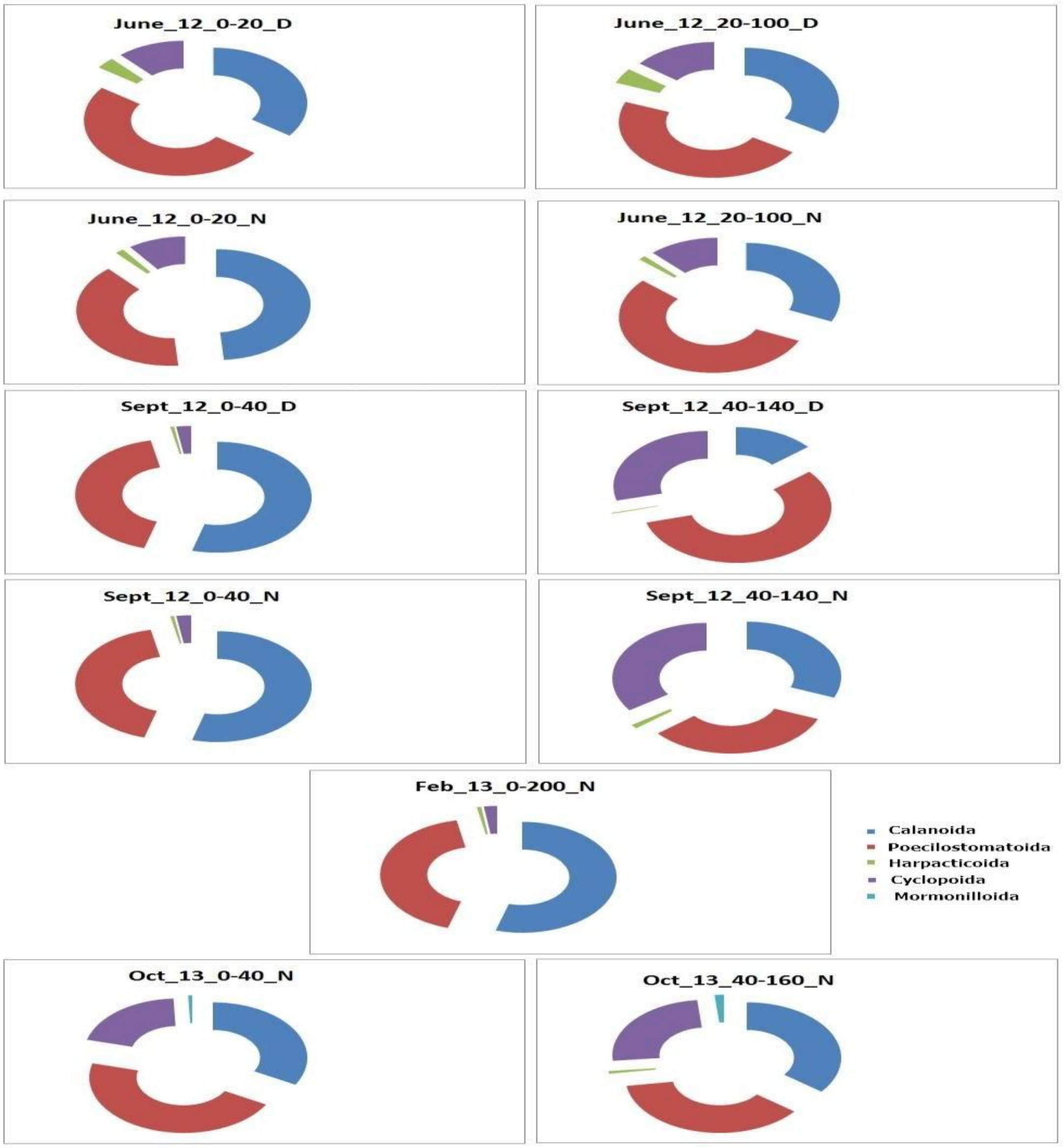


Fig. 2.16 Variations in relative abundance of copepod orders recorded at ASTS in the Arabian Sea

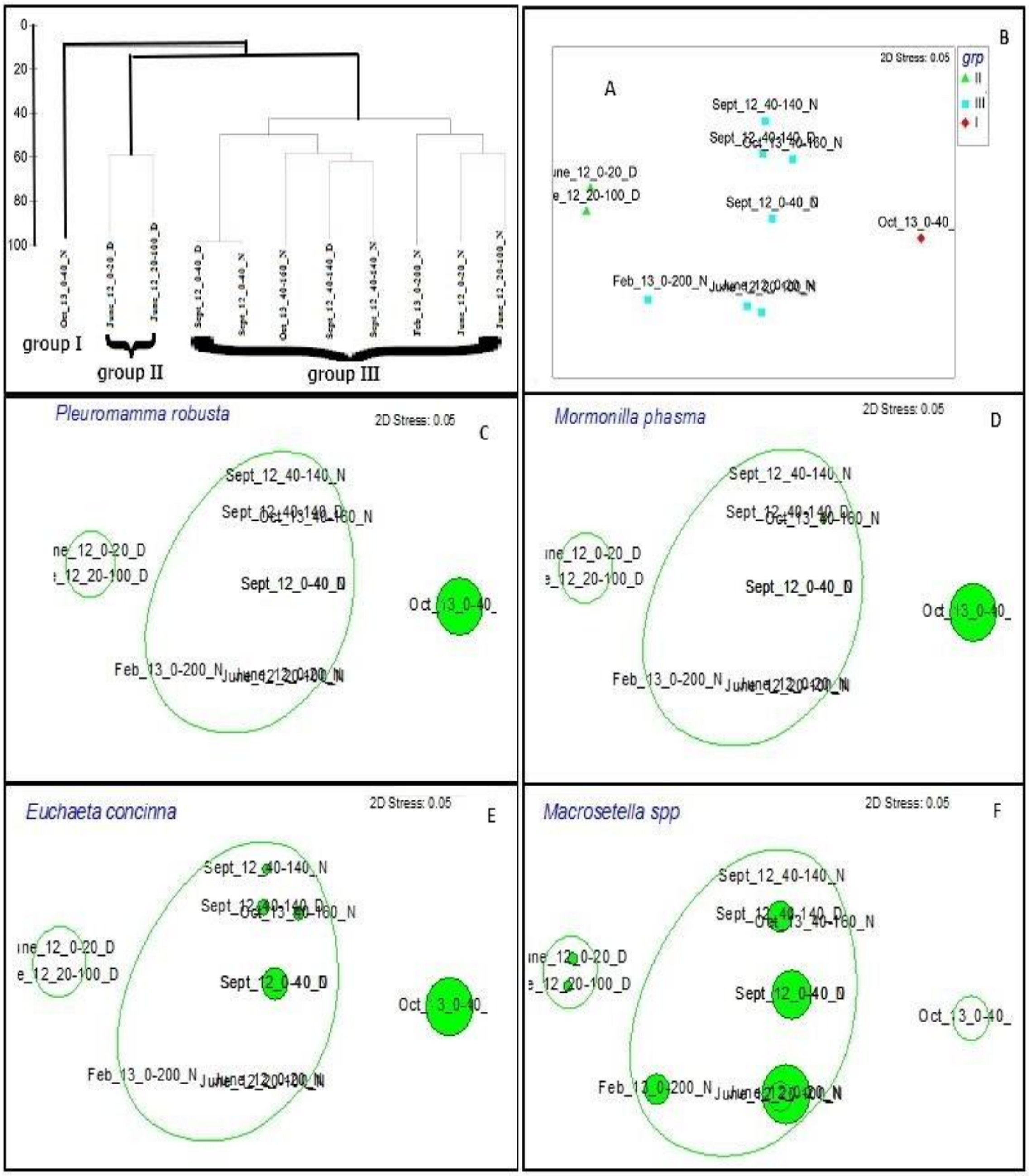


Fig. 2.17 Clusters formed on the basis of copepod assemblage at ASTS (A) Bray–Curtis cluster and (B) nMDS plot. Bubble plot of distinct copepod species (C–F)

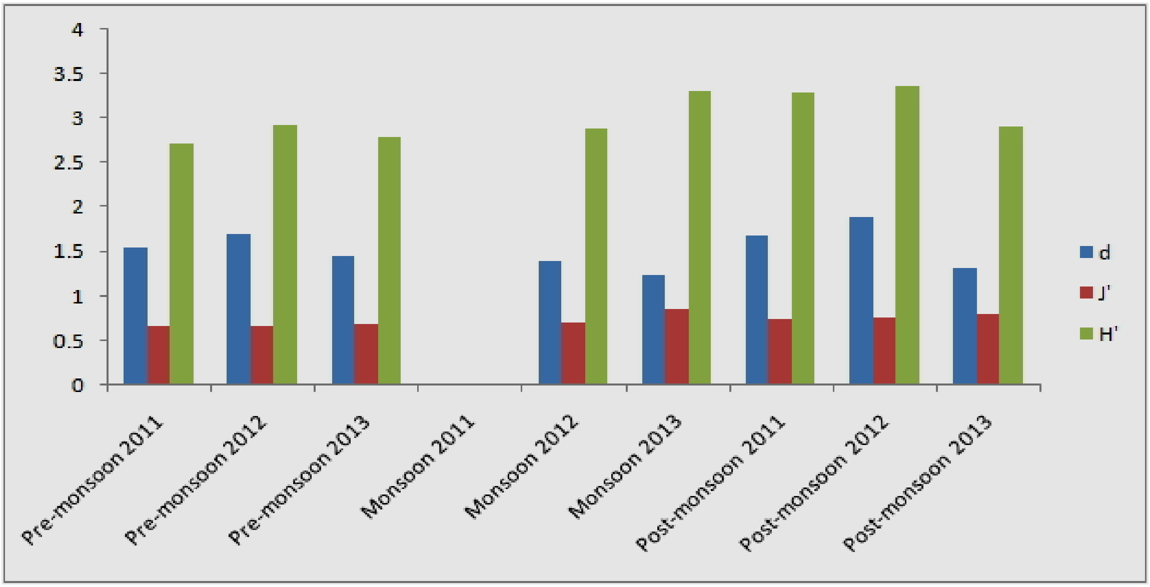


Fig. 2.18 Seasonal variation in diversity of copepod assemblages at continental shelf (G5). ***H'*****: species diversity;** ***d*****: species richness and** ***J*****: evenness**

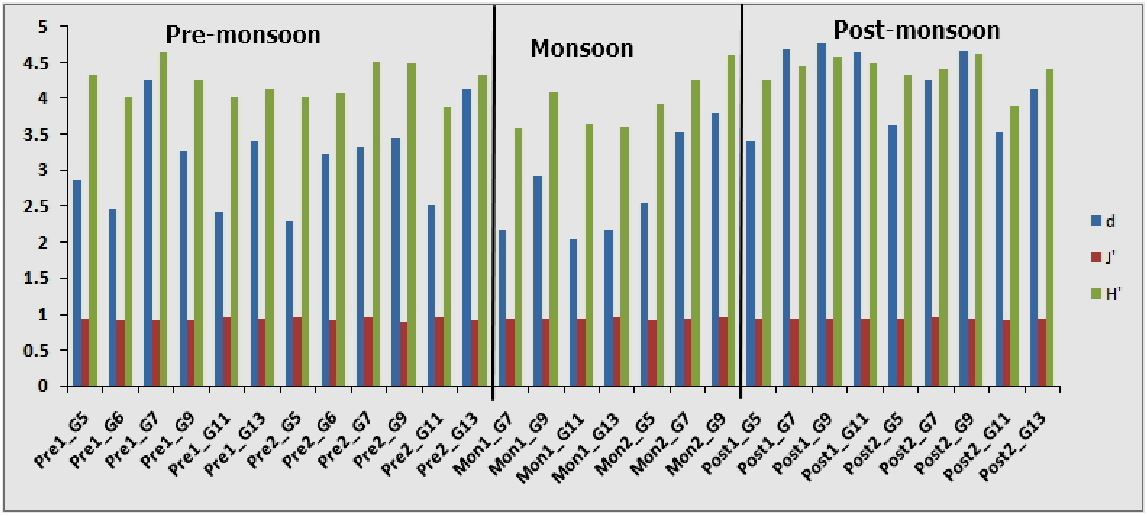


Fig.2.19 Spatial and seasonal variation in diversity pattern of copepod assemblages at transect with continental shelf and slope stations. ***H'*****: species diversity;** ***d*****: species richness and** ***J*****: evenness**

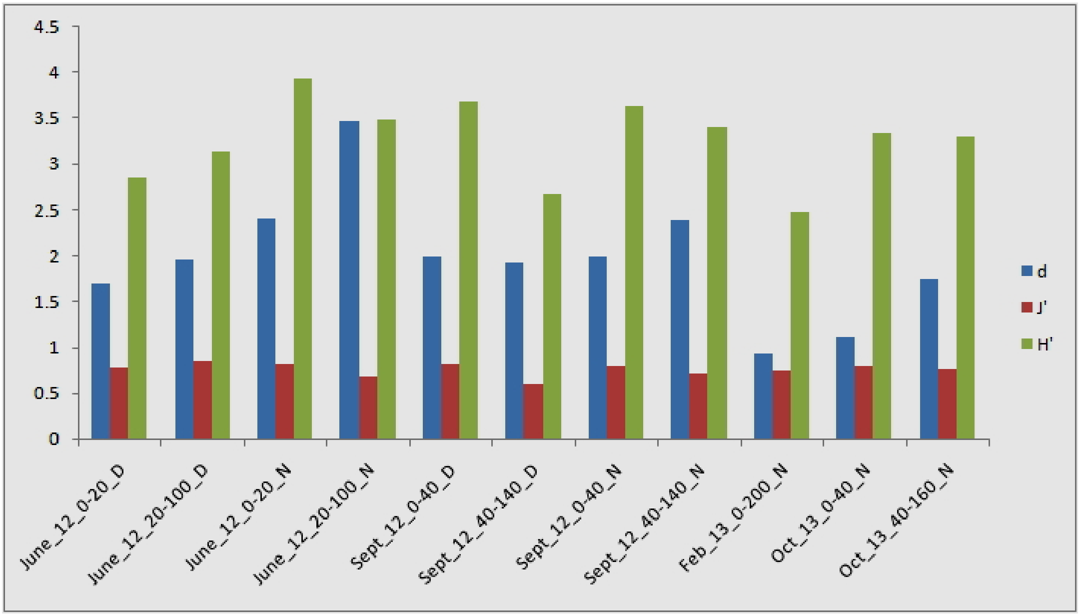


Fig. 2.20 Seasonal variation in diversity pattern of copepod assemblages at the oceanic station. *H'*: species diversity; *d*: species richness and *J*: evenness

Legends read as *June_12_0-20_D* and *June_12_0-20_N:* sampled during day and night, respectively at 0-20 m stratum in June'12; *June_12_20-100_D* and *June_12_20-100_N*: sampled during day and night, respectively at 20-100 m stratum in June'12; *Sept_12_0-40_D* and *Sept_12_0-40_N* : sampled during day and night, respectively at 0-40 m stratum in September'12; *Sept_12_40-140_D* and *Sept _12_40-140_N*: sampled during day and night, respectively at 40-140 m stratum in September'12*Feb_13_0-200_N*: Sampled during night at 0-200 m stratum in February'13; *Oct_13_0-40_N* and *Oct_13_40-160_N* Sampled during night at 0-40 m a 40-140 m stratum in October'13

2.4 DISCUSSION

2.4.1 Hydrographic variations

Physico-chemical characteristics of the eastern Arabian Sea make a favorable environment for the continued existence of mesozooplankton. Continental shelf waters of the Indian west coast are very productive and endure a rich and abundant planktonic life. The rich fishery of this region increases its significance to the country (Nair and Peter 1980). Previous studies on hydrography have revealed consistent seasonal changes in the oceanography that is important for fisheries, especially during upwelling in the southwest monsoon (Banse 1968; Nair and Peter 1980). During the post-monsoon, the abundance of mesozooplankton recorded to be high probably due to influencing the biological cycle (Nair and Peter 1980).

Along the continental realm values of temperature, salinity and chlorophyll *a* concentration ranged between 24.83–30.07°C, 35.07–35.67 and 0.03–2.12 µg/l, respectively during pre-monsoon. Concurrently, it is well-known that mesozooplankton from these locale show spatial and temporal variations (Madhupratap and Haridas 1986; Madhupratap et al.1990; Padmavati et al. 1998; Nair et al. 1999; Jagadeesan et al. 2013; Gauns et al. 2015b) similar to primary production. Biological productivity of the Arabian Sea is governed by upwelling during southwest monsoon (Banse 1968) and winter cooling during northwest monsoon (Madhupratap et al. 1996b). The present study indicates a longitudinal variation in the distribution of these mesozooplankton similar to earlier reports (Fasham and Angel 1975; Madhupratap et al. 2001a). In central and eastern Arabian Sea during the month of May, environmental conditions are reported to be oligotrophic with high abundance of bacteria and picoplankton (Ramaiah et al. 1996), microzooplankton (Gauns et al. 1996) and low phytoplankton (Bhattathiri et al. 1996) with an increased number of *Trichodesmium* spp. (Sawant and Madhupratap 1996) followed by a high abundance of mesozooplankton during April-May (Madhupratap et al. 1996a). The latter study suggests that due to the ability of large copepods to feed on smaller microzooplankton or even bacteria enables them to maintain the relatively invariable biomass between the seasons in the eastern Arabian Sea. Jointly, such biological conditions may link the mesozooplankton abundance during the present study with control of the microbial loop in the eastern Arabian Sea.

The temperature and salinity during pre-monsoon, monsoon and post-monsoon were always high at the oceanic station as compared to the continental margin. The DO concentrations in the OMZ and intermediate depths varied seasonally, with the lowest concentration was recorded during the October 2013 than those in June 2012 and September 2012 as reported earlier by Jain et al. (2014) and de Sousa et al. (1996). In the Northeastern Arabian Sea, higher surface productivity (Bhattathiri et al. 1996) together with sluggish renewal of intermediate waters (Naqvi et al. 1990) leads to intense oxygen depletion during the winter season. Surface waters were devoid of nitrate during June 2012 and September 2012 and quite low during the October 2013 (0.006 μM). The inter-monsoon period experiences extreme solar heating and weak winds which stratify the surface layer (Muraleedharan and Prasanna Kumar 1996) and depletes nutrients/nitrate in the upper euphotic zone. Conversely, convective mixing aids the upward pumping of nutrient-rich subsurface layers during winter (PrasannaKumar and Prasad 1996) that is responsible for high primary productivity. The low primary productivity period inter-monsoon (Madhupratap et al. 1996a) show a higher abundance of bacteria (Jain et al. 2014). Here the bacterial abundance is sustained by the dissolved organic carbon from earlier phytoplankton blooms of the north-east monsoon (Ramaiah et al. 2000). In general, bacterial abundance is higher at the end of the southwest monsoon. The decay of phytoplankton blooms and increased exudation and/or particle breakdown (Ducklow 1993) would also lead to facilitation of prolonged bacterial proliferation.

2.4.2 Mesozooplankton and copepod abundance

The extensively sampled continental shelf station (G5) captured significant variation in mesozooplankton and copepod abundance. Comparatively, post-monsoon showed higher abundance than pre-monsoon and monsoon (Fig. 2.1). Conspicuous low copepod abundance during monsoon may be attributed to freshening of the system and coastal upwelling. Interestingly, the highest abundance of copepods during post-monsoon corresponds to the breeding season of the organism. The breeding season for most of the copepods in coastal waters of India is reported to be in post-monsoon, although a few species breed continuously (Ummerkutty 1965).

The seasonal variation in mesozooplankton and copepod abundance along the transect covering continental shelf and slope (Fig. 2.2, 2.3 and 2.4) revealed different pattern of variation than that of the monthly sampled G5 station. At the continental shelf station (G5), highest copepod and mesozooplankton abundance was recorded in pre-monsoon, intermediate during monsoon and least in post-monsoon. Overall, all three seasons hold high counts of mesozooplankton as observed by Madhupratap et al. (2001).

Along the study transect, pre-monsoon, monsoon and post-monsoon revealed peculiar observation of low counts of mesozooplankton in the continental slope region than the shelf. This trend of mesozooplankton abundance seems to be influenced by phytoplankton biomass, as the shelf region is characterized by high chlorophyll concentration as observed during the present study. Similar observations that support the high mesozooplankton counts at near-shore stations were earlier reported by Nair et al. (1996), Rakhesh et al. (2006) and Jagadeeshan et al (2013). Conspicuously, areas with distinct bathymetry with steep incline or decline (seamouts and trenches) stand out with abruptly high abundance (Saltzman and Wishner, 1997), as observed at G9, which lie almost between the continental shelf and slope, however, marked as a station on the continental slope. Some researchers (Dower et al. 1992; Dower and Mackas 1996; Martin and Christiansen 2009) proposed that increased biomass in such sites are caused by modifications to the water current regime that cause a geographic resurgence. However, direct evidence on this aspect is not available and long-term studies would be needed to confirm such effect in the Arabian Sea.

In the oceanic realm of the eastern Arabian Sea, overwhelmed abundance of mesozooplankton seemed to be persistent (Fig. 2.5) by primary productivity caused by open ocean upwelling (Smith and Madhupratap 2005). Conversely, a lack of association between mesozooplankton and phytoplankton biomass is mostly attributable to herbivorous zooplankton grazing on phytoplankton (Gasparini and Castel 1999). Also, as Banse (1994) suggests, such a steady state of Chl *a* concentration despite regional differences in subsurface nutrient input, is achieved due to zooplankton grazing. Madhupratap et al. (1996a) reported that high zooplankton biomass in the Arabian Sea was sustained by microzooplankton and bacteria, during the low Chl *a* periods.

Mesozooplankton are known to be concentrated in the uppermost stratum in the oceanic station of high chlorophyll and primary production (Longhurst and Harrison, 1989; White et al. 1995; Fernandes 2008). The decline in mesozooplankton abundance below the thermocline was observed in the present study like in earlier studies (Vinogradov 1970, 1997; Banse, 1994; Wishner et al. 1998). It is interesting that the inter-monsoon seasons support high mesozooplankton biomass in open waters, especially in the upper layers, although the primary productivity generally is lower than in the Southwest or Northeast Monsoons. This and the fact that seasonal variations in zooplankton biomass are small in the upper layers of northern latitudes (Madhupratap et al. 1996b; Wishner et al. 1998) bring us back to the paradox of the Arabian Sea and the applicability of the microbial loop spatially and temporally (Madhupratap et al. 1996).

2.4.3 Distribution of copepods

Copepoda was the predominant taxon during the present study and contributed about 72–99 % to the total mesozooplankton abundance, similar to previous studies from the Arabian Sea (Padmavati et al. 1998; Wishner et al. 2008; Smith and Madhupratap 2005; Gauns et al. 2015), Bay of Bengal (Rakhesh et al. 2006; Fernandes et al. 2009; Fernandes and Ramaiah 2013) and the other part of the world ocean (Longhurst 1976; Weikert 1982; Mackas and Galbraith 2002; Lenz 2012; Mendes de Castro Melo et al. 2012). Copepods may be abundant due to their capability of detecting the hydrodynamic disturbances created by the approaching predators and of their escapes with high velocities (Verity and Smetacek 1996). These traits are facilitated by the sensory-armed antennae and their streamlined, muscular body (Kiorboe et al. 2010). These crustaceans are equipped with powerful mandibles edged with silica, which allow them not only to feed on diatoms but also on a variety of microzooplankton (Smetacek et al. 2004).

The copepod community composition showed spatial and seasonal variability over the study period. Compared to previous reports, Calanoida and Poecilostomatoida dominated the copepod orders (Deevey and Brooks1977; Madhupratap and Haridas 1990). The other copepod Orders present were Cyclopoida, Harpacticoida and Mormonilloida (Madhupratap et al. 2001a). The abundance and composition of individual order are further discussed below in detail.

Calanoida: Calanoida was the most overwhelming order of copepods (Fig. 2.6, 2.8, 2.12, 2.14 and 2.16) in the Arabian Sea (Madhupratap et al. 2001a; Wishner et al. 1998; Smith and Madhupratap 2005) and another marine habitat (Fernandes and Ramaiah 2014; Mazocchi et al. 2014). This order is more diverse and the species belonging to this order show selective in the habitat and feeding preferences (Timonin 1971).Results revealed 70 copepod species belonging to Calanoida (Table 2.2), all of which has been previously reported from the Indian waters (Madhupratap et al. 2001a; Smith and Madhupratap 2005; Gauns et al. 2015). It comprised of coastal and oceanic species, mostly of Indo-Pacific origin and a few of a cosmopolitan nature (Pillai et al 2014). Among calanoids, the families were mainly represented by Paracalanidae, Clausocalanidae, Centropagidae and Temoridae in terms of abundance. Previously, these families dominated the winter monsoon (Padmavati et al. 1998) even though known to persist throughout the year in the Arabian Sea (Madhupratap et al. 2001a; Jagadeesan et al. 2013). These families are known to dominate the waters of Red Sea (Cornis et al. 2007), Bay of Bengal (Fernandes 2008), Santos Bay (Miyashita et al. 2009) and Mediterranean Sea (Mazzocchi et al. 2014). In the oceanic station, dominant copepod families in the 0–200 m stratum includes Paracalanidae (Stephen and Kunjamma 1987; Madhupratap et al. 1990; Padmavati et al. 1998), Clausocalanidae (Fernandes 2009), Eucalanidae (Saltzman and Wishner, 1997; Smith and Madhupratap 2005), Euchaetidae (Madhupratap et al. 1990; 2001), Lucicutiidae (Wishner et al. 1998) and Metridinidae (Saraswathy 1986), which is consistent with the present study.

Overall, composition and patterns of dispersal of calanoid copepod species obtained in this study are analogous with the preceding studies from the Arabian Sea (Madhupratap and Haridas 1986; 1990; Madhupratap et al. 1996; Padmavati et al. 1998; Smith and Madhupratap 2005). Among calanoid, species of genera *Acrocalanus*, *Centropages*, *Paracalanus* and *Temora* were ubiquitous and distributed over larger areas (Padmavati et al. 1998).The species, *Temora turbinata* was assumed to be an opportunistic predator of phytoplankton and particulate matter (Paffenhoffer et al. 1988). Also, swarming of *T. turbinata* was observed from the west coast of India was positively related to the monsoon (Stephen and Iyer 1979).

Further, it is reported that the herbivores and omnivores calanoids coexist with their predatory counterpart in the study region. The coastal species herbivore *Subeucalanus* spp., omnivore *Centropages furcatus*, predatory *Labidocera pectinata* and predatory *Euchaeta wolfendeni* reported showing coexistence. Additionally, herbivore *Undinula vulgaris*, omnivore *T. discaudata* and carnivore *Labidocera acutifrons* were associated in shelf waters (Stephen and Iyer 1979). Coexistence of *Centropages calaninus*, *Temora turbinata*, *Rhincalanus nasutus*, *Centropages tenuiremis* and *Euchaeta concinna* is reported from the shelf water of Arabian Sea in monsoon (Stephen and Iyer 1979). The copepod species namely, *Acartia* spp., *Acrocalanus* gibber, Centropages *tenuiremis*, *Subeucalanus pileatus*, *Paracalanus* parvus, *Temora turbinata Oithona plumifera*, *Euterpina acutifrons*, *Microsetella* sp., *Oncaea* spp. and *Corycaeus* spp. were abundant at the continental shelf. A similar record of copepod species was observed by Madhupratap et al. (2001).

Likewise, filter-feeder *Cosmocalanus* spp. and predatory *Euchaeta* spp. showed coexistence in offshore habitat (Stephen and Iyer 1979). Concurrently, *Pleuromamma indica*, *Metridia* spp., *Euchaeta* spp., *Calocalanus* sp., *Acrocalanus* spp. *Oithona* spp., *Oncaea* spp. and *Farranula* spp. showed dominance at the continental shelf break and slope. This is consistent with the copepod species composition reported earlier by Padmavati et al. (1998) at the slope. Apparently, dominance of small-sized (< 2mm) copepods found in this study are known to be capable of exploiting the phytoplankton and microzooplankton (Stoecker and Capuzzo 1990; Roman and Gauzens 1997; Hopcropt et al. 1998). Also, they can switch their feeding habits by preying on microzooplankton in the period of low phytoplankton especially in the inter-monsoon. Further, during less productive inter-monsoons microbial loop would be important feed to sustain the high abundance of mesozooplankton (Madhupratap et al. 1996).

Predation by carnivorous plankton is known to structure the mesozooplankton community (Jagadeesan et al. 2013) as a negative relation between copepod abundance and carnivore plankton has been previously reported (Hansson et al. 2005). The carnivore copepods especially *Candacia* spp. and *Euchaeta* spp. were generally abundant towards the continental slope where the chlorophyll concentration is reportedly low (Naqvi et al. 2006), suitable locality for the sustenance of these organisms. The herbivores occurred in high densities in the shelf waters where food is copious (D’souza and Gauns, 2016). The copepods having herbivore feeding habits such as *Acrocalanus* spp., *T. turbinata* and *Paracalanus* spp. are eminent in the Arabian waters (Madhupratap and Haridas 1990;

Smith and Madhupratap 2005). Members of Calanidae family, *Canthocalanus pauper* and *Undinula vulgaris* are amongst the distinct residents that scrap-off autotrophs from the Arabian Sea (Madhupratap and Haridas 1990; Madhupratap et al 1999). However, their preponderance towards the continental slope confirms its ubiquity. Furthermore, these organisms are well-known to switch their feed preferences based on the feeding locale (El-Sabaawi et al. 2009), an add-on advantage to thrive in oceanic low productive waters. However, omnivorous copepods namely *Acartia* sp. and *Centropages* spp. showed no particular trend of dispersal and seem to be more adaptable to change in geography.

Poecilostomatoida: Poecilostomatoida are ubiquitous in coastal and offshore waters and the free-living forms appear to be carnivorous (Madhupratap 1999). Poecilostomatoida was overwhelmed by three families, namely Oncaeidae, Corycaeida and Sapphrinidae during the study (Fig. 2.6, 2.8, 2.12, 2.14 and 2.16). These families are known to be free-living and are common in the Arabian Sea (Madhupratap 1999; Bottger-Schnack 1998). In the oceanic station, dominant copepod families in the 0–200 m stratum includes Corycaeidae (Madhupratap et al. 2001a) and Oncaeidae (Bottger-Schnack 1994; Madhupratap et al. 2001a). They account up to 20% of the total copepods in continental shelf and 40–56 % in continental slope and oceanic waters. Up to 40 % contribution recorded in other marine environments (Paffenhofer 1993; Jagadeesan et al. 2013; Fernandes and Ramaiah 2014) like in Santos Bay (Miyashita et al. 2009) and in Brazilian waters (Lopes et al. 1999).

The peculiar observation of Poecilostomatoids as most overwhelmed copepod order in the continental shelf, slope and oceanic waters of study region probably signify the importance of using 200 µm as opposed to previously used 330 µm mesh size during IIOE. There is a possibility that even the 200 µm mesh size used during the present study may provide biased absolute numbers of these small copepods. Therefore, as a caution, use of smaller mesh size along with 200 µm for future studies from the Arabian Sea is recommended that will validate if there is any loss of this small zooplankton.

Presence of *Oncaea venusta* and *Corycaeus gibbulus* were common in samples from coastal, neritic and oceanic waters. These species are termed intermediate as their occurrence might be due to surface circulation and mixing of the waters across the continental realm. Many new species were overlooked earlier because of the larger mesh size usually employed to collect zooplankton and also due to the paucity of long-term monitoring on the continental margin. Bottger-Schnack (1998) found nearly 70 species from the family Oncaeidae alone from the Arabian Sea as compared to earlier listings of 4-5 species.

Cyclopoida: The order Cyclopoida was overwhelmed by the single-family Oithonidae with four species, namely *Oithona brevicornis*, *O. plumifera*, *O. spinirostris* and *Paraoithona rigida* were identified. Among, *O. brevicornis* and *O. plumifera* were the most abundant cyclopoids. Comparatively, this order revealed in the stable population on the continental shelf, slope and oceanic realm (Fig. 2.6, 2.8, 2.12, 2.14 and 2.16). This order is very common in estuarine waters as well (Madhupratap et al. 1996a; Vineetha et al. 2015). However, at continental slope and oceanic station they were among the principal contributor of copepod community. In the oceanic station, Oithonidae were among the dominant copepod families in the 0–200 m stratum (Madhupratap et al. 2001a). Copepods belonging to this order are generally considered as carnivores (Timonin 1971; Madhupratap et al. 1999).

Consistently, high abundance of *Oithona* spp. as expected was observed in our samples. Bigelow (1926) expressed *Oithona similis* as copious and ubiquitous copepod in the world. Additionally, Gallienne and Robins (2001) suggested that *Oithona* spp. have been traditionally under-sampled by employing large mesh sizes (>200 µm). According to Paffenhofer, cyclopoid success in marine environments relates to their relatively low feeding rates, reproduction, growth and mortality, which contribute to their population stability (Paffenhofer 1993). In Southwest Atlantic waters, they are a key food source for the larvae of the Brazilian sardine *Sardinella brasiliensis* (Kurtz and Matsuura, 2001).

Conspicuously, the high percent abundance of carnivore copepods dominated by Poecilostomatoida and Cyclopoida persists in the eastern Arabian Sea (Madhupratap and Haridas, 1986; 1990; Madhupratap et al. 1990; Padmavati et al. 1998; Smith and Madhupratap 2005). Moreover, it seems to be a general observation as Longhurst and Pauly (1987) scrutinized that the biomass of predators is almost double compared to herbivore and detrivores in the tropics than that of the polar region. However, it is important to point out a certain drawback in the present data and interpretations. Firstly, the mesh size (200 µm) employed for sampling could have restricted the collection of small-sized carnivores like poecilostomatoids and cyclopoids (Bottger-Schnack, 1996). Researchers have commented on losses of these smaller copepods with nets of mesh sizes 200-330 µm (Banse 1963; Vannucci 1968; Greene 1990; Turner 1994; Paffenhofer 1998). Secondly, in view of dwindling food supply, copepods might have undergone coprophagy instead of carnivorous feeding habit (Madhupratap et al. 2001a). Thirdly, depending upon the prey availability, most of the forms may prefer the omnivorous feeding habit. Moreover, the classification of trophic groups in the present study was based on the literature (Longhurst

1967; Timonin 1971; Longhurst and Williams 1979; Madhupratap and Haridas 1990) and may be debatable. However, for comparison of the data with previous studies (Padmavati et al. 1998; Madhupratap et al. 2001a; Smith and Madhupratap, 2005) same trophic classification was followed.

Harpacticoida: Members of this order are concentrated on the continental shelf as compared to the slope and oceanic realm (Fig. 2.6, 2.8, 2.12, 2.14 and 2.16). The species, *Euterpina* spp., *Macrosetella* spp., *Clytemnestra* spp. and *Microsetella* spp., were the common habitant in the coastal regions. The genus, *Metis* was found only in the continental shelf realm during pre-monsoon and post-monsoon. Harpacticoida is known to occupy diverse niches from interstitial (Karanovic and Cho 2016), subterranean (Cotarelli and Bruno 1993), deep-sea (Madhupratap et al. 2001a; Gollner et al. 2008) to hydrothermal vent (Conroy-Dalton and Huys 1999). Also, some species are pelagic and few parasitic (Stock 1991). In the Arabian Sea, their contribution to the copepod community is generally less (Madhupratap et al. 2001a). The species, *Macrosetella gracilis* was generally distributed throughout the water column as also reported earlier (Bottger-Schnack 1994; Weikert 1982). Overall, Haridas and Rao (1981) listed commonly occurring five genera in the epipelagic Arabian Sea viz. *Macrosetella*, *Microsetella*, *Miracia*, *Clytemnestra* and *Aegisthus*. Additionally, the genera *Longipedia*, *Euterpina*, *Metis* and *Distioculus* also occur in surface layers, whereas *Bathyidia* and *Tisbe* occupy the bathypelagic zone (Bottger-Schnak 1996).

Mormonilloida: The order, Mormonilloida contributed least to the total copepod community. Only two species, namely *Mormonilla phasma* and *Neomormonilla minor* occurred during this study. Also, these species were absent in continental shelf stations.

These copepods are fragile and cosmopolitan in meso-bathypelagic waters, especially of the Arabian Sea (Padmavati et al. 1998).These copepods may shift vertically upwards to avoid the anoxic layers (Bottger-Schnack 1996; Saltzman and Wishner 1997).The species, *Mormonilla minor*, the meso-bathypelagic particle feeder (Boxshall 1985) is known to occur in large numbers in the thermocline, seems to feed on the partially decomposed particles and reside at the upper boundary of oxycline (Smith and Madhupratap 2005). The females possess filter baskets formed by feeding appendages (Boxshall 1985) and adult male of *Mormonilla*, probably characterized by reduced feeding (Huys et al. 1992).

2.4.4 Habitat heterogeneity of copepod community

Bray–Curtis clustering on the basis of copepod dynamics grouped the stations, either by different bathymetric provinces or by the time of sample collections (months). The copepod showed a notable association between the stations with time and space due to a few remarkable species as identified by SIMPER test.

Distinct copepod species, particularly *Euterpina acutifrons* (Fig. 2.7C), *Centropages furcatus* (Fig. 2.7D), *Temora turbinata* (Fig. 2.7E) and *Pseudodiaptomus serricaudatus* (Fig. 2.7F) at G5 were responsible for clustering the months. Group I months (April’ 13, May’13 and October’13) typically showed the minor contribution of *Euterpina acutifrons*. Although it is a characteristic species of the continental shelf, it is most abundant during January (Rakesh et al. 2006). Group II was restricted to post-monsoon months (December’10 and October’11), where *Centropages furcatus* were abundant. Generally, this species show low abundance in coastal waters (Madhupratap et al. 1990). The major group formed was group III that was composed of pre-monsoon, monsoon and post-monsoon months. The group III months were favored by the euryhaline *Temora turbinata*.

This species has a greater tendency toward a coastal distribution and was more tolerant to water with lower salinities (Resgalla Jr. et al. 2008) and narrower temperature (25.0–26.3 ºC; Lopes et al. 1998; Resgalla Jr. et al. 2008; Dias and Boneckar 2009). This species is considered as invasive in the Brazilian waters (Lopes 2004). The other species that favored the group III was the copepods *Pseudodiaptomus serricaudatus* Herrick, 1884, that mostly occur in shallow, coastal, freshwater to hypersaline conditions (Soh et al. 2001; Walter et al. 2002; Nishida and Rumengan 2005).

The transect study revealed pre-monsoon to be very dynamic during the study period. The formation of clusters based on stations varied widely between February 2011 (Fig. 2.10) and May 2011 (Fig. 2.11). In February 2011, the co-existence of *Oithona* spp., *Acartia erythrea* and *Microsetella* spp. was responsible for the formation of three groups (fig. 2.10), which clustered together G5, G6 and G7 as a group I, G9 and G11 as group II and G13 as group III. During May 2011, the group I was composed of the G6, G11 and G13, where *Oncaea* spp. was abundant (fig. 2.11). Interestingly, group II was restricted to the G9, where *Pleuromamma indica* was conspicuously abundant. The group III was comprised of the G5 and G7, where an abundance of euryhaline species particularly, *Microsetella* spp. was abundant. In monsoon, the group I was composed of the continental slope (G13), where the dominance of *Pleuromamma indica* and absence of *Lucicutia flavicornis* was observed (Fig. 2.13). Moreover, the variable dominance of *Corycaeus* spp. and *Oithona* spp. accounted for clustering the groups II (G7 in June and September'12) and III (G5, G6, G9 and G11). During the post-monsoon, a group I was dominated by shelf stations and group III was dominated by slope stations, due to the abundance of *Acrocalanus* spp. and

Oncaea spp. Conspicuously, the group II was restricted to the continental slope (G11) by the absence of *Oithona* spp. and dominance of *Lucicutia flavicornis* (Fig. 2.15).

The continental shelf and slope stations were distinguished during pre-monsoon (February 2011) and monsoon because of the occurrence of *Oithona* spp. This genus is known to be abundant and ubiquitous in the marine habitat (Nishida 1985; Madhupratap and Haridas 1990; Fransz and González 1995; Nielsen and Sabatini 1996; Metz 1996; Atkinson 1998; Padmavati et al. 1998; Atkinson and Sinclair 2000; Gallienne and Robins 2001; Peterson and Keister 2000; Hansen et al. 2004; Hirst and Ward 2008; Fernandes and Ramaiah 2014). Lenience intolerance for temperature and salinity ranges by this genus would be a possible explanation for its cosmopolitan nature (Bigelow 1926; Nishida 1985). In addition, the egg-carrying *Oithona* lacks the danger of egg predation, sinking and advection (Hay et al. 1991) supporting it's high abundance. Comparatively, *Oithona* seems to exhibit stable population in time and space than the co-occurring copepods. This may be due to the specialized feeding behavior. Mostly, they show an omnivorous and/or detritivorous feeding (Petipa et al. 1970; Turner 1986; Paffenhofer 1993; Atkinson 1998; Kattner et al. 2003; Reigstad et al. 2005) but prefer motile prey (Uchima and Hirano 1986). They are known to feed on particles of the lower size spectrum, mainly small protozooplankton, this makes them an important link between microbial food webs and higher trophic levels (Nielsen and Sabatini 1996). During its whole lifespan, it plays a dual role of predator and prey (Uchima and Hirano 1986; Hirst and Ward 2008). The juveniles may be a major food source for fish larvae (Takahashi and Uchiyama 2007) and for many commercially important ichthyoplankton like cod, mackerel, seabream and hake (Young and Davis 1992; Sánchez-Velasco 1998; Reiss et al. 2005; Porri et al. 2007).

The Calanoida copepod, *Acartia erythraea* was dominant at the continental shelf stations and comprehended for the formation of a distinct cluster during February 2011. This species is euryhaline in nature (Padmavati and Goswami 1996) and the comparatively high temperature-salinity combination known to favor their abundance (Gonzalez, 1974; Cervetto et al. 1999). Similar to our observation, species of *Acartia* are recognized to occur abundantly during the warm season along the North Atlantic and European coasts (Conover, 1956; Lee and McAlice, 1979; Brylinski, 1981). On the contrary, these species were found in high numbers in the mid and outer Tampa Bay during the winter (Badylak and Phlips 2008) and is linked to the lack of seasonal patterns in phytoplankton (Badylak et al. 2007). A study from coastal waters of China suggests that these species prefer the dinoflagellates and the food size preference of ~10 µm (Sheng et al. 2010).

The *Microsetella* spp. seems to work synergistically with elevated temperatures during May 2011 in the continental shelf region. It is known to tolerate a wide temperature range of 9–27°C (Uye et al. 2002), and show a strong relation to DO and phytoplankton biomass (D'souza and Gauns 2018). Elevated *Pleuromamma indica* counts in oxygen-deficit waters during pre-monsoon and monsoon was comprehended for the distinct clusters. Also, the low DO (57.2 µm) at G9 in May 2011 seem to favor the dominance of *Pleuromamma indica*, as this species is known to thrive in a low oxygen milieu (Saraswathy, 1986; Saraswathy and Iyer 1986; Goswami et al. 1992). Further, niche partitioning on vertical ranges among congeneric species of *Pleuromamma* could be assigned to different migratory habits of the species (Roe 1974). This species is eminent for being endemic to the Indian Ocean, a tendency towards vertical migration and being tolerant to low oxygen waters (Goswami 1994; Padmavati et al 1998) despite stray doubtful records from the

Atlantic (Sewell 1948) and Pacific Oceans. This species is generally confined to the oxygen deficit waters of the northern Indian Ocean (both Arabian Sea and the Bay of Bengal) and rarely occurs in the south of 10°N (Goswami et al. 1992).

The clustering of continental slope stations during pre-monsoon and post-monsoon was due to the higher abundance of *Oncaea* species. This genus is ubiquitous and abundant in a marine milieu (Paffenhofer 1993; Gonzalez and Smetacek 1994; Madhupratap et al. 1999) probably due to its capability to exploit a wide range of feed. Specifically, *Oncaea* spp. has been contemplated to feed on marine snow, feces (Alldredge 1972; Gonzalez and Smetacek 1994) and mesozooplankton like chaetognaths and appendicularians (Go et al. 1998). Also, *Oncaea* spp. is considered to be an omnivore (Turner 1986) and detritivore (Yamaguchi et al. 2002). Therefore, the comparatively low chlorophyll slopes region's environment would be conducive for *Oncaea* spp. to proliferate abundantly.

Spatial and seasonal variability of *Lucicutia flavicornis* was noticeable on the continental slope. On one hand, its absence formed the distinct group during monsoon and on the other hand, its presence during post-monsoon apprehended for the observed distinction. Conspicuously, this species is habitant of the continental slope and oceanic waters. *Lucicutia* is considered to be an omnivore, feeding on detritus and gram-negative bacteria in low oxygen waters of the Arabian Sea (Gowing and Wishner 1998). Additionally, seasonal variation in the gut content of *Lucicutia* points toward the seasonal variability in prey composition of *Lucicutia* to be the crucial factor to influence its abundance (Gowing and Wishner 1998).

Corycaeus spp. possibly played a crucial role by segregating at the continental slope region during monsoon. This genus employs ambush filtering behavior and shows carnivory by feeding on ciliates and heterotrophic dinoflagellates (Turner 1984; Laundry et al. 1985; Chen et al. 2017). In addition, the general dominance of picoautotrophs (Ahmed et al. 2016) and depleted ciliates density (Gauns et al. 2000) in the Arabian Sea water during this period seem apparent due to copepod grazing (Pitta et al. 2001) overall, suggesting the importance of microbial loop in the region.

Acrocalanus spp. was abundant at continental shelf and slope during post-monsoon. Copepods of this genus thrive in tropical and sub-tropical waters (Araujo 2006) and its fine-particle filtering ability favor co-occurrence without competition in the surface layers (Fernandes and Ramaiah 2014). The experimental study revealed that juveniles of *Acrocalanus* feed on phytoplankton (Gusmao and Mckinnon 2009). In addition, adults and juveniles of *Acrocalanus* are known to feed on microzooplankton (Mckinnon 1996). Also, this species seems to utilize scarce trophic resources efficiently that could explain their successful proliferation in tropical waters (Gusmao and Mckinnon 2009).

At the oceanic station, ASTS, the seasons were grouped together with high level of homogeneity between depth and sampling time (Fig. 2.17). The dominance of *Pleuromamma robusta* and *Mormonilla phasma* formed a group with the mixed layer stratum sampled during the night. Strikingly, the absence of *Euchaeta concinna* during day formed another cluster and *Macrosetella* spp. accounted for the clubbing of the major group with the rest of the seasons. The co-occurrence of *Pleuromamma robusta* and *Mormonilla phasma*, which are tolerant to the oxygen-deficit, were noticed during post-monsoon (October 203) in the mixed layer depth (0–40 m) sampled at day time. Generally, their presence is extremely rare in the continental shelf, probably as a consequence of oxygenated waters. *Pleuromamma robusta* is well-known for its ability to carry out diel vertical migration (Saltzman and Wishner 1997). This species is reported to depict the *Pleuromamma indica* (Vinogradov and Voronina 1962) in terms of distribution pattern in the eastern tropical Pacific (Saltzman and Wishner 1997). Likewise, *Mormonilla* spp. is a mesopelagic genus (Boxshall 1986), thus appear in low numbers in the epipelagic waters of the Indian Ocean (Madhupratap and Haridas 1990). Similar to our observation, *Pleuromamma robusta* and *Mormonilla* spp., co-occurred in the eastern tropical Pacific seemed to be divided into groups, separated from the core of the depleted oxygen (Saltzman and Wishner 1997). These species probably concentrates at the surface water column for copious food.

The absence of carnivorous *Euchaeta concinna* during the day time sampling in monsoon (June 2012) is noteworthy. This species is habitant of the continental shelf, slope and oceanic realm of the Arabian Sea. The increased abundance of *Euchaeta* spp. away from the coast suggests that the populations in coastal waters are derived from offshore waters. A little knowledge about the seasonal and spatial distribution of *Euchaeta* spp. and their relationship with environmental factors is known. Also, a seasonal variation in abundance of *Euchaeta* spp. was reported from East China Sea (Xu 2006). This species is common in the coastal waters of eastern Hong Kong only during winter and spring (Wong et al. 2012). Also, the entire adult population of this species is reported to thrive in dark, deeper waters during the day, probably to minimize the risks of fish predation (Wong et al. 2012). Further, this species is known to be a nocturnal surface migrant, where they prey on *Acrocalanus*, *Paracalanus* and *Parvocalanus* (Wong et al. 2012). The conspicuous observation on

Euchaeta concinna in the oceanic waters of the Arabian Sea suggests its possibility of vertical migration.

The harpacticoid copepod *Macrosetella* spp. is found in pelagic habitats in open waters of the Arabian Sea (Madhupratap et al. 2001a), central North Pacific near Hawaii (Eberl and Carpenter 2007) and Red Sea (Bottger-Schnack and Schnack 1989). Also, this genus was confined to 0–200 m in the Arabian Sea (Madhupratap and Haridas 1990), however, occurs below 1000 m in the Red Sea (Bottger-Schnack 1994). This harpacticoid was absent during post-monsoon (October 2013) in the mixed layer depth (0–40 m) during the daytime. *Macrosetella* reported using colonies of the nitrogen-fixing cyanobacterium *Trichodesmium* spp. as a floating substrate and nursery (Eberl et al. 2007). This association enables the copepod to lead a pelagic existence. Here, in the present study region, the presence of *Trichodesmium* spp. is well-known during pre-monsoon. The cyanobacterium *Trichodesmium* spp. is capable of producing toxins (Cox et al. 2005). It has been shown that *Macrosetella* is resistant to these toxins to a certain extent (O’Neil et al. 1996).

2.4.5 Diversity of copepods

Copepod diversity, varied from the continental shelf (G5: H’: 1.90–3.71; Fig. 2.18), transect (G5, G6, G7, G9, G11 and G13: H’: 3.56–4.63; Fig. 2.19) and oceanic realm (ASTS: H’: 2.48–3.93; Fig. 2.20) of the Arabian Sea. In addition, seasonal variations of H’ were very well recorded during the study, accounting for the highest value (4.63) in pre-monsoon. Akin to earlier observations, copepod diversity in the warm surface waters was high (Deevey and Brooks 1977; Madhupratap and Haridas 1990). In a study from the eastern tropical Pacific Ocean, Longhurst (1985) suggested that a stable vertical structure of the water column might be one of the more important causes of variation in regional plankton diversity. On a contrary, McGowan and Walker (1979) laid emphasis on predation as the controlling factor for diversity.

Species richness was generally highest in the continental realm accounting for highest value (4.76) during post-monsoon. Evenness, a major component of diversity (Ortner et al. 1982), registered its highest value during pre-monsoon at the continental slope (0.95). Padmavati et al. (1998) and Angel (1993) attributed the high diversity to the stable structured environment. In the present study, the species richness was higher in the surface as compared to the deep stratum at the oceanic station.

In terms of copepod diversity, the Arabian Sea displays a range of species diversity indices. Nonetheless, the observed copepod diversity (H’: 1.90–4.63) in the present study were comparable to that of previous studies from the Arabian Sea (Padmavati et al. 1998) and Bay of Bengal (Fernandes 2008; Fernandes and Ramaiah 2013). The species richness values of the present study (<2.4) is comparable to a study from the subtropical Inland Sea of Japan (Madhupratap and Onbe 1986), however, evenness (<0.5) is lower than those observed during this study. Also, H' values reported from the Southeast China Sea (1.39 to 3.13; Shih and Chiu 1998) lies on a lower range as compared to the values of the present study. Further, the spatiotemporal alterations in water temperature, salinity and phytoplankton are reflected as the important factors for the changes in community structure and biodiversity (Davis 1987; Siokou-Frangou 1996). Researchers depicted that the numbers of species vary depending on the stability of the environment (Margalef 1958; Deevey, 1971). In this regard, the studied region seems to be a stable ecosystem.

Mesozooplankton provide an integrated picture of the regional features as it is mediatory between the higher trophic level and primary producers. In general, mesozooplankton was dominated by copepods in all three seasons across the continental shelf, slope and open waters of the eastern Arabian Sea. Collectively, calanoids dominated the copepod population with an utmost number of the genera and species. Communally, Poecilostomatoida and Cyclopoida contributed highly to the total copepod counts, while minor contribution came from Harpacticoida and Mormonilloida. Observations of the copepod community have revealed a strong coupling between the stations and copepod species. The phytophagus genera, *Acrocalanus gibber*, *Paracalanus parvus* and *Temora turbinata* were abundant at the shelf stations. Conversely, carnivorous genera, *Euchaeta concinna*, *Oncaea vensuta* and *Oithona plumifera* were abundant at the slope stations. This clear discrepancy seemed to be exhibited in response to the relative contributions of the euryhaline species that detained for the continental shelf (*Microsetella* spp. and *Temora turbinata*), slope (*Oithona* sp., *Oncaea* sp., *Lucicutia flavicornis* and *Pleuromamma indica*) and open-ocean (*Pleuromamma robusta* and *Mormonilla phasma*). Distinctly, high species richness and diversity of copepods was noteworthy of the study region. However, monitoring the mesozooplankton assemblages more frequently will ascertain whether the recorded observation is transitory or is a regular feature in this region. Apparently, the elevated abundance and diversity of copepods seem to be an indicator of potential fisheries resources in this region.

Chapter 3

GENDER AND SPECIES-WISE INFLUENCE ON $\delta^{13}C$ AND $\delta^{15}N$ ISOTOPES OF COPEPODS IN THE ARABIAN SEA

3.1 INTRODUCTION

The diversity of copepod community in the continental margin and oceanic waters of the Arabian Sea is profound (Padmavati et al. 1998). They are significant members of marine ecosystems and have accomplished features for exploiting a wide array of diets (Kleppel 1993). This dietary flexibility of copepods can equilibrate the energy flow in aquatic ecosystems (Sprules and Bowerman 1988). Substantial effort has gone in understanding copepod diets and their trophic position in the ocean (Graeve et al. 1994; Stevens et al. 2004; El-Sabaawi et al. 2009; Kurten et al. 2016). However, data from the Arabian Sea on copepod feeding habit are scarce (Goes et al. 1999; D'souza and Gauns 2016) and were not based on stable isotope technique. Stable isotope technique is advantageous in studying the feeding mechanism of the copepods as it accounts the assimilated food integrated over a time period (Fry 1988; Post 2002). Use of this technique in studying feeding ecology of copepods has become quite familiar (Minagawa and Wada 1984; Fry 1988; Post 2002; Fry 2006; El-Sabaawi et al. 2009). Combination of carbon and nitrogen stable isotope ratio is commonly used in ecological studies as tracers of trophodynamics (Fry 2006). Isotopic signatures of food-webs vary spatially based on change in prey to predator during chemical reactions of metabolic processes due to different reacting rates of isotopes (Peterson and Fry 1987). The signature of stable isotope ratio of nitrogen($\delta^{15}N$) in organisms, for instance, is characteristically enriched by 3–4 ‰ compared to $\delta^{15}N$ value of their prey, thereby acting as a measure of trophic position (Miyake and Wada 1967; Minagawa and Wada 1984; Owens 1987).Similarly, the prey sources typically have discrete stable isotope ratio of carbon($\delta^{13}C$) that is integrated into the consumers tissues with slight alteration nearly1‰ (DeNiro and Epstein 1978; 1981; Peterson and Fry 1987; Michener and Schell 1994; El-Sabaawi et al. 2009). Thus by using this technique it is possible to detect the carbon source of the predator. That is, the different reacting rates result in the accumulation of the heavier isotope in the consumer, due to a preferential loss of lighter isotopes during respiration and excretion, and lead to a stepwise enrichment between prey and consumer tissue, termed trophic fractionation. Trophic fractionation occurs in a predictable way for the different elements and can be used to evaluate carbon sources and trophic position of an organism (Peterson and Fry 1987; Zanden and Rasmussen 2001; Post 2002). On the other hand, the physiology of the organism has strong impact on the isotopic composition regardless of its trophic position or dietary history. The lipids component of the organism embrace light isotopic carbon than other tissues due to the enzymes involved in lipid synthesis that fractionate in favor of lighter isotopes (De Niro and Epstein 1978; Post et al. 2007). Therefore, samples with variable lipid content can display differences in $\delta^{13}C$ that are unrelated to feeding history. This is especially true for high latitude copepods, which often store large lipid reserves (Sato et al. 2002). To date, there is no consensus on whether stable isotope samples should be corrected for lipid content (Post et al. 2007).

Normally, niche differences promote species coexistence in nature (Schoener 1974; Narwani et al. 2013; Carroll and Nisbet 2015) by the partitioning of resources such as food and space (Schoener 1974). A broad classification of copepod orders and species demonstrate differences among specific traits such as feeding habit and niche selection. Nonetheless, many species demonstrate differences between the sexes with regards to body size, morphological traits, feeding or micro–habitat utilization (Shine 1989; Van Kleunen et al. 2010; Fryxell et al. 2015; Dalu et al. 2017). Globally, sex ratios have been observed to be biased towards females (Arendt et al. 2014; Fryxell et al. 2015; Vineetha et al. 2015). With regard to the feeding of copepod order, species or sex–specific differences, consumer foraging is shifting in relation to individual physiological state or basal food resource availability (Resh et al. 1988; Dalu et al. 2017). Thus, the dominant copepod species were considered for the feeding habit studies to get a clear picture of the species-species difference in the copepod feeding habit in the study region. Specific feeding studies on different copepod genders of dominant species were carried out to understand segregation in their feeding habits. To date, the diets of calanoid copepod species namely *Centropages* spp., *Subeucalanus pileatus*, *Pleuromamma indica*, *Euchaeta concinna*, *Acartia erythraea* and *Temora turbinata* that are abundantly found in the Arabian Sea are not characterized, and little is known about their seasonal variability in their diets in the Arabian Sea. The present study describes seasonal variability in the diet of these dominant copepods diet using stable isotope δ^{13}C and δ^{15}N values.

3.2 METHODOLOGY

Mesozooplankton samples were collected using the net with 200 µm zooplankton net from the continental shelf, slope and Open Ocean (Fig. 1.2) and stored in the ice box, details are mentioned in chapter 2. In a laboratory, samples were frozen at −20ºCuntil analysis. The study area is described in chapter1.Details on mesozooplankton collections for stable isotope analyses are provided in table 3.1.

3.2.1 Copepod taxonomy and sorting

The copepod samples collected in 500 mL plastic bottles were brought back to the laboratory for detailed analysis. Samples were split into four parts using Folsom splitter (Goswami 2004). The first sub-samples of mesozooplankton were preserved in buffered formalin and remaining two sub-samples were frozen at −20ºC.The frozen samples were thawed and washed thoroughly with filtered seawater for further investigation. Stable isotope analyses were carried out following the protocol outlined in Smyntek et al. (2007). Copepods were then sorted at gender and species level using a stereo microscope under minimum light (Williams et al. 2014). Around 30–60 adult copepods were sorted and were oven dried at 60ºC for 48 hrs.

3.2.2 Analytical method on copepods for isotope ratio mass spectrometry(IRMS)

Elemental and isotopic measurements were made from the dried copepods(0.5mg), packed tightly in tin cups (size 12.5×4.25mm) for analysis. The stable isotope ratios of carbon and nitrogen were quantified using a Thermo Finnigan DELTA V Plus isotope ratio mass spectrometer in continuous-flow mode after high-temperature flash combustion in an EURO3000 Eurovector elemental analyzer. The packed samples were combusted at 1050ºC and the resultant products were passed in a constantly flowing stream of 5.5-grade dry helium (He) at a rate of 100 ml min^{-1}. The evolved gases then travel through a reduction column packed with copper wires at 680ºC. The reduced products (CO_2, N_2 and H_2O) were dehydrated by a magnesium perchlorate trap before being separated by a gas chromatography column at 50ºC. Finally, the He stream containing these gases is led via a Conflow III interface into the open split of the DeltaIRMS. The $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios are estimated simultaneously from the same sample. The isotopic ratios are expressed in per mil notation, $\delta^{15}N$ or $\delta^{13}C$ (‰) = $[(R_{sample}/R_{standard}) - 1] \times 1000$ where, R = $^{15}N/^{14}N$ or $^{13}C/^{12}C$ and atmospheric N_2 and Pee Dee Belemnite (PDB) were the standards used.

A working standard, "ε-Amino-n-Caproic Acid" (ACA), was run after every 5 samples. The ACA values recorded for ^{15}N and ^{13}C are 4.6 ‰ and −25.3 ‰, respectively and standard deviation for both ^{15}N and ^{13}C was less than 0.2 ‰ (for n=10 samples) (Karapurkar et al. 2008). Carbon and nitrogen contents in the samples were calculated from a calibration curve made of ACA standards ranging from 1 to 4 µM for nitrogen and 6 to 24µM for carbon. The precision of the elemental analyzer was ±0.1 µg and the C/N ratios were calculated as atomic ratios.

3.2.3 Statistical analysis

Variability in δ^{13}C and δ^{15}N at continental shelf was compared within the *Subeucalanus* gender and season was tested using factorial analysis of variance (ANOVA). Similarly, factorial ANOVA was used to study the variation in δ^{13}C and δ^{15}N within the copepod genders at continental shelf, slope and open waters. The analysis of variance was followed by a post hoc Tukey HSD test. Prior to analysis, all data were square-root transformed. Values were considered significant at 95 % level of confidence (Statastica 6.0, Statsoft, OK, USA). After square root transformation, non-multidimensional scaling (nMDS) and Bray–Curtis cluster were assembled based on the isotopic composition of copepod order collected from continental shelf region (PRIMER 6).

3.3 RESULTS

Acartia spp., *Euchaeta* spp., *Labidocera* spp., *Lucicutia* spp., *Subeucalanus* spp., *Temora* spp., *Pleuromamma* spp. and *Undinulla* spp. were the dominant calanoid copepods, while, *Oithona* spp., *Euterpina* spp., *Microsetella* spp., *Macrosetella* spp. and *Oncaea* spp. were the dominant non-calanoids found in the study area. The detailed study on abundance of copepod species is elucidated in chapter 2. The feeding habit of *Subeucalanus* spp. at gender-level and *Acartia* spp. and *Temora* spp. at genera-level were investigated at the continental shelf. In continental slope waters, δ^{13}C and δ^{15}Nin *Subeucalanus* spp.(gender-wise), *Euchaeta* spp. (gender-wise), *Lucicutia* spp.(genera-wise), *Oithona* spp.(genera-wise), *Euterpina* spp. (genera-wise), *Undinulla* spp.(genera-wise) and *Labidocera* spp. (genera-wise) were studied. In open waters, *Subeucalanus* spp., *Pleuromamma* spp. and *Euchaeta* spp. was studied at gender level and *Oithona* spp., *Macrosetella* spp. and *Oncaea* spp. at genera level for the $\delta^{13}C$ and $\delta^{15}N$.

3.3.1 Feeding appendages

Distinctive morphological feature of the second maxillae of *Subeucalanus pileatus*, *Euchaeta concinna*, *Pleuromamma indica*, *Acartia erythrea* and *Temora turbinata* are demonstrated in plate 3.1.The development of thickened spine-like and dagger-like setae on the distal ends and medial lobes of feeding appendages in *Euchaeta concinna* can be interpreted as adaptations for grasping prey indicating carnivory (plate 3.1).All other species had feeding appendages with fine plumose setae; among these the setae in *Acartia erythrea* were relatively fine (plate 3.1).

3.3.2 Copepod sex ratio

A detailed study of the sex ratio in *Subeucalanus* spp. (continental shelf, slope and open waters), *Pleuromamma* spp. (open waters) and *Euchaeta* spp. (continental slope and open waters) was carried out to understand whether gender-specific variations had any influential role in the feeding preference of these species in the different habitats of the Arabian Sea. Overall, the sex ratio (male: female) varied between 0 and1.5. Moreover, the sex ratio and abundance pattern in *Subeucalanus* spp., *Euchaeta* spp. and *Pleuromamma* spp. was biased towards females (Table 3.2). In all the seasons, females outnumbered the males in continental shelf, slope and open waters of the Arabian Sea. However, *Euchaeta* *concinna* revealed exception during monsoon (at ASTS) and post-monsoon (at G11), where males outnumbered the females. The micrographs of male and females of *Subeucalanus* sp., *Pleuromamma* spp. and *Euchaeta* spp. are presented in plate 3.2.

3.3.3 Stable isotopes (δ^{13}C and δ^{15}N)in copepod genders

Both, δ^{13}C and δ^{15}N showed consistent pattern of high enrichment in males as compared to their female counterparts. On one hand, large gradients of δ^{13}C transpired atcontinental shelf and open ocean station, while isotope values at continental slope stations did not differ much. On the other hand, large gradient of δ^{15}N occurred in open waters as compared to shelf and least variation was observed at continental slope stations.

Continental shelf: Overall, distribution of δ^{13}C and δ^{15}N showed variations among the genders of *Subeucalanus* spp. at continental shelf realm (Fig.3.1). The common trend of enriched values in the male of *Subeucalanus* spp. was consistent as compared to females.

During pre-monsoon, δ^{13}C and δ^{15}N content in *Subeucalanus pileatus* showedsegregation between males and females (Fig. 3.1 A and B). Particularly, δ^{13}C fluctuated on a minor scale between −19.70 and −18.22 ‰ with the depleted value in February 2013 and enriched during March 2012. In contrast, the δ^{15}N values that varied between 7.80and 10.10 ‰ showed low and high values during March 2012 and February 2013, respectively. Additionally, the C/N ratio (Fig.3.1 C) fluctuated between 4.20 and 5.84 with low value observed in males and high in females during March 2012 and February 2013, respectively. Similar to δ^{13}C, the carbon content of copepods was high in March 2012 (22.32 µM) and low (2.09 µM) in February 2013. Overall, an inter-annual and gender variation in carbon content was conspicuous. However, the nitrogen content varied over a narrow range 0.35–5.30 µM with lowest value observed in February (2013) and highest in March. (2012).

Comparatively, the δ^{13}C and δ^{15}N showed wider range variations among the *Subeucalanus* spp. during monsoon (Fig.3.1 A and B). Also, slight enrichment in δ^{13}C (−20.27 to −18.14 ‰) as compared to pre-monsoon was observed. Amongst the studied months, the depleted value of δ^{13}C occurred during September (2011) and enriched in July (2013). The δ^{15}N in copepods gender varied on the narrow scale (7.34–9.27 ‰) and was depleted in this season as compared to pre-monsoon. Moreover, like δ^{13}C the low and high values were observed in September (2011) and July (2013), respectively. The C/N ratio (4.63 to 5.14) for monsoon was consistent with pre-monsoon; however, both low and high value croppedup in females during July 2013 and September 2011, respectively (Fig.3.1 C). The carbon content ranged widely from 10.06 to 24.59 µM of copepod weight. The higher values of carbon were observed in females (in July 2013) and low in males (in September 2011). The high nitrogen content in copepods during this season was striking; the lowest value (2.16µM) in males and highest value (5.25 µM) in females were observed during September 2011.

The monsoonal treat with respect to changes in phytoplankton and surrounding nutrients levels was visible in the distribution of δ^{13}C and δ^{15}N of *Subeucalanus* spp. during post-monsoon (Fig.3.1 A and B). Distinctly, the δ^{13}C values were more enriched (−19.97 to −17.18 ‰) than pre-monsoon and monsoon. However, the minimum (in November 2012) and the maximum value (in October 2013) were observed in female counterparts. Contradictory to δ^{13}C, the δ^{15}N value revealed low enrichment in post-monsoon specifically during November 2012 (4.91 ‰). The C/N ratio (5.26–7.66) was comparatively higher than that of pre-monsoon and monsoon (Fig.3.1C). Both, the low C/N value in January 2013 and high during December 2012was observed in female

Subeucalanus. A linear relation between δ^{13}C and δ^{15}N revealed poor correlation (r^2 = <0.01) for copepod genders at the continental shelf (Fig.3.1 D). The carbon content of *Subeucalanus* ranged from 4.23 to 10.34 µM with higher values observed in December (2012) and low in January (2013). Similar to pre-monsoon, low nitrogen content was consistent during this period. The lowest value (0.59µM) was recorded during November 2012 and highest (1.80 µM) in October (2013).

Bray–Curtis cluster analysis on stable isotopes of *Subeucalanus* spp. males and females clubbed the sampling months into two groups (fig. 3.2 A). Particularly, March'12, July'13, September'11, December'12 and February'13 clustered together to form the group I with 98 % similarity. Distinctly, the post-monsoon months, November'12, January'13 and October'13 clustered at 93 % similarity forming group II. The results of nMDS revealed a similar pattern of clustering of months (fig. 3.2 B) and the plots for δ^{13}C and δ^{15}N of *Subeucalanus* sp. females (fig. 3.2 C and E) and males (fig. 3.2 D and F) perceived similar distribution pattern.

Continental Slope: The δ^{13}C and δ^{15}N of*Subeucalanus* spp. and *Euchaeta* spp. did not differ considerably (table 3.3). Theδ^{13}C ranged between −21.16 and −20.01 ‰, and δ^{15}N from 6.56 to 8.96 ‰ in these species, respectively. The carbon content of copepods ranged from 8.23 to 17.17 µM. Interestingly, high nitrogen content (1.82–4.06 µM) was observed in *Subeucalanus* spp. and *Euchaeta* spp. from slope realm. However, C/N ratio (4.23–5.53) was consistent with copepods from shelf waters. Also, there was no significant correlation (r^2 = 0.09) observed between δ^{13}C and δ^{15}N of copepod genders (Fig.3.3).

Open Ocean: The males and females of copepod species belonging to genus *Euchaeta*, *Pleuromamma* and *Subeucalanus* sampled from oceanic realm were studied for their feeding habits. Collectively, $\delta^{13}C$ ranged between −22.19 and −19.52 ‰ (Fig. 3.4B); the depleted value was observed in *Euchaeta* females (September 2011) and enriched in *Subeucalanus* males (September 2012). The $\delta^{15}N$ varied from 5.82 to 10.47 ‰ (Fig. 3.4A), where the depleted value was observed in omnivorous *Pleuromamma* males and enriched values in *Euchaeta* males during September 2012 and 2011, respectively. Amongst the copepods considered, *Euchaeta concinna* males displayed the most carnivorous signature. Conspicuously, C/N ratio revealed species-wise variability, which was of comparatively broad range (4.86–7.06) (Fig.3.4C). The low value was recorded in *Pleuromamma* females (September 2012) and high value in *Euchaeta* males (September 2011). The carbon content showed a variation on a wide range of 2.24 to 19.06 μM and nitrogen content varied over a narrow range of 0.43–3.62 μM. The lowest value of carbon and nitrogen were observed in females of *Pleuromamma* spp. (September 2012) and highest in females of *Euchaeta* spp. (September 2012). A poor positive correlation ($r^2 = 0.15$) was observed between $\delta^{13}C$ and $\delta^{15}N$ for copepod genders in oceanic waters (Fig.3.4D).

3.3.4 Stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) in copepod species

Continental Shelf: In pre-monsoon, $\delta^{13}C$ values in *Acartia* spp. and *Temora* spp. varied in the range of −20.24 to −18.10 ‰. Low enrichment in $\delta^{15}N$ (5.69–8.20 ‰) prevailed for these species on the shelf during this season. Amongst both these copepods, the depleted value was observed in *Acartia* spp. (February 2012) and enriched value in *Temora* spp. (May 2013). The C/N ratio varied on the narrow range(4.08–5.13) with low values recorded in *Temora* spp. and high value observed in *Acartia* spp. during May 2013 and February 2012, respectively (Fig.3.5). Comparatively, *Acartia* spp. was comprised of low carbon (1.46 μM) and nitrogen content (0.28 μM) during pre-monsoon.

The calanoid, *Temora* spp. was not dominant member of copepod community during monsoon. Thus, only *Acartia* spp. was speculated for isotopic study. In monsoon, feeding ecology of *Acartia* spp. possibly changed resulting in enriched $\delta^{13}C$ (−18.25 to −17.61 ‰) and $\delta^{15}N$ (7.95 to 9.70 ‰). The enriched value was observed in July (2013) and low during August (2013). From the literature, it is known that monsoon show dominance of diatoms in phytoplankton community of eastern Arabian Sea. The change in prey composition isotopically different from pre-monsoon was very well reflected in the isotopic composition of copepods. The C/N ratio (4.12 to 4.48) showed the lowest range of variation with low value observed in July (2013) and high in August (2013). Amongst the copepod species dwelling at continental shelf, highest carbon content (7.58 μM) was recorded during monsoon in Acartia spp. Comparatively, high nitrogen content (1.34 to 1.82 μM) was recorded in *Acartia* during monsoon. The lowest and highest values were observed during August and July (2013), respectively.

Seasonal variability in the feeding of *Acartia* spp. and *Temora* spp. was prominent during post-monsoon. Moreover, the distribution of $\delta^{13}C$ and $\delta^{15}N$ showed inter-annual variations among the copepod species (Fig. 3.5A and B). The common trend of enriched $\delta^{13}C$ of copepods in post-monsoon was consistent. Both, the enriched $\delta^{13}C$ (−16.59 ‰) and depleted value (−21.14‰) was observed in *Temora* spp. during November 2011 and October 2012, respectively. This observation implies that multiple carbon source was utilized by *Temora* spp. in post-monsoon of 2011 and 2012. Concurrently, the $\delta^{15}N$ (6.12 to 9.10 ‰) was less enriched as compared to monsoon. The low and high values of $\delta^{15}N$ were observed in *Temora* spp. during October 2012 and November 2011, respectively demonstrating inter-annual variability. Such enrichment pattern of $\delta^{15}N$ may imply that the genus *Temora* is capable of switching its prey dependent on the availability of autotrophic prey. The low value of C/N ratio was observed in *Acartia* spp. (4.94) and high in *Temora* spp. (5.74) during January 2013 and December 2012, respectively (Fig. 3.5C). *Temora* spp. attained high carbon content (5.10 μM) in during December (2012) and *Acartia* spp. attained low (2.59 μM) during November (2011). Interestingly, *Acartia* spp. achieved lowest (0.48 μM) and highest value (0.96 μM) of nitrogen content during December 2012 and November 2011, respectively. No significant correlation (r^2 = 0.39) was observed between $\delta^{13}C$ and $\delta^{15}N$ of copepod species from shelf waters (Fig. 3.5 D).

Bray Curtis similarity and nMDS analysis on stable isotopic values of *Acartia* spp. and *Temora* spp. clubbed the sampling months into two groups at 65 % similarity (Fig. 3.6A and B). Post-monsoon 2012 (October'12 and November'12) months formed a group at 98 % similarity based on the dominance of isotopic content of *Temora* spp. (Fig. 3.6D and F). While, the major group clubbed the months, December'12, May'13, March'12, February'12, August'13, January'13 and July'13 at 93 % similarity based on the dominance of isotopic content in *Acartia* spp. (Fig. 3.6C and E).

Continental Slope: Consistently, the $\delta^{13}C$–copepod values from continental slope waters reveal depleted values as compared to their shelf counterpart. The $\delta^{13}C$ of *Candacia* spp., *Lucicutia* spp., *Labidocera* spp., *Undinulla* spp., *Euterpina* spp. and *Oithona* spp. showed a narrow range of variation (−21.96 to −20.33 ‰). Amongst, less enriched values of $\delta^{13}C$ were observed in *Lucicutia* spp. and more enriched in *Undinulla* spp. (Table 3.4). Conspicuously, least enrichment of $\delta^{15}N$ was observed in *Euterpina* spp. (0.96 ‰) and high in *Undinulla* spp. (8.36 ‰). A poor correlation (r^2 = 0.03) between $\delta^{13}C$ and $\delta^{15}N$ of copepod species was consistent in continental slope waters (Fig.3.7). A regular pattern of a narrow range of variation in C/N ratio apprehended for low value in *Lucicutia* spp. (4.09) and high in *Labidocera* spp. (5.45). Consistently, high nitrogen content in copepods of slope realm was recorded. Likewise, species-wise variations were observed in carbon and nitrogen content in copepods. In particular, low values of carbon and nitrogen contents were observed in *Oithona* spp. (5.10 μM) and *Labidocera* spp. (1.08 μM), respectively. On the other hand, high values of carbon (15.87 μM) and nitrogen content (3.01 μM) were observed in the calanoid, *Undinulla* spp. Commonly, no significant correlation ($r^2 = 0.028$) between $\delta^{13}C$ and $\delta^{15}N$ of copepod species from slope waters was observed (Fig. 3.7).

Open oceanic realm: The $\delta^{13}C$ and $\delta^{15}N$ in *Macrosetella* spp., *Oithona* spp. and *Oncaea* spp. were studied from the oceanic realm. The most depleted $\delta^{13}C$ values occurred in copepods of oceanic waters. Precisely, the $\delta^{13}C$ in these copepods species ranged from −24.36 to −21.46 ‰ (Table 3.5) with depleted traces in *Macrosetella* spp. and enriched in *Oncaea* spp. (2012). The $\delta^{15}N$ of copepods varied from 2.31 (*Oithona* spp.) to 7.22 ‰ (*Oncaea* spp. in 2011). Comparatively, positive correlation ($r^2 = 0.49$) between $\delta^{13}C$ and $\delta^{15}N$ was observed for copepods in oceanic waters (Fig. 3.8). The C/N ratio (4.98–5.91) was consistent with high ratio recorded in *Oncaea* spp. (2011) and low in *Oithona* spp. (2011). Typically, low carbon (0.83μM) and nitrogen content (0.16μM)occurred in *Macrosetella* spp. while, higher range of carbon (21.63 μM) and nitrogen (3.66 μM) was recorded in *Oncaea* spp.

Table 3.1 Sampling records of copepods for stable isotope analyses in the Arabian Sea

Location	Station	Sampling month	Represented as	Sampling time
Continental Shelf	G5	September'11	Sept'11	Day
	G5	November'11	Nov'11	Day
	G5	March'12	Mar'12	Day
	G5	August'12	Aug'12	Day
	G5	October'12	Oct'12	Day
	G5	November'12	Nov'12	Day
	G5	December'12	Dec'12	Day
	G5	January'13	Jan'13	Day
	G5	February'13	Feb'13	Day
	G5	April'13	Apr'13	Day
	G5	May'13	May'13	Day
	G5	July'13	Jul'13	Day
	G5	August'13	Aug'13	Day
Continental Slope	G13	May'11	Pre-monsoon 2011	Day
	G11	Jan'12	Post-monsoon 2012	Day
	G7	Feb'13	Pre-monsoon 2013	Day
	G9	Feb'13	Pre-monsoon 2013	Day
	G7	Oct'13	Post-monsoon2013	Day
	G8	Oct'13	Post-monsoon2013	Day
Open Ocean	ASTS	Sept'11 (0–50 m)	Sept'11_a	Day
		June'12 (0–20 m)	June'12_a1	Day
		Sept'12 (0–40 m)	Sept'12_a1	Day
		Sept'12 (40–140 m)	Sept'12_a2	Day
		Sept'12 (0–40 m)	Sept'12_b1	Night
		Feb'13 (0–200 m)	Feb'13	Day

Table 3.2 Male: female sex ratio of copepods in the Arabian Sea

Location	Station	Sampling month	Copepods	Male: female ratio
Continental Shelf	G5	Mar'12	*Subeucalanus* spp.	0
		Dec'12	*Subeucalanus* spp.	0.17
		Feb'13	*Subeucalanus* spp.	0.23
		Jul'13	*Subeucalanus* spp.	0.5
Continental slope	G13	Pre-monsoon 2011	*Subeucalanus* spp.	0.83
	G11	Post-monsoon2012	*Euchaetaconcinna*	1.33
Open Ocean	ASTS	June'12_a1	*Euchaeta concinna*	0.25
		Sept'12_a1	*Euchaeta concinna*	1.5
			Pleuromamma indica	0.2
			Subeucalanus spp.	0.64
		Feb'13	*Euchaetaconcinna*	0

Table 3.3 The variation of δ^{13}C and δ^{15}N in copepods genders at the continental slope

Season	Station	Gender	δ^{13}C (‰)	δ^{15}N (‰)	C (uM)	N (uM)	C/N
Pre-monsoon'11	G11	*Euchaeta_F*	-20.92	7.55	13.14	3.06	4.30
	G11	*Subeucalanus*_F	-21.13	6.56	8.23	1.82	4.51
	G13	*Subeucalanus*_F	-20.57	7.59	17.17	4.06	4.23
	G13	*Subeucalanus*_M	-21.26	8.96	15.02	3.18	4.72
Post-monsoon'12	G11	*Euchaeta_F*	-21.24	7.95	13.84	2.26	6.13
	G11	*Euchaeta*_M	-20.01	8.71	13.06	2.36	5.53

Where, F: female and M: male.

Table 3.4 The variations of $\delta^{13}C$ and $\delta^{15}N$ in copepod species along the continental slope

Season	Station	Species	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C (uM)	N (uM)	C/N
Pre-monsoon'11	G13	*Lucicutia* spp.	-21.96	5.91	6.72	1.65	4.09
	G13	*Oithona* spp.	-21.47	5.34	5.10	1.17	4.37
	G13	*Euterpina* spp.	-20.76	0.96	7.28	1.34	5.42
Post-monsoon'12	G11	*Undinulla* spp.	-20.33	8.36	15.87	3.01	5.28
	G11	*Labidocera* spp.	-20.88	7.18	5.86	1.08	5.45

Table 3.5 The variation of $\delta^{13}C$ and $\delta^{15}N$ in copepods species at the open ocean station (ASTS)

Season		$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C (uM)	N (uM)	C/N
Sept'11_a	*Macrosetella* spp.	-24.36	3.45	0.83	0.16	5.18
	Oithona spp.	-23.40	2.31	0.86	0.17	4.98
	Oncaea spp.	-22.40	7.22	21.63	3.66	5.91
June'12_a1	*Oncaea* spp.	-21.46	5.80	9.76	1.76	5.54

Where Sept'11_a: September 2011 (0-50 m); June'12_a1: June 2011 (0-20 m)

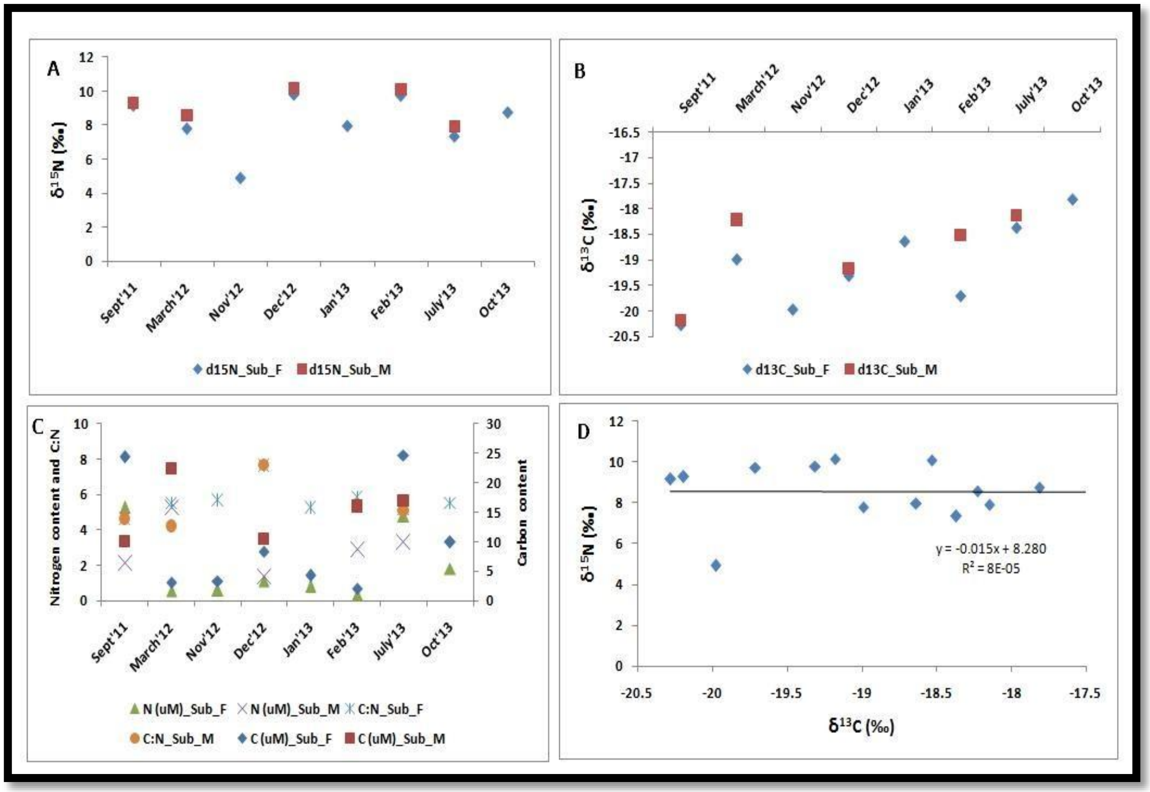


Fig. 3.1 Monthly variation of (A) δ^{15}N (B) δ^{13}C (C) elemental carbon and nitrogen (D) correlation between δ^{13}C and δ^{15}N in the males and females of *Subeucalanus* sp. at continental shelf (G5). (The legends shows *Sub_F-Subeucalanus* female; *Sub_M-Subeucalanus* male)

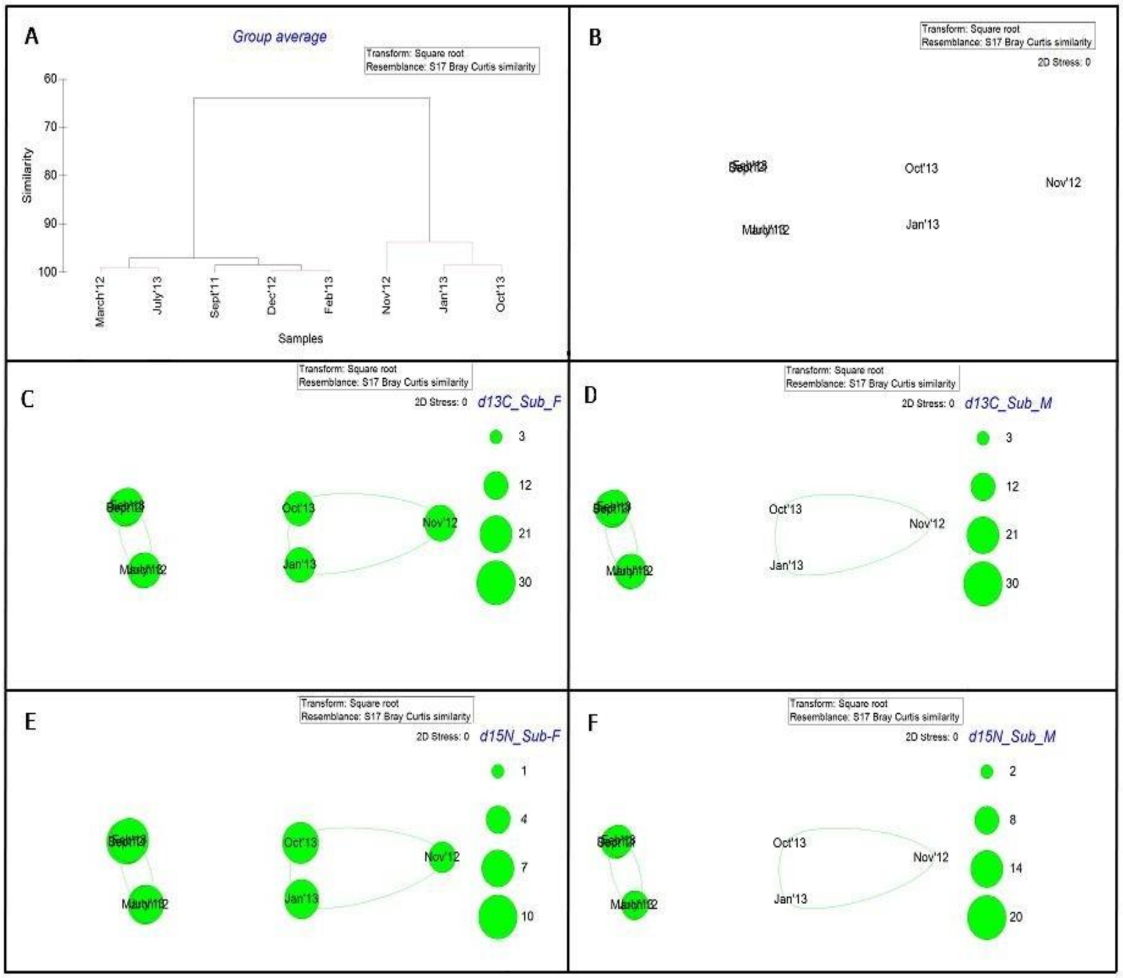


Fig. 3.2 Bray–Curtis similarity (A) based on clustering of months manifested through dendrogram and nMDS plot (B) based on copepod isotopic contents. Bubble plot of isotopic carbon values in *Subeucalanus* spp. females and males (C–D) and isotopic nitrogen in *Subeucalanus* spp. females and males (E–F) at continental shelf (G5)

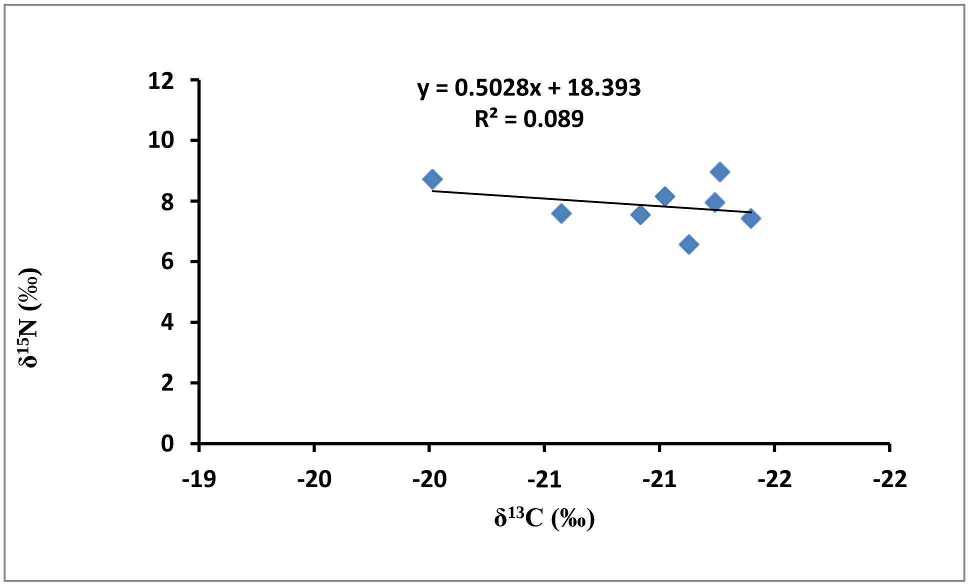


Fig. 3.3 The correlation between $\delta^{15}N$ and $\delta^{13}C$ in copepod genders at continental slope

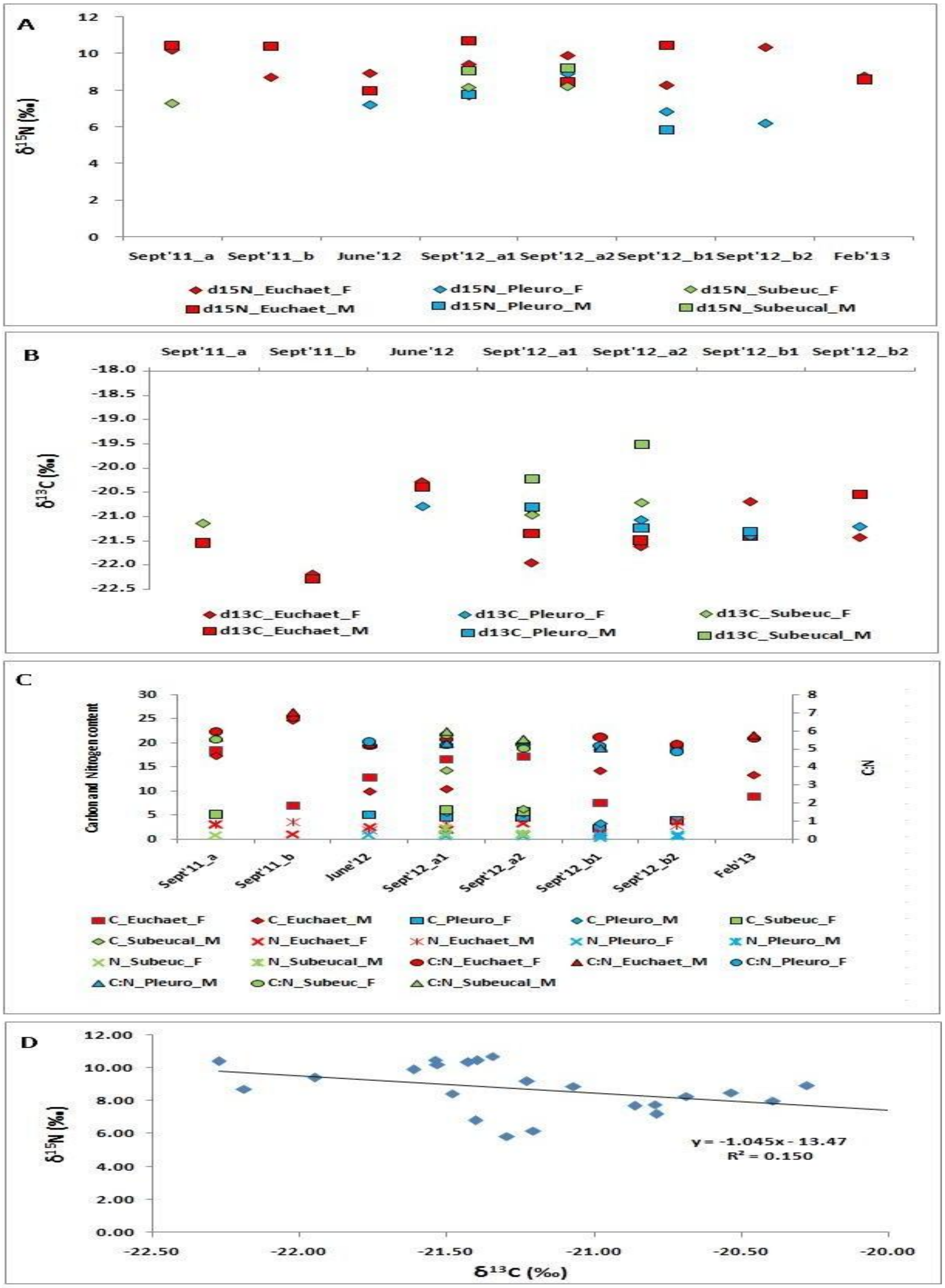


Fig. 3.4 The variations of (A) δ^{15}N, (B) δ^{13}C, (C) carbon and nitrogen content and (D) correlation between δ^{15}N and δ^{13}C in copepod genders at open ocean station (ASTS) (*Euchat-F-Euchaetaconcinna* female; *Euchaet_M -Euchaetaconcinna* male; *Pleuro_F- Pleuromamma indica* female; *Pleuro_M-Pleuromamma indica* male; *Subeuc_F-Subeucalanus* spp. female; *Subeuc_M-Subeucalanus* spp. male)

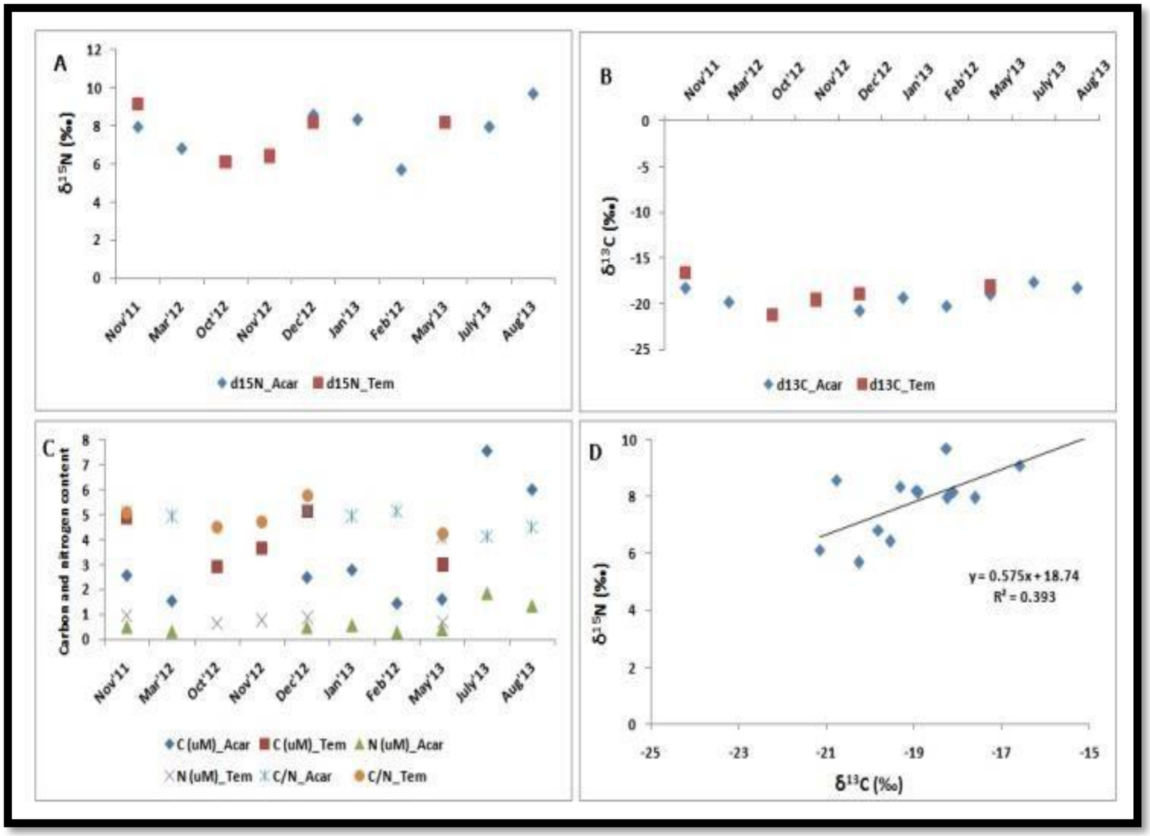


Fig. 3.5 The monthly variations of (A) δ^{15}N, (B) δ^{13}C, (C) carbon and nitrogen content and (D) correlation between δ^{15}N and δ^{13}C in copepod species at continental shelf (*Acar-Acartia erythraea*; *Tem-Temora turbinata*)

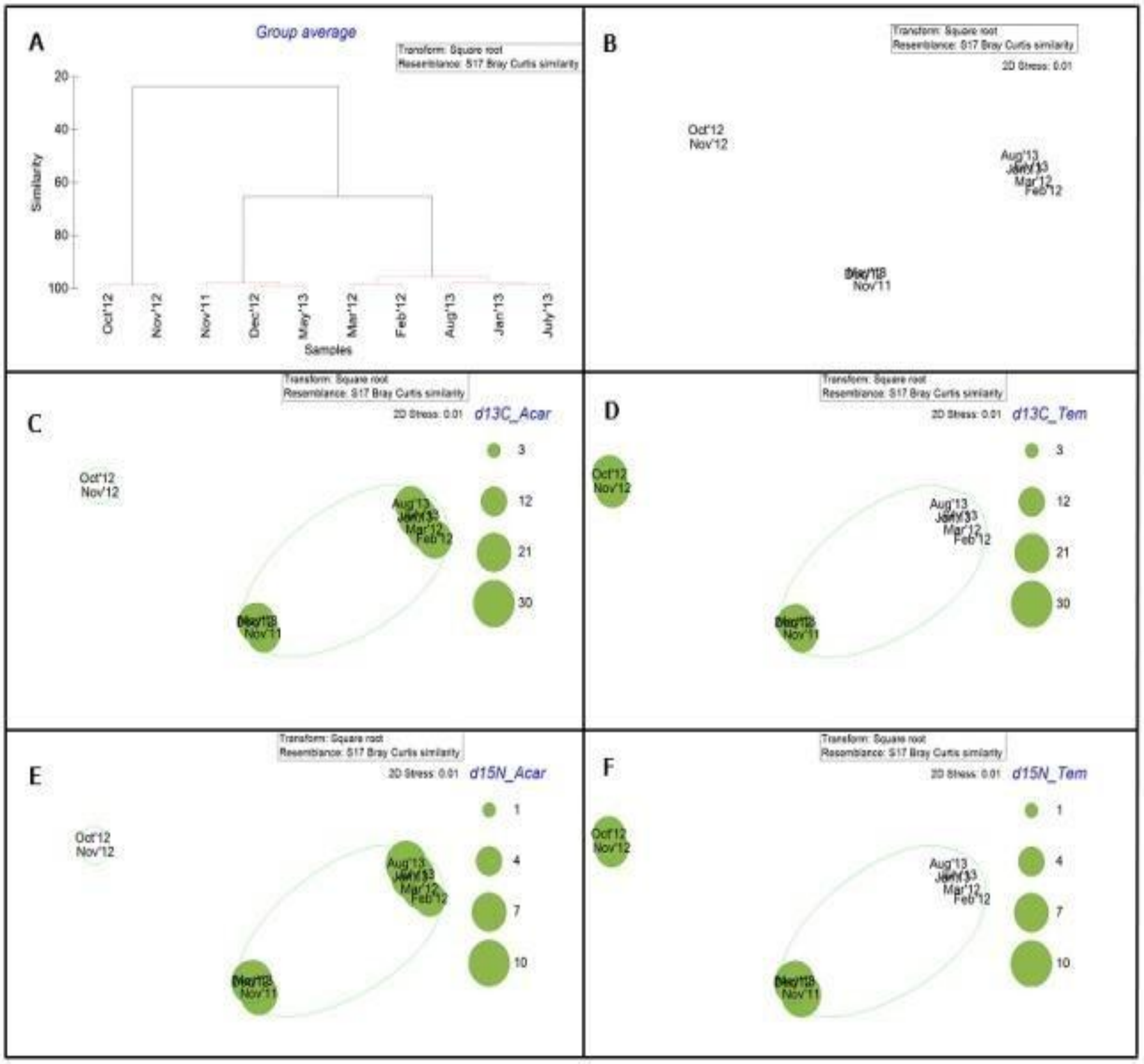


Fig. 3.6 Bray–Curtis similarity (A) based on clustering of months manifested through dendrogram and nMDS plot (B) based on copepod isotopic contents. Bubble plot of isotopic carbon values in *Acartia erythraea* and *Temora turbinata*(C–D) and isotopic nitrogen in *Acartia erythraea* and *Temora turbinata* (E–F) at continental shelf (G5)

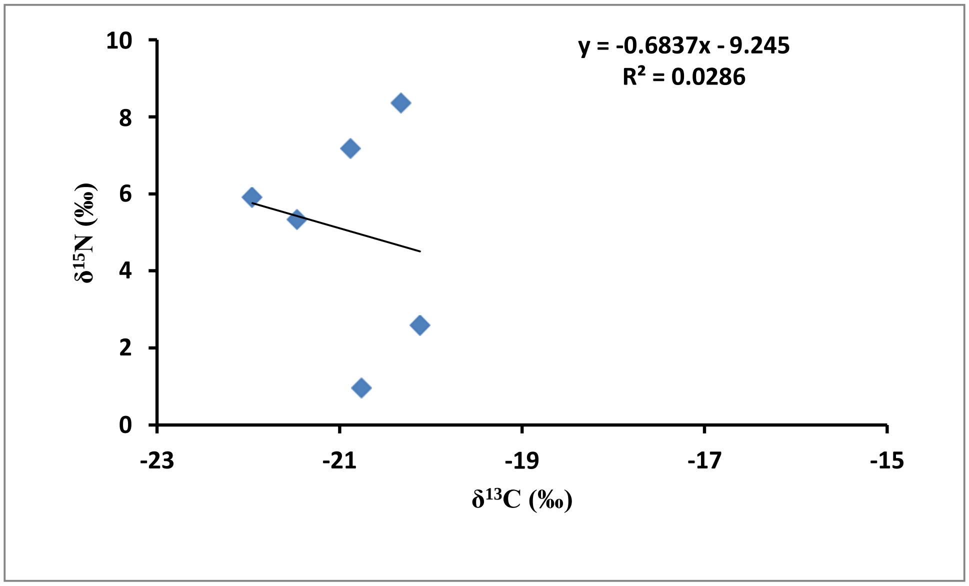


Fig 3.7 Correlation between δ^{15}N and δ^{13}C in copepod species at continental slope

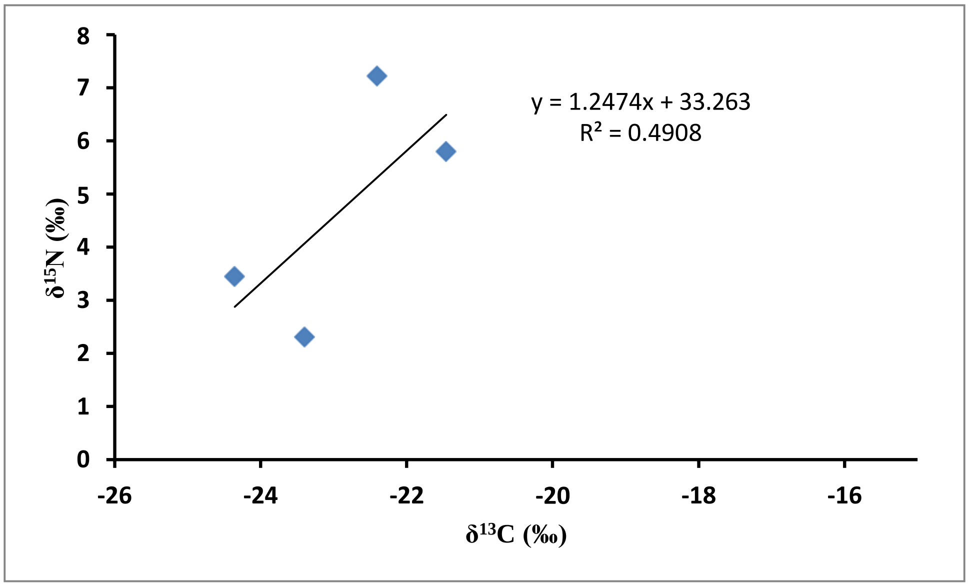
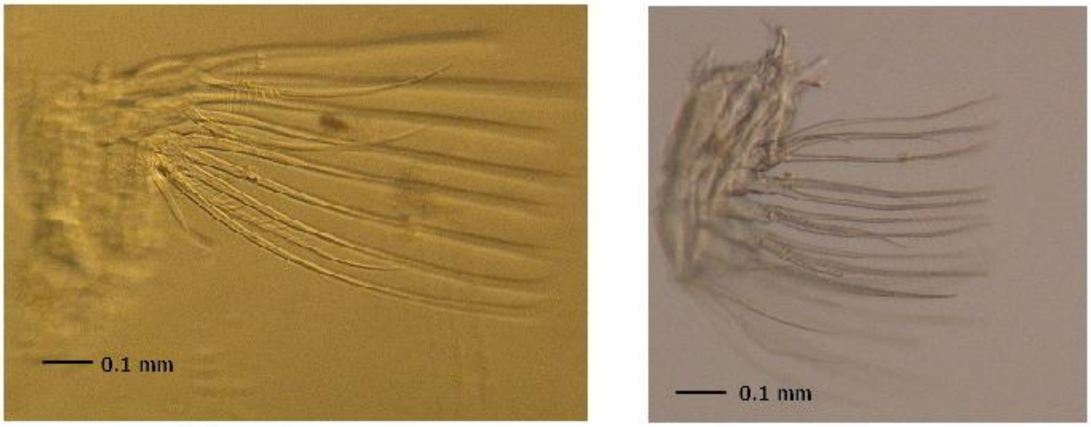
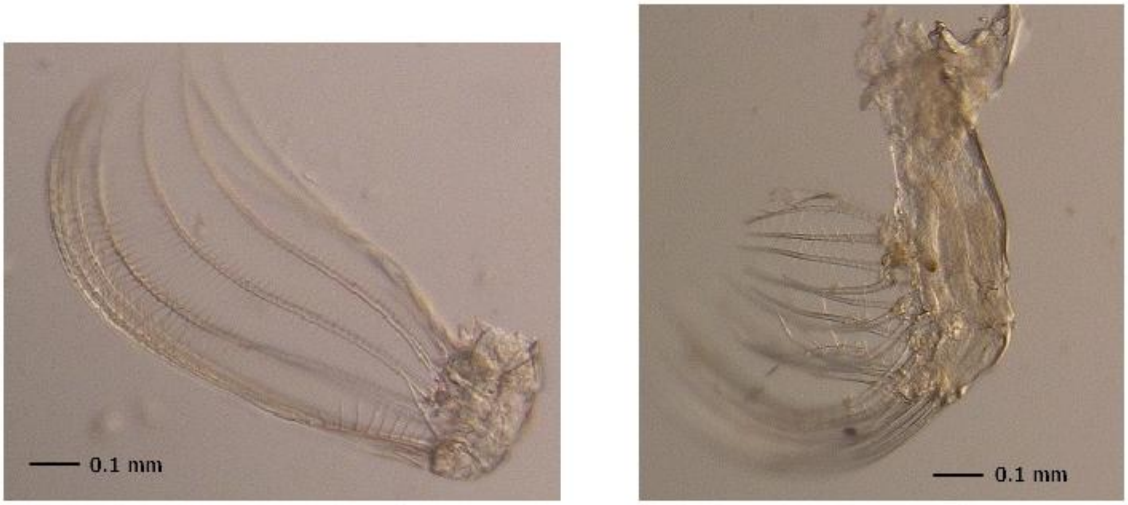


Fig. 3.8 The correlation between δ^{15}N and δ^{13}C in copepod species at open ocean station (ASTS)

Plates



Subeucalanus *sp.* *Temora sp.*



Acartia sp. *Euchaeta sp.*

Plate 3.1 Second maxilla of studied copepod species.

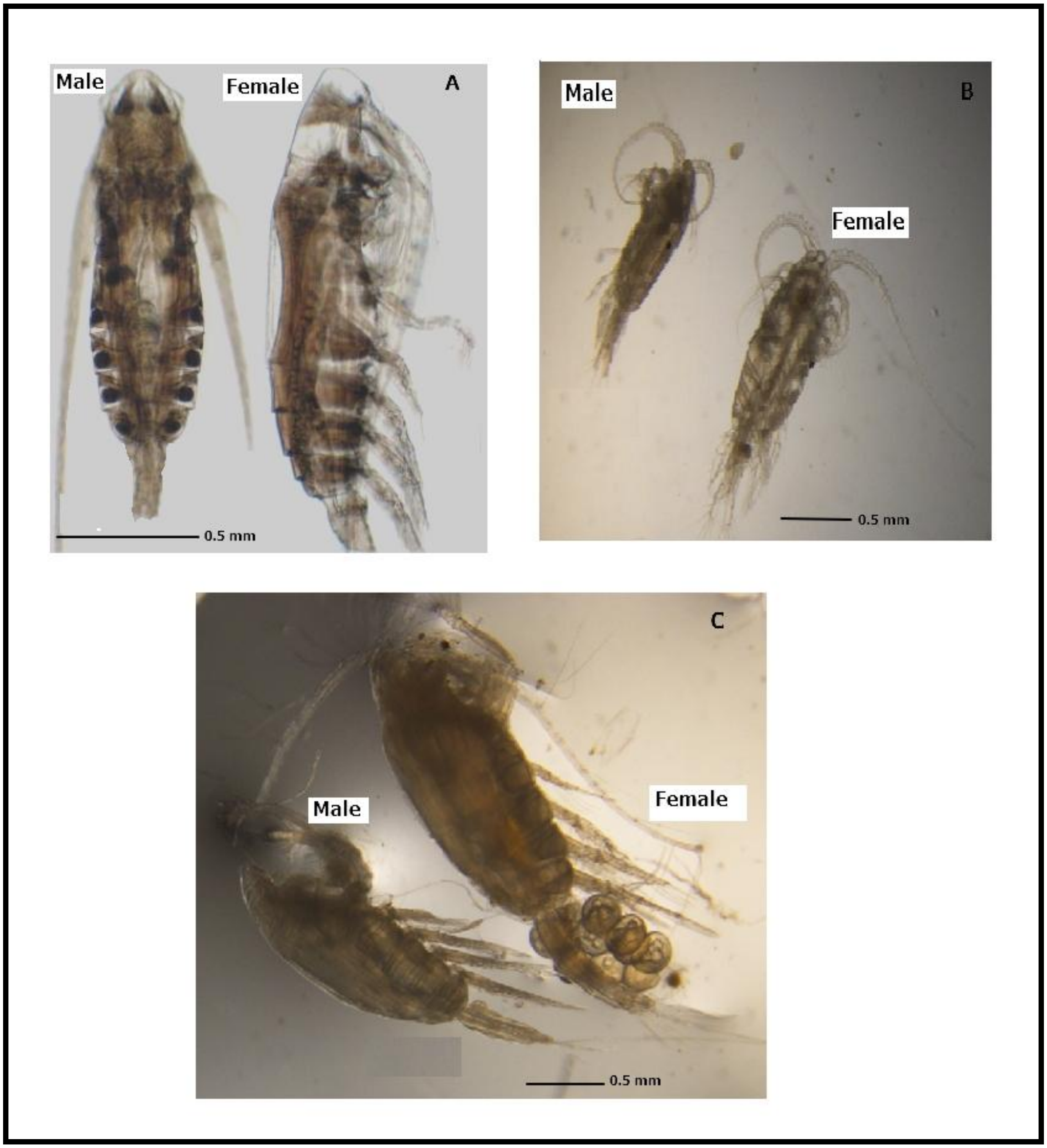


Plate 3.2 Photomicrographs of (A) *Subeucalanus* sp. (B) *Pleuromamma* sp. and (C) *Euchaeta* sp.

3.4 DISCUSSION

3.4.1 Biogeochemistry of the study region: Important features

Being among the chief upwelling zones, the Arabian Sea also inhabits the major oceanic oxygen minimum zone where intense denitrification leaks the fixed nitrogen (Naqvi 1987). Distinctly, the vigorous upwelling in the Arabian Sea occurs along its western periphery (Naqvi 2008) during June–September that enhances the biological production (Banse 1987; Naqvi and Jayakumar 2000; Wiggert et al. 2005; Habeebrehman et al. 2008). During December–March, the convective mixing driven by cool and dry winds supports the productivity in the northeastern Arabian Sea (Madhupratap et al. 1996; Lee et al. 2000; Prasannakumar et al. 2001). The high carbon fixation rates mediate the export of particulate matter to the deep sea that sustains the oxygen minimum zone (Naqvi et al. 2009).While, pre-monsoon is characterized by depleted nitrate and rich phosphates concentrations in the surface waters of continental margins (Ahmed et al. 2017). During this season, the nutrient deficient condition in conjunction with calm weather creates a favorable environment for the growth of nitrogen-fixing cyanobacteria *Trichodesmium* (Devassy et al. 1978). Earlier studies documented low $\delta^{15}N$ values in particulate organic matter associated with *Trichodesmium* bloom in the eastern Arabian Sea (Maya et al. 2011). Oceanic waters of Arabian Sea harbor picoplankton abundantly (Jain et al. 2014), and are recognized to fix atmospheric nitrogen (Wasmund et al. 2001; Montoya et al. 2004). Further, nitrogen-fixing diazotrophs have been reported from the Arabian Sea during non *Trichodesmium* bloom period (Bird et al. 2005) thus signifying the presence of nitrogen fixation during the other period of the year. Accordingly, in the euphotic zone, light isotopic nitrogen fueled by nitrogen fixation gets reflected in isotopic depleted nitrate values (5‰) as compared to the deep waters (250 to 350 m; 15‰; Brandes et al. 1998). In addition, Bonnet et al. (2011) accounted that >45% of N_2 fixation rates by the picoplankton size fraction signifying important role in total N_2 fixation by these smaller forms.

3.4.2 Characteristics of copepods in the Arabian Sea

The majority of tropical copepods have depleted lipid contents (Lee et al. 2006) as they stay active and do not necessitate diapausing (Lee and Hirota 1973). Also, a typical feature of copepod feeding is the sloppy feeding behavior, which provides the dissolved nutrients to the autotrophic forms (Vincent et al. 2007). Characteristic of small-sized copepods are their omnivorous nature with flexible trophic niches and their trophic levels often vary with habitat and season (Wang and Conover 1986; Head and Harris 1987; Kleppel 1993; Calbet and Saiz 2005). Typically, *Temora* spp. has been characterized as a suspension feeder primarily exploiting non-motile prey (Tiselius and Jonsson 1990; Koski et al. 2005) particularly heterotrophic prey in oligotrophic and pre-bloom situations (Gentsch et al. 2009). Another calanoid, *Acartia* spp. was reported to prefer phytoplankton and ciliates using passive sinking strategy (Tiselius and Jonsson 1990). Other noteworthy calanoid, *Subeucalanus pileatus* was noticed to favor ciliates as well as dinoflagellates over diatoms and were observed to favor heterotrophic feed over autotrophs (Verity and Paffenhofer 1996). The predatory calanoid, *Euchaeta* spp. is known to prey on *Acrocalanus*, *Paracalanus* and *Parvocalanus* (Wong et al. 2012) and on non-calanoids like *Oithona* and *Oncaea* (Oresland 1991). The vertical migrating species, *Pleuromamma* spp. are also considered as carnivores (Hannides et al. 2009).

Characteristics morphology of mouthparts namely the mandibles, first maxillae, second maxillae, and maxillipeds have been described in detail by Anraku and Omori (1963), Arashkevich (1969), Wong (1984) and Green and Shiel (1999). Herbivorous copepods (*Subeucalanus* spp.) have plumose setae on the distal ends of feeding appendages, while the carnivorous ones (*Euchaeta* spp.) harbor thickened spine-like and dagger-like setae (Green and Shiel 1999). Mouthparts continuously tremble and small particles are inertly funneled by the second maxillae towards the mouth (Price and Paffenhofer 1984). However, larger particles are actively grasped by maxillipeds and second maxillae (Kerfoot 1977; Koehl and Strickler 1981; Strickler 1984). Faunal prey is chewed by mandibles, which is held in the basket formed by the posterior maxillipeds and lateral maxillae (Wong 1984). Evidently, in carnivores like *Euchaeta* spp. would require pronounced structures like solid spines on the maxillipeds and maxillae for grasping and/or piercing prey than in herbivores like *Subeucalanus* spp. Also, *Pleuromamma indica*, *Temora turbinata* and *Acartia erythrea* are with fine setules capable of filtering the suspended matter.

Typically, copepod sex-ratios are skewed towards females' ascendancy in wild populations especially calanoids (Kiorboe 2006) like *Subeucalanus* spp. and *Pleuromamma* spp. except for *Euchaeta* spp. (present study). It is well known that carnivorous copepods like *Euchaeta* spp. show dominance of males as compared to females, however, like present study vary seasonally (Kouwenberg 1993). The biased sex-ratios towards females imply differential mortality rates among the gender (Kiorboe 2006), food availability (Gusmao and McKinnon 2009), predation (Blais and Maly 1993; Boix et al. 2006), differential parental care (Sapir et al. 2008) and even sex interchange (Flemminger 1985; Svensen and Tande 1999; Irigoien et al. 2000; Miller et al. 2005; Gusmao and McKinnon 2009). Occasionally, the males do not feed, thus providing an explanation of their higher mortality rate (Kiorboe 2006). Sometimes, individuals of certain species adjust their sex ratios in response to the quality of the environment, producing more offspring of the gender likely to contribute most to their individual fitness (Sapir et al. 2008). Apart, planktonic copepod males are known to moult to adulthood prior to females (Paffenhofer and Mazzocchi 2003). Moreover, calanoid males come across a predator more efficiently than females as males swim vigorously compared to females.

Dissimilarity in sex ratio between the calanoid families pursues the phylogeny (Ohtsuka and Huys 2001). To elaborate, the families belong to the superfamily Centropagoidea have the least biased sex-ratios as they require multiple mating. On the contrary, those families with the female-skewed sex ratios are able to reproduce continuously after just one mating (Kiorboe 2006) as the case with *Euchaeta* spp. and *Pleuromamma* spp. Paffenhofer and Mazzocchi (2003) reported dominance of females of *Paracalanus* spp., *Clausocalanus* spp. and *Calocalanus* spp. with males contributing <2%. However, the calanoid *Lucicutia* spp. revealed a higher percentage of males than that of females and occasionally for *Centropages velificatus*, which repeatedly fertilize their females in neritic waters (Paffenhofer and Mazzocchi 2003). According to a study by Kiorboe (2006), average sex-ratio (males: females) varies between 0.15 and 1.1. Also, sex-ratios vary seasonally within species (Conover 1956; Lee and McAlice 1979; Jimenez-Melero et al. 2014). Such high female skewness in the copepod community might be a benefit towards effort-less mate-finding for the male counterpart and consecutively facilitates elevated reproductive output.

3.4.3 Seasonal variability of $\delta^{13}C$ of copepods

Phytoplankton, algae and seagrasses undertake C3 pathway, but their $\delta^{13}C$ values markedly vary from terrestrial C3 plants. Availability of ambient CO_2 and slower diffusion of CO_2 in water are the primary cause for such dissimilarity (Fogel et al. 1992). Phytoplankton especially diatoms, dinoflagellates, green algae and euglenoids seem to prefer uptake of dissolved CO_2 over HCO_3^- (Khan et al. 2015). Consequently, phytoplankton have $\delta^{13}C$ values ranging from –30‰ to –18‰ (Degens et al. 1968; Anderson and Arthur 1983; Maya et al. 2011). Distinction in marine (–24‰ to –18‰) and freshwater phytoplankton $\delta^{13}C$ (–30‰ to –25‰) occurs due to higher dissolved CO_2 concentrations compared to HCO_3^- in freshwater systems. Similar to phytoplankton, the $\delta^{13}C$ of algae (freshwater: –30‰ to –26‰; marine: –23‰ to –16‰) and sea grasses (–21‰ to –6‰; Hemminga and Mateo 1996) reflects its uptake of CO_2 relative to HCO_3^-. Mesozooplankton maintain the signature of their diet with slight enrichment of ^{13}C (Fry 2008).

Continental shelf: Gender segregation in *Subeucalanus* sp. and species-wise variation in $\delta^{13}C$–copepods enrichment was observed at continental shelf. Particularly, the seasonal variations in $\delta^{13}C$–copepods were conspicuous. Typically, depleted $\delta^{13}C$ in copepods was recorded during pre-monsoon (gender specific: −19.70 and −18.22 ‰; species-specific: −20.24 to −18.10 ‰), the intermediate $\delta^{13}C$ values in monsoon (genders: −20.27 to −18.14 ‰; species: −18.25 to −17.61 ‰) and most enriched $\delta^{13}C$ in post-monsoon (genders: −19.97 to −17.18 ‰; species: −21.14 to −16.59 ‰) were observed. Additionally, the most enriched values were observed in *Temora* spp. (−18.10‰) in pre-monsoon. Interestingly, $\delta^{13}C$in copepod was more enriched than $\delta^{13}C$ in SPOM (Maya et al. 2011); masking the bulk $\delta^{13}C$ in SPOM signatures with different feed (Gentsch et al. 2009). Alternatively, metabolic processes involved in tissue production, excretion or egestion for copepods might have enriched δ^{15}N and δ^{13}C in their bodies (Vanderklift and Ponsard 2003; Tamelander et al. 2006; Forest et al. 2010). Comparatively, heavier δ^{13}C–copepods in monsoon seem to be influenced by the switching of phytoplankton dominated by heavier isotopic diatom (Parab et al. 2006; Laws et al. 1995). The decline in autotrophic biomass during post -monsoon as compared to monsoon when dinoflagellates dominate results enriched δ^{13}C in copepods. Again, the most enriched δ^{13}C was noticed in *Temora* spp. (−16.59 ‰) during post-monsoon. Previous studies showed dinoflagellates to be depleted in δ^{13}C as compared to diatoms (Gearing et al. 1984; Rolff 2000). However, more enrichment in δ^{13}C during diatom-depleted period observation similar to the present study was reported by Grey and Jones (2001) from Loch Ness. Nevertheless, it is important to determine values separately for different phytoplankton taxa from the Arabian Sea to understand the carbon fractionation.

Continental slope: Continental slope was conspicuous with depleted δ^{13}C for copepod assemblages that apprehended for *Subeucalanus* spp. and *Euchaeta* spp. (genders specific: −21.16 to −20.01 ‰ and species-specific: −21.96 to −20.33 ‰). Similar to the present observation, previous studies also reported depleted values in off-shore waters in comparison to coastal shelf waters (Miller et al. 2008). Such observation implies a singular carbon source might be available for these primary consumers. Moreover, such depleted isotopic content signifies less nourished feed, pointing towards utilization of marine snow, that these copepods depend upon (Williams et al. 2014).

Open Ocean: Typically, δ^{13}C of copepod species (−24.36 to −21.46 ‰) are depleted as compared to shelf and slope waters. In open waters, bacteria play a crucial role in isotopic fractionation of copepod faecal pellets, which can cause a depletion of ^{13}C in the residual material (Macko and Estep 1984). Thus, the autotrophs utilize re-mineralised nutrients thereby depleted ^{13}C is transferred to higher trophic level like copepods. Open waters of the Arabian Sea are known to harbor picoplankton and dinoflagellates as principal autotrophs contradictory to continental shelf that is dominated by diatoms. However, the $\delta^{13}C$ values of copepod genders (−22.19 to −19.52 ‰) are comparatively enriched and show similarity with the shelf copepods. Similar to present observations, Struck et al. (2001) and Koppelmann et al. (2003) observed enriched $\delta^{13}C$ values in open waters. The most enriched $\delta^{13}C$ values were observed in *Subeucalanus* as compared to *Pleuromamma* and *Euchaeta* species. The previous study of gut content analysis of *Pleuromamma* revealed wide array of feed including autotrophs and protozoans (Sano et al. 2013). Besides their $\delta^{13}C$ values varied on a wide range convey that different food substrates are being processed. Collectively, selective feeding in copepod species according to their nutritional need was noticed. Amongst, *Subeucalanus* spp. seems to selectively capture the phytoplankton and remaining species might opt for the available heterotrophic biomass and marine snow.

3.4.4 Seasonal variability of $\delta^{15}N$ in copepods

The $\delta^{15}N$ of copepods mostly come from the $\delta^{15}N$ of the suspended matter (Fry 1988). Typically, depleted values of $\delta^{15}N$-suspended matters were observed from continental shelf region during pre-monsoon (Maya et al. 2011; D'souza et al. (under communication)). Such low values seem to arise from nitrogen fixation by diazotrophs like *Trichodesmium* spp., which is eminent to occur during pre-monsoon in the coastal waters bordering India (Qasim 1970; Devassy et al. 1979; Perumal et al. 1999; Jyothibabu et al. 2003; Sarangi et al. 2004; Parab et al. 2006). Comprehensive study on *Trichodesmium* bloom revealed that these bloom are not consumed by organisms thus, decompose resulting in elevated ammonium levels (Nair et al. 1992) thereby isotopically lighter nitrogen for the phytoplankton. Monsoon corresponds to high concentration of dissolved inorganic nitrogen and restricted light availability due to cloud cover (Maya et al. 2011) supports partial nitrate utilization by phytoplankton (Wada and Hattori 1978; Wada 1980). Partly, such processes can account for depleted δ^{15}N-Suspended matters. In addition, the riverine run-off can contribute to the relatively depleted δ^{15}N of the terrestrial organic matter. Contrary, post-monsoon was relatively enriched in δ^{15}N-suspended matters, probably due to phytoplankton uptake of heavier nitrate as a consequence of denitrification (Wada et al. 1975; Liu and Kaplan 1989; Brandes et al. 1998; Maya et al. 2011; Bardhan et al. 2015).

The low δ^{15}N values in the open waters of the Arabian Sea like the eastern Mediterranean seem to be caused by the fixation of atmospheric nitrogen (Sachs and Repeta 1999; Pantoja et al, 2002; Koppelmann et al. 2003). Nitrogen-fixing cyanobacteria like *Anabaena* spp. and *Trichodesmium* spp. exhibit values close to 1.0 ‰ (Minagawa and Wada, 1986). Indeed, nitrogen-fixing cyanobacteria such as *Synecchococcus* spp. (Li et al. 1993) and *Richelia intracellularis* (Zeev et al. 2008) found in the eastern Mediterranean provides evidence on biological nitrogen fixation as *R. intracellularis* has nifH sequences (nifH is the marker gene which encodes nitrogenase reductase). Consequently, The baseline δ^{15}N-suspended matters dominated by phytoplankton alter depending upon the nitrogen source and its isotopic fractionation during uptake and assimilation (Montoya and McCarthy 1995; Schmidt et al. 2003). Additionally, it is influenced by seasonal and regional variations in phytoplankton, light intensity and temperature (Waser et al. 1998). The δ^{15}N of particulate matter revealed seasonal variability in the Arabian Sea (Maya et al. 2011) and also in Baltic Sea (Rolff 2000).

The δ^{15}N–copepods seem to be strongly linked with phytoplankton biomass and water column temperature. Highly enriched δ^{15}N–copepods coincided with depleted chlorophyll concentration and increased water column temperature in the present study. It's challenging to characterize the trophic level of copepods in the present study due to lack of isotopic characterization of the phytoplankton taxa from the Arabian Sea. Typically, the stepwise increment of δ^{15}N in marine food webs is considered to be 3–4‰ per trophic level (Michener and Schell 1994). Although the increase in δ^{15}N between trophic levels can be variable (McCutchan et al. 2003), a mean trophic fractionation of 3.4‰ is widely applicable (Post 2002). Considering 3.4 ‰ as the baseline value of δ^{15}N in the present study reveal omnivorous feeding habit favored by these copepods in the Arabian Sea.

Continental shelf: The waters of continental shelf were productive during all the seasons (as elaborated in chapter 5). Segregation of δ^{15}N among males (7.92–10.16 ‰) and females (4.91–9.72 ‰) belonging to *Subeucalanus* was revealed in the waters of continental shelf waters of the study region. Likewise, *Acartia* spp. (5.69–9.70 ‰) and *Temora* spp. (6.12–9.10 ‰) revealed intermediate δ^{15}N indicating omnivorous feeding behavior among these species. In addition to gender-wise and species-wise variations, seasonal variation in δ^{15}N was conspicuous. Such variation may be the consequential output of δ^{15}N of plankton that depends on nitrogen production (Montoya et al. 2002). Further, pre-monsoon has abundance of picoplankton (Parab et al. 2006) and *Trichodesmium* (Devassy1979; Nair et al. 1992), which produce light isotopic nitrogen. However, the *Trichodesmium* mostly remains ungrazed (Nair et al. 1992) and thereby copepods may need to consume animal diet along with phytoplankton to cater its metabolic requirement. *Acartia* spp. (5.69 ‰) showed low $\delta^{15}N$ enrichment during this season as compared to monsoon and post-monsoon. Such spatial and temporal variability in omnivorous copepods like *Acartia* were reported from Sagami Bay (Sano et al. 2013) and eastern Pacific Ocean (Olson et al. 2010). Comparatively, intermediate enriched values of stable nitrogen and carbon isotopes in copepods were recorded in monsoon, suggesting that they are driven by increased phytoplankton biomass. The seasonal shifts in $\delta^{15}N$ as a result of a simultaneous switch in diet can be due to the assimilation of a new $\delta^{15}N$ baseline instead of a change in trophic position (Dale et al. 2011; Reid et al. 2013). The seasonal upwelling along the west coast of India replenish nitrate with high $\delta^{15}N$ to the coastal waters (Naqvi et al. 2006; Maya et al. 2011), which is in turn utilized by the autotrophic forms (Michener and Schell 1994). In late monsoon, the surface waters rapidly become oligotrophic and denitrification overrides the nitrogen cycle (Maya et al. 2011). At this point, primary production becomes dependent on recycled nitrogen especially ammonia which is generally depleted in ^{15}N. Mostly, the tiny plankton feed on the suspended matter and since they usually posses rapid tissue turnover, copepods could exhibit isotopic compositions following such seasonal pattern (Polunin et al. 2001).

Contradictory to SPOM, relatively lighter $\delta^{15}N$ and heavier $\delta^{13}C$ was observed in copepods during post-monsoon (D’souza et al. manuscript in preparation). Utilization of nitrogen-limited phytoplankton which are of low nutritional quality as compared to nitrate-replete phytoplankton (Malzahn et al. 2007; El-Sabaawi et al. 2013) of monsoon may be the probable explanation for the observed variations. Additionally, a shift in phytoplankton, dominated by dinoflagellates in post-monsoon (Parab et al. 2006) might have contributed to the change in isotopic (carbon and nitrogen) content of feed as the δ^{15}N of dinoflagellates are less enriched as compared to diatoms (Kurten et al. 2016). Contrary, *Temora* spp. (6.12 ‰) showed less enrichment in post-monsoon than that of monsoon and pre-monsoon. This indicates the switching ability of this copepod according to the feed availability. However, the δ^{15}N for *Temora* spp. fell below the range observed by Gentsch et al. (2009) from North Sea (δ^{15}N: 7.7–16.1 ‰). On the other hand, *Subeucalanus* spp. (10.16 ‰) revealed the most enriched δ ^{15}N for post-monsoon. The δ^{15}N for *Subeucalanus* spp. concurs with the observation of *Eucalanus* spp. from Red Sea (Kurten et al. 2016).

Continental Slope: Like δ^{13}C, δ^{15}N also showed a narrow range of variations in copepods on the continental slope. The genders of *Euchaeta* (7.55–8.71 ‰) and *Subeucalanus* (6.56–8.96 ‰) showed almost similar values. However, the enriched values were noticed in the male counterparts. Among the copepod species, *Euterpina* was conspicuous with depleted δ^{15}N (0.96 ‰) during pre-monsoon corresponding to *Trichodesmium* bloom period. As cyanobacteria are isotopically lighter, compared to other phytoplankton and detritus (Fry and Wainwright 1991; Fawcett et al. 2010), the selective grazing on this prey may put forward an explanation as to why *Euterpina* isotopic signatures were low. While, *Undinulla vulgaris*showed enriched δ^{15}N ratios (8.36 ‰) indicating similar trophic positions as *Euchaeta concinna* and *Subeucalanus* spp., reflecting its omnivorous feeding mode.

Similar to present observation, depleted δ^{13}C (–22.55‰) and low δ^{15}N (5.47 to 6.57‰) in copepods was observed by Polunin et al. (2001) in the off-shore waters. Changes in the feeding type of copepods have been observed with increasing distance from the shore, which favors the carnivorous forms (Vinogradov and Tseitlin 1983). In the continental slope and open waters, the refractory substances like the chitinous exoskeleton of copepod are abundant in marine snow (Miquel et al. 1994). This chitin is an important source of nitrogen in the marine environment (Shimmelmann et al. 1998), and the capability to exploit chitin has been confirmed for bacteria (Kichner 1995) and many crustaceans in the open waters (Bucholz and Vetter 1993; Watanabe et al. 1998). However, the processes that caused the low $\delta^{15}N$ values within the copepod community of the eastern Arabian Sea are not fully understood.

Open waters: Overall**,** the $\delta^{15}N$ value in copepod genders revealed omnivorous feeding behavior that apprehended for carnivore *Euchaeta* (8.27–10.70 ‰), omnivores *Pleuromamma* (5.84–9.18 ‰) and *Subeucalanus* (7.27–9.05 ‰). A common trend of the most enriched values in the male counterpart was observed. While, other copepod species particularly, *Macrosetella* spp. (3.45 ‰) and *Oithona* spp. (2.31 ‰) revealed depleted $\delta^{15}N$. *Pleuromamma* spp. actively undergoes diel vertical migration (Madhupratap and Haridas 1990; Auel and Verheye 2007) and pursues a diverse approach to metabolic processes (Teuber et al. 2013). Based on previous studies, the migrating copepod species- *Pleuromamma*is known to occupy various trophic positions ($\delta^{15}N$: 6–11‰; Teuber et al. 2014). Conversely, a related species *Metridia gerlachei* was characterized to be more carnivorous (Lopez and Huntley 1995).

The enriched $\delta^{15}N$ was also found for *Euchaeta concinna* at the open water station. Higher $\delta^{15}N$ in zooplankton with increasing depth has previously been found in calanoid copepods, *Pareuchaeta* species and in large mesozooplankton in general (Polunin et al. 2001; Koppelmann et al. 2009; Laakman and Auel 2010). This might indicate a higher proportion of carnivory with increasing depth and/or $\delta^{15}N$ enrichment at the base of the foodweb due to rapid loss of the lighter isotope during decomposition of particulate nitrogen pools (Polunin et al. 2001; Fry 2006).

Measure and nutritive value of feed along with body weight are the chief aspects assumed to drive copepod feeding rates (Saiz and Calbet 2011). In addition, the common trend of considering either adult females or both the genders together in studies related to feeding behavior seems to provide bias information. As this study reveals the probability of gender-wise dimorphism in feeding manners. Such gender-wise differences in feeding behavior need to be anticipated to gain a synoptic view of the functioning of plankton food web that in turn mediate the biogeochemistry. Similar to the present study, *Temora longicornis* (another species)is reported to show dimorphic feeding rates with respect to genders (Moison et al. 2013).

3.4.5 Seasonal variability of C and N in copepod

In the marine environment, copepods act as sink and source of carbon and nitrogen by being a mediator between primary producer and secondary consumer (Walve and Larsson 1999). Additionally, body stoichiometry imitates the requirement for specific elements based on growth rates and life history of copepods (Carrillo et al. 2001). The fast turnover in copepods incorporates new carbon and nitrogen (Fry and Arnold 1982). In many studies, size estimates using the length-weight regression were translated to carbon biomass (Berggreen et al. 1988; Sabatini and Kiorboe 1994; Hopcroft et al. 1998; Saptapoomin 1999; Lugomela et al. 2001). Generally, C/N for marine phytoplankton is 6.6–8.7 (Redfield et al. 1963; Holligan et al. 1984), for freshwater phytoplankton, is in range of 5–8 (Harris 1986; Kendall et al. 2001), for bacteria in the range 2.6–4.3 (Lee and Fuhrman 1987) and for terrestrial organic matter in range of 12–200 (Hedges and Mann 1979) have been published. According to Bamstedt (1986), the C/N ratio of marine copepods from medium latitude were relatively low (3–4) and high latitudes showed high ratio (3–13).

Continental shelf: The highest carbon (22.32 μM) and nitrogen (5.30 μM) content in *Subeucalanus* spp. genders was observed during pre-monsoon. Likewise, species-wise variations revealed highest carbon (7.58 μM) and nitrogen (1.82 μM) content during monsoon in *Acartia* spp. Nonetheless, C/N ratio was consistent in copepod genders of *Subeucalanus* spp. that comprehended during pre-monsoon (4.20–5.84) and monsoon (4.63–5.14). Conspicuously, C/N ratio for *Subeucalanus* spp. genders during post-monsoon (5.26–7.66) showed higher ratio and variation. Similarly, copepod species showed minor variations in C/N ratio during pre-monsoon (4.08–5.13), and post-monsoon (4.94–5.74). During monsoon, the C/N ratio in *Acartia* spp. was typically low (4.12–4.48). The probable reason for such low C/N ratio may be the higher nitrogen content in *Acartia* during monsoon. Simultaneously, the land derived suspended material with low C/N ratio may have resulted in such low values (Maya et al. 2011). Cataletto and Umani (1994) pinpointed a high seasonal fluctuation of C/N ratio mainly due to periodic alteration in nitrogen content in *Acartiaclausi* in Northern Adriatic Sea. Boucher et al. (1976) monitored *Centropages* sp. and *Temora* sp. in Banyuls-Sur-Mer neritic waters and pointed out consistent C/N ratio, but carbon and nitrogen content swerved coinciding to season and physiology of the copepod. The copepod species dominated by *Acartia* spp. and *Temora* sp. revealed similar values of C/N ratio, which are comparable to previous studies (Kiorboe et al. 1985; Stottrup and Jensen 1990; Dam and Lopes 2003).

Continental Slope: Copepod genders recorded the highest carbon (17.17 μM) and nitrogen (4.06 μM) content in females of *Subeucalanus* spp. Further, copepod species-wise comparison revealed highest carbon (15.87 μM) and nitrogen (3.01 μM) content in *Undinulla* spp. Consistently, C/N ratio for copepod genders (4.23–5.53) and species (4.09 –5.45) varied on a narrow scale. Typically, low C/N ratio at continental slope waters seems to be governed by high nitrogen content in the copepods. Nitrogen is an integral component of organic molecules; phytoplankton tends to adjust to the lowest requirement of nutrient (Galbraith and Martiny 2015). As a corollary of the plasticity of the elemental composition of phytoplankton, the low C/N ratio in the copepods residing at continental slope might be observed. However, exact reason is difficult to pinpoint.

Open waters: Copepod genders displayed highest carbon (12.71 μM) and nitrogen (3.51 μM) content in carnivore *Euchaeta* spp. females. On the contrary to herbivore, carnivores mostly deal with a reduced ration of higher quality food (Boerma and Elser 2006) and probably do not face nutrient deficiency (Laspoumaderes et al. 2010). Respiration is measured as a most important path of carbon loss by zooplankter (He and Wang 2006) and hence it could be physiological policy to handle surplus carbon in their diet (Laspoumaderes et al. 2010). Also, species-wise variation detected highest values of carbon (21.63 μM) and nitrogen (3.66 μM) content in *Oncaea* spp. Copepod genders–C/N (4.86–7.06) and species–C/N ratio (4.98–5.91) in open waters markedly differed from the continental shelf and slope waters. Hays et al. (1998) expressed *Metridia lucens* to undergo diel variations in carbon and nitrogen content in New Zealand waters and revealed carbon content in the range of 21.93 to 25.71 µg C ind^{-1} and nitrogen from 5.95 to 6.87 µg N ind^{-1}. Similar to *Metridia lucens, Pleuromamma* spp. also undergo diel vertical migration and the periodic feeding and fasting might cause a cyclic alteration in its elemental composition (Hays et al. 1997). In addition, the *Pleuromamma* spp. appears to profit from the rich food supply from in the surface waters at night. The reduced C/N ratio seems to be due to high protein content required to support a strong musculature in migrating species (Morris and Hopkins, 1983; Teuber et al. 2014). The results of present study showed distinct abundance of *Macrosetella* in the open waters, which attained very low elemental carbon (0.83 µM) and nitrogen (0.16 µM) content may be explained by the capability of this genus to nibble on *Trichodesmium* with depleted cellular carbon and nitrogen and with low consistent C/N ratio (5.18).

Copepod physiology can be surmised as a nexus at which elemental imbalances are deciphered into ecology by selective feeding and nutrient cycling. In adult copepod, as the somatic growth cease, carbon will be required to sustain the metabolism, but there will be reduced nitrogen demand for protein synthesis (Faerovig and Hessen 2003; Laspoumaderes et al. 2010). Consequently, a stoichiometric outlook on physiology should be explicitly associated with the metabolism with the elemental limitation forced by the environment. In tropical oceans, there seems to be no variation in elemental ratios in phytoplankton, zooplankton and fish (Gorsky et al. 1988). The implication of such observation would be a more homogeneous regeneration of elements in tropical oceans on the contrary to temperate oceans (Gismervik 1997).

3.4.6 Relation between δ^{13}C and δ^{15}N of copepods

Association between δ^{15}N and δ^{13}C indicates probable aid of multiple carbon or nitrogen sources to copepod feed in a different ecological niche (William 2013).The common linearity between carbon and nitrogen isotopes may be credited to kinetic isotope effects of amino acid synthesis (Macko et al. 1986; Minagawa et al. 1992; Aita et al. 2011). The copepods from continental margins and oceanic realm potentially consumed matter with varied carbon or nitrogen source. Thus, the correlation between copepod–δ^{13}C and δ^{15}N contents is affected by the accumulating material arising from different pathways of carbon fixation or from changes in nitrogen sources. Since δ^{13}C and δ^{15}N values get enriched equally with trophic level, δ^{13}C and δ^{15}N of the copepod population would be positively correlated ($r^2>0.5$) if the baseline isotopic composition is derived from single carbon and single nitrogen source (Polunin et al. 2001; Fanelli et al. 2009; William 2013). The weak correlation between δ^{15}N and δ^{13}C of copepod genders collected from continental shelf ($r^2 = <0.01$; Fig. 3.1D), slope ($r^2 = 0.09$; Fig. 3.3) and open waters ($r^2 = 0.15$; Fig. 3.4D) of the Arabian Sea suggests use of multiple carbon or nitrogen source contributed to the trophic food web (Williams et al. 2014).

Correlation between copepod–δ^{13}C and δ^{15}N values is often used to identify the merging of multiple carbon sources, for instance, terrestrial plant matter or chemoautotrophic carbon fixation to copepod food webs (Burd et al. 2002; Bergquist et al. 2007; Macavoy et al. 2006; William et al. 2014). All the stations examined in this study were far from land to see appreciable inputs of terrestrial carbon to copepod food webs but continental shelf (G5) do support different processes of nitrogen cycles. These include atmospheric nitrogen fixation during pre-monsoon. The δ^{15}N–SPOM (1.5–4.28 ‰) values during pre-monsoon at station G5 were lower than that of typical marine organic matter (5‰; Maya et al. 2011). Such low values seem to arise from N_2 fixation by diazotrophs, as the nitrogen fixer, *Trichodesmium* spp. is eminent to occur during pre-monsoon in the coastal waters bordering India (Qasim, 1970; Devassy et al. 1979b; Perumal et al. 1999; Jyothibabu et al. 2003; Sarangi et al. 2004; Parab et al. 2006). A comprehensive study on *Trichodesmium* bloom revealed that these blooms decompose resulting in elevated ammonium levels (Nair et al. 1992) leading to lighter isotopic nitrogen for the phytoplankton. Such depleted values of δ^{15}N–SPOM were reported from the Red Sea during *Trichodesmium* bloom (Kurten et al. 2016). However, the impact of nitrogen fixation was not observed in δ^{13}C–SPOM which showed typical marine organic matter signatures (−22‰ to −19‰; Maya et al. 2011). Additionally, post-monsoon was characterized by relatively enriched δ^{15}N-SPOM, this possibly be due to phytoplankton uptake of nitrate from the heavier isotopic pool in oxygen-depleted waters that arises from denitrification (Liu and Kaplan 1989; Brandes et al. 1998; Maya et al. 2011; Bardhan et al. 2015).

Copepod species revealed a comparatively significant positive correlation between δ^{15}N and δ^{13}C at continental shelf ($r^2 = 0.39$; Fig. 3.5D) and open waters ($r^2 = 0.49$; Fig. 3.8) implies a similar source of carbon used by copepods (Williams et al. 2014). The other explanation would be the utilization of similar nitrogen source as indicated by δ^{15}N values of copepod species collected from a continental shelf or open waters. While, distinctly poor correlation ($r^2 = 0.03$; Fig. 3.7) between δ^{13}C and δ^{15}N of copepod species from continental slope was noticed. Contradicting the result of the present study, the strong positive correlation between δ^{15}N and δ^{13}C of plankton, nekton and other crustaceans is reported in Mediterranean slope waters (Polunin et al. 2001).

To sum up, the Arabian Sea is a eutrophic habitat for the most part of the year, with diatoms, dinoflagellates and cyanobacteria blooms. Thus, the importance of herbivory for copepod species with low selectivity might be anticipated. Use of stable isotope technique in the present study has provided relative information on copepod feeding from different geographic settings of the Arabian Sea. The isotopic values of carbon in copepods were enriched at the continental shelf and depleted values at the slope and open water realms.

While, the isotopic values of nitrogen varied on a narrow scale indicating predominantly omnivorous feeding habit. In particular, the small-sized copepods exhibited omnivory seasonally and regionally. This is consistent with the overall feeding behavior observed in the continental shelf. Collectively, male copepods belonging to *Subeucalanus*, *Euchaeta* and *Pleuromamma* showed segregation in feeding behavior than their female counterpart. Further, male copepods always accumulated enriched values of carbon and nitrogen isotopes. Furthermore, *Temora* spp. and *Acartia* spp. could be characterized as an omnivore on the basis of flexibility in its feeding pattern during different seasons in the continental shelf waters, with a regular swing from a heterotrophic feed to an autotrophic feed. This relatively broad trophic niche of *Temora* spp. and *Acartia* spp. permits utilization of potential microplankton and phytoplankton efficiently. In continental slope and open waters realm, *Pleuromamma* spp. exhibited omnivorous feeding behavior. *Subeucalanus* spp. revealed variation in isotopic content in nitrogen and carbon across the continental shelf, slope and open waters. Invariably, *Euchaeta concinna* exhibited carnivorous feeding behavior in the continental shelf, slope and open waters of Arabian Sea as affirmed with stable isotope technique. The different trophic strategies of copepods dwelling in different habitats of the Arabian Sea likely play a crucial role in utilizing and transporting the fixed carbon and nitrogen to another trophic level.

Chapter 4

SPATIAL DISCREPANCY IN ISOTOPIC COMPOSITION OF CALANOIDA AND POECILOSTOMATOIDA IN THE ARABIAN SEA

4.1 INTRODUCTION

Structure of the plankton food web in productive coastal waters and oligotrophic open waters are highly variable. Primarily, nutrition and predation seems to influence the trophic position of copepods, dominant forms of mesozooplankton. In addition, copepod grazing on primary producers favoring larger cells can determine phytoplankton community structure (Kiorboe 2008). Consequently, the ultimate fate of primary production depends on the trophic structure of copepods. Stibor et al. (2004) suggested that copepods act like a shunt for the primary production, alternating between the second and third trophic level. Therefore, the trophic level occupied by copepods would have a strong implication for the trophic transfer in a food web.

Traditional approaches such as gut content analysis and laboratory feeding experiments provide a broad perspective of ingested food (Schmidt et al. 2003). Examination of gut contents gives only the snapshots of the ingested diet, while, study of natural isotopic content offer insights on the assimilated food (DeNiro and Epstein 1978; Fry and Sherr 1984), based on feeding, assimilation, tissue turnover and growth rates of the organisms (Peterson and Fry 1987; Post 2002). The stable isotopes ^{15}N and ^{13}C have been used to integrate variation in isotope signal at the base of the food web as the baseline (Post 2002). Typically, the ^{13}C/^{12}C ratio of an organism is directly linked to that of its food with 1‰ enrichment than its diet (DeNiro and Epstein 1978; Rau et al. 1983) and the ^{15}N/^{14}N ratio has an enrichment of ~3–4‰ per trophic level (Minagawa and Wada 1984; Michener and Schell 1994).

Food availability for the copepods mainly affects the success of its population in an area. In spite of this, studies pertaining to feeding of the copepods from the natural environment of Indian waters are limited (Goes et al. 1999; Fernandes and Ramaiah 2016; D’souza and

Gauns 2016). Few studies are based on laboratory reared copepods using cultured food (Anandan et al. 2013; Jeyaraj and Santhanam 2013; Jasmine et al. 2016). Every effort to couple primary production to commercial fishery asks for better understanding on food web structure from phytoplankton to copepods to fish. Thus, despite difficulties with shifting baselines of the primary producers and problems identifying predator–prey relationships, there is a need to describe trophic interactions among the smallest plankton. In this study, copepods were collected from three regions viz., continental shelf, slope and open waters of the Arabian Sea to understand their food preference and the seasonal variations. The chapter 3 deals with the feeding behavior of dominant and comparatively big–sized individual copepod species and genders. The remaining small–sized copepod species was difficult to target at species level were collectively classified at order level and examined for their feeding preferences. Mostly, these tiny species belonged to Calanoida and Poecilostomatoida, the dominant copepod orders thriving in the study region. To my knowledge, this study represents the first attempt to use stable isotopic approach to investigate feeding in the copepod orders from Indian waters.

4.2 METHODOLOGY.

4.2.1 Sampling

The study area includes continental shelf, slope and open waters of the Arabian Sea (Fig. 1.2). The study location is mentioned elaborately in chapter 1. Mesozooplankton samples were collected using net with 200 µm mesh and stored immediately in ice box. Detailed mesozooplankton collection procedure is elaborated in the chapter 2 while, particulars of sampling months is stated in table 3.1 of chapter3.

4.2.2 Copepod sorting and analytical method for IRMS

Approximately 30–60 individual adult copepods belonging to Calanoida and Poecilostomatoida were later sorted and oven dried at 60 ºC for 48 h. The pre-treatment for copepods to be analyzed using Thermo Finnigan DELTA V plus isotope ratio mass spectrometer in continuous-flow mode (Owens and Rees 1989) and analysis on IRMS analytical procedure (Smyntek et al. 2007) is detailed in chapter 3.

4.2.3 Statistical analyses

Variability in δ^{13}C and δ^{15}Nat continental shelf was compared within the copepod orders and season using factorial analysis of variance (ANOVA). Similarly, variation in δ^{13}C and δ^{15}N at continental shelf, slope and open waters were compared within the copepod orders using factorial ANOVA. The analysis of variance was followed by a post hoc Tukey HSD test. Prior to analysis, all data were square-root transformed. Values were considered significant at 95 % level of confidence (Statastica 6.0, Statsoft, OK, USA). After square root transformation, non-multidimensional scaling (nMDS) and Bray–Curtis cluster were assembled based on isotopic composition of copepod order collected from continental shelf region (PRIMER 6).

4.3 RESULTS

4.3.1 Seasonal variations in abundance of copepod orders

Enumeration and seasonal variability of copepod orders is elaborated in depth in chapter 2. Hence, this chapter will touch upon the gist of copepod abundance. Copepods, the dominant mesozooplankton group, showed seasonal variation in abundance along the study area, particularly the continental shelf. Results revealed low copepod population in monsoon, while their population seems to have peaked significantly in post-monsoon at continental shelf. The continental slope and open ocean, on the other hand, did not exhibit significant seasonal trends as observed in continental shelf. Amongst, Calanoida and Poecilostomatoida dominated the copepod community along the continental shelf, slope and oceanic realm throughout the study period. The dominant Calanoida and Poecilostomatoida families represented annually were Paracalanidae and Oncaeidae, respectively. The species present throughout the year were considered for studying feeding habits. This includes, *Acrocalanus* spp., *Paracalanus* spp., and *Centropages* spp. of Calanoida and*Oncaea* spp. and *Corycaeus* spp. of Poecilostomatoida.

4.3.2 Seasonal variability of δ^{13}C, δ^{15}N and C:N of copepod orders in continental shelf waters

Calanoida: In pre-monsoon, δ^{13}C varied from −21.35 to −18.46 ‰ and δ^{15}N varied from 1.97 to 10.05 ‰ (Fig.4.1A and B). The minimum and maximum value of δ^{13}C and δ^{15}N were observed in April (2013) and May (2013), respectively. Synoptic view on monthly variation revealed least enrichment (1.97) of δ^{15}N during April’2013 corresponding to low surface Chl *a* (0.69 ng/mL) in Calanoida. Moreover, Calanoida attained highest carbon (14.91 μM) and nitrogen (3.44 μM) content during May 2013. While, the low carbon (1.07 μM) and nitrogen content (0.20 μM) coincided with the low surface Chl *a* (0.69 ng/mL) in April 2013. The C/N ratio oscillated from 4.33 (May 2013) to 5.28 (March 2012; Fig. 4.1C).

During monsoon, δ^{13}C (−20.14–−17.64 ‰) and δ^{15}N (6.65–9.23 ‰) were comparatively enriched and low values were noted during September 2011 and high in August 2013(Fig.4.1A and B). Carbon (4.96 to 8.54 μM) and nitrogen (0.84 to 2.03 μM) isotopes varied widely with higher values in July 2013 and low in August 2012. Consistently, C/N ratio fluctuated on a narrow range from 4.20 to 5.91 (Fig. 4.1C); low value was observed in July 2013 and high in August 2013.

During post-monsoon, most enriched δ^{13}C (−15.76 ‰) and intermediateδ^{15}N (9.56 ‰) was conspicuous. Alternatively, carbon (2.56 to 4.59 µM) and nitrogen (0.50–0.86 µM) was comparatively depleted in this season. The C/N ratios (5.01–5.59) were consistent with pre-monsoon and monsoon.

Poecilostomatoida: In pre-monsoon, depletedδ^{13}C (−21.32 to −19.01 ‰) and δ^{15}N (6.10 to 8.59 ‰) values were recorded. Specifically, the depleted isotopic values were observed in May 2013 and enriched values in February 2013. Following the enriched isotopic values, highest carbon (3.27 µM) and nitrogen (0.62 µM) content were observed during February 2013. However, low carbon (1.51 µM) and nitrogen content (0.29 µM) in Poecilostomatoids were reflected during April 2013.Consistently, C/N ratio (4.33–5.28) during this period was similar to calanoid C/N ratio during pre-monsoon (Fig. 4.1).

During monsoon, δ^{13}C (−21.24–−17.64 ‰), δ^{15}N (6.53 to 7.27 ‰) and C/N ratio (4.43–5.50) showed enrichment compared to pre-monsoon (Fig.4.1). As compared to Calanoida, Poecilostomatoida attained the low carbon (2.62 and6.28 µM) and nitrogen contents (0.51 to 1.39 µM).

During post-monsoon, most enriched δ^{13}C (−22.02–−17.21 ‰) and δ^{15}N (3.76–8.80 ‰) was observed. It is a striking observation that Poecilostomatoida, traditionally known to be omnivore/carnivore attained the least δ^{15}N enrichment of 3.76 ‰. This observation implies that the small-sized copepods utilize the autotrophic biomass as primary feed. The C/N ratio (5.09–5.63) fluctuated on a narrow scale. The carbon content of copepods ranged from

1.75 to 3.24 μM with higher values observed in December 2012 and lower in November 2012. The nitrogen content (0.34–0.62 μM) was lowest during October 2013and highest in December 2012. Statistical analysis depicted a poor correlation ($r^2 = 0.21$) between $\delta^{13}C$ and $\delta^{15}N$ of Calanoida and Poecilostomatoida collected from continental shelf waters (Fig. 4.1D).

Calanoida and Poecilostomatoida showed marked seasonal variability in elemental and isotopes of carbon and nitrogen at continental shelf realm. Significant seasonal variations in $\delta^{13}C$ of copepod orders were observed at continental shelf unlike $\delta^{15}N$ contents of copepod orders (Table 4.1). Bray Curtis similarity analysis on stable isotopic values of Calanoida and Poecilostomatoida clubbed the sampling months into three groups at 98 % similarity (fig. 4.2A). The major group (first group) was formed by clubbing together the months namely, March'12, August'12, November'11, August'13, and July'13. While, October'12 and September'11 formed a second group and January'13, May'13 and December'12 formed the third group. Conspicuously, April'13 and November'12 remained ungrouped. The nMDS analysis revealed a similar pattern of clustering of months comparable to cluster analysis (fig. 4.2B). Also, a similar pattern of nMDS plots for $\delta^{13}C$ and $\delta^{15}N$ in Calanoida (fig. 4.2C and E) and Poecilostomatoida (fig. 4.2D and F) was observed.

4.3.3 Seasonal variability of $\delta^{13}C$, $\delta^{15}N$ and C:N of copepod orders in continental slope waters

Distinctly, the Calanoida–$\delta^{13}C$ varied on a narrow scale from −21.21 to −20.10 ‰. while, their $\delta^{15}N$ values varied widely ranging from 3.31 to 6.55 ‰ (Table 4.2). Noticeably, Calanoida–C/N ratio fluctuated on wide scale range from 4.19 to 7.13. The lowest value was observed at G11 during pre-monsoon (2013) and highest value at G7 in post-monsoon (2012). The carbon content ranged from 3.51 to 11.02 μM and nitrogen content from 0.49–2.00 μM in Calanoida.

In Poecilostomatoida, the δ^{13}C (−21.61 to−20.87 ‰) and δ^{15}N (2.29 to 6.54 ‰) were comparable to Calanoida. Noticeably, C/N ratio in Poecilostomatoida oscillated widely from 4.37 to 6.50; the lowest value was observed at G11 during pre-monsoon (2013) and highest value at G9 in post-monsoon (2012). In Poecilostomatoida, the carbon (2.92 to 7.82 μM) and nitrogen (0.45–1.38 μM) content was low. At the continental slope as well no significant correlation ($r^2 = 0.00$) was observed between δ^{13}C and δ^{15}N of copepod orders (Fig.4.3), which is an indication of utilization of different nitrogen source.

4.3.4 Seasonal variability of stable isotopes (δ^{13}C and δ^{15}N) in copepod orders of open waters

In Calanoida, δ^{13}C ranged between −22.45 and −20.89 ‰, the minimum value observed in upper 40 m stratum at night and maximum in sub surface (40–140 m) stratum in the day during monsoon (September 2012; Fig.4.4A). Concurrently, the δ^{15}N varied from 5.00 to 8.20 ‰ and the low and high values were observed in monsoon, September 2012 and 2011, respectively (Fig. 4.4B). Likewise, C/N ratio fluctuated between 4.31 and 6.49, the low and high value was observed during February 2013 and September 2012, respectively (Fig.4.4C). Elemental carbon content was 4.08 μM in September 2012 and 7.55 μM in September 2011.Consecutively, elemental nitrogen was found to be low (0.71 μM) during monsoon (September 2012) and high (1.42 μM) in post-monsoon (February 2013).

In Poecilostomatoida, the $\delta^{13}C$ content of copepods was in range −22.48–−18.45 ‰, the minimum value observed in monsoon (September 2012) and maximum in post-monsoon (February 2013). Concurrently, the $\delta^{15}N$ varied from 4.21 to 7.45 ‰ and the low and high values were observed in June 2012 and September 2011, respectively. The C/N ratio varied from 4.87 (February 2013) to6.12 in (June 2012; Fig.4.4C). The elemental carbon content ranged from 2.28 to 14.30 μM and nitrogen between 0.37 and 2.53 μM, with higher values observed in September (2012) and low in June (2012) for both elements. A poor correlation ($r^2 = 0.01$) was observed between $\delta^{13}C$ and $\delta^{15}N$ of copepod orders in open waters of Arabian Sea (Fig.4.4D).

Overall, significant variations were found in $\delta^{13}C$ and $\delta^{15}N$ of copepod orders collected from three study sites namely continental shelf, slope and open waters of Arabian Sea (Table 4.3). Further post hoc test revealed significant variations between $\delta^{13}C$ and $\delta^{15}N$ in open waters.

Table 4.1 Results of ANOVA comparing order-wise and seasonal variation in a stable isotope of carbon and nitrogen

Effect	**SS**	***df***	**MS**	**F**	***p***
$\delta^{13}C$					
Orders	10.06	1.00	10.06	1.00	0.33
Season	78.55	2.00	39.28	3.90	0.04*
Orders X Season	30.44	2.00	15.22	1.51	0.25
$\delta^{15}N$					
Orders	4.42	1.00	4.42	0.40	0.54
Season	75.37	2.00	37.69	3.40	0.06
Orders X Season	46.84	2.00	23.42	2.11	0.15

The variables that were significant are represented with '*' mark.

Table 4.2 seasonal variation in an elemental and stable isotope of carbon and nitrogen in copepod orders in continental slope waters

Order	**Season**	**Station**	**$\delta^{13}C$ (‰)**	**$\delta^{15}N$ (‰)**	**C (uM)**	**N (uM)**	**C/N**
Calanoida	Post-monsoon'12	G7	-21.21	3.78	3.51	0.49	7.13
	Pre-monsoon'13	G7	-20.15	5.16	8.25	1.17	7.06
		G9	-20.10	3.31	11.02	1.75	6.30
		G11	-20.05	6.55	8.39	2.00	4.19
		G13	-20.91	4.98	4.73	1.00	4.71
Poecilostomatoida	Post-monsoon'12	G9	-21.17	4.98	2.92	0.45	6.50
		G11	-21.61	6.54	7.82	1.38	5.69
	Pre-monsoon'13	G7	-20.94	3.94	3.93	0.66	5.98
		G9	-20.87	2.29	5.13	0.84	6.12
		G11	-21.29	5.03	4.44	1.02	4.37
		G13	-21.47	4.30	3.95	0.90	4.38

Table 4.3 Results of ANOVA comparing order–wise and region– a wise variation of a stable isotope of carbon and nitrogen

Effect	**SS**	***df***	**MS**	**F**	***p***	**Post hoc test**
$\delta^{13}C$						
Orders	2.75	1.00	2.75	4.51	0.05*	Poecilostomatoid a
study region	26.72	2.00	13.36	21.93	0.00*	Open Ocean
Orders X study region	0.05	2.00	0.03	0.04	0.96	
$\delta^{15}N$						
Orders	0.48	1.00	0.48	0.54	0.47	
study region	51.47	2.00	25.73	28.86	0.00*	Continental slope
Orders X study region	5.48	2.00	2.74	3.07	0.07	

The variables that were significant are represented with ‘*’ mark.

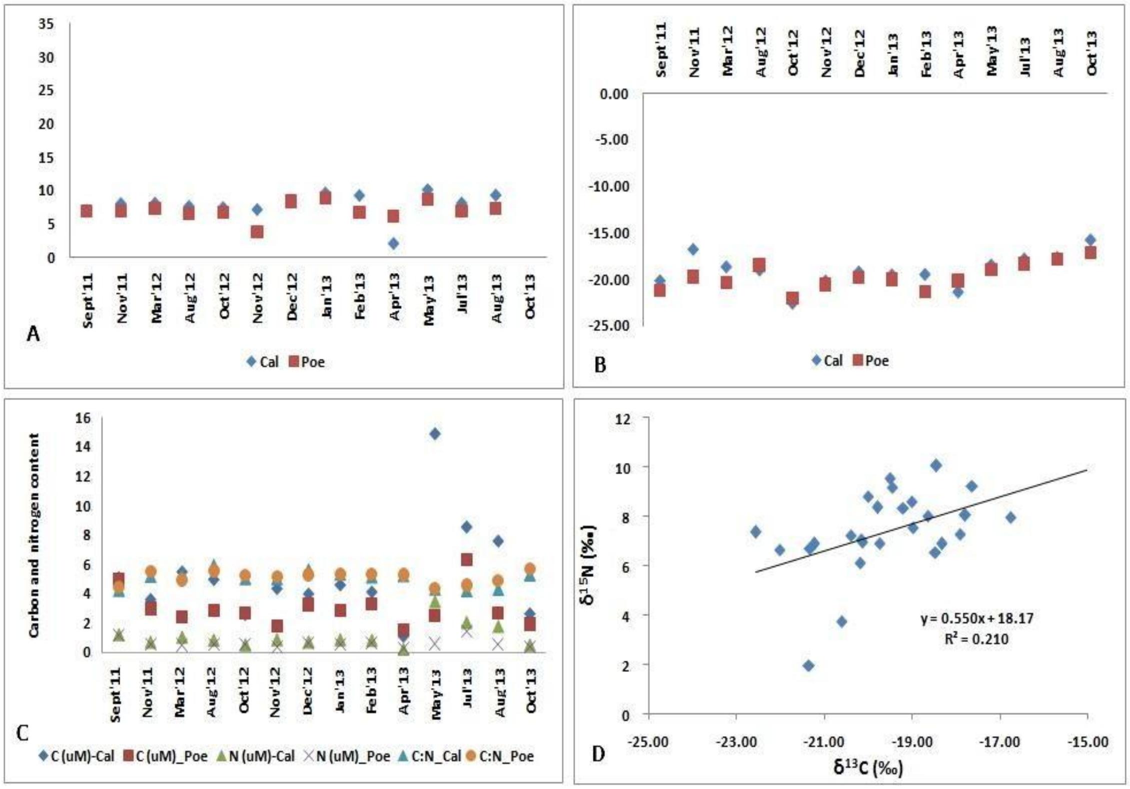


Fig 4.1 The monthly variations of (A) $\delta^{15}N$, (B) $\delta^{13}C$, (C) carbon and nitrogen content and (D) correlation between $\delta^{15}N$ and $\delta^{13}C$ in copepod orders at the continental shelf

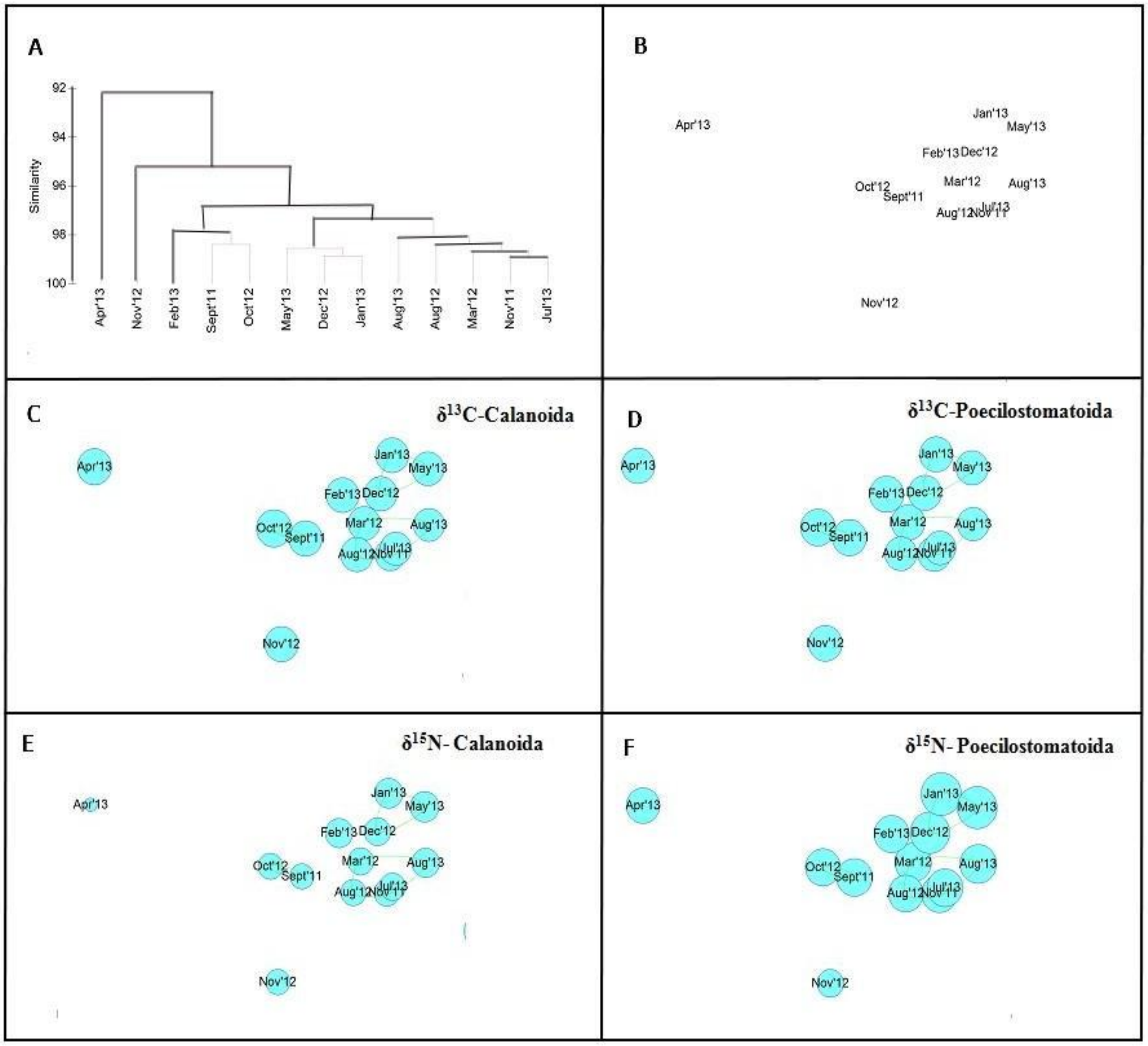


Fig. 4.2 Clusters formed on the basis of copepod stable isotope content at continental shelf (A) Bray–Curtis cluster and (B) nMDS plot. Bubble plot of distinct copepod order (C–F)

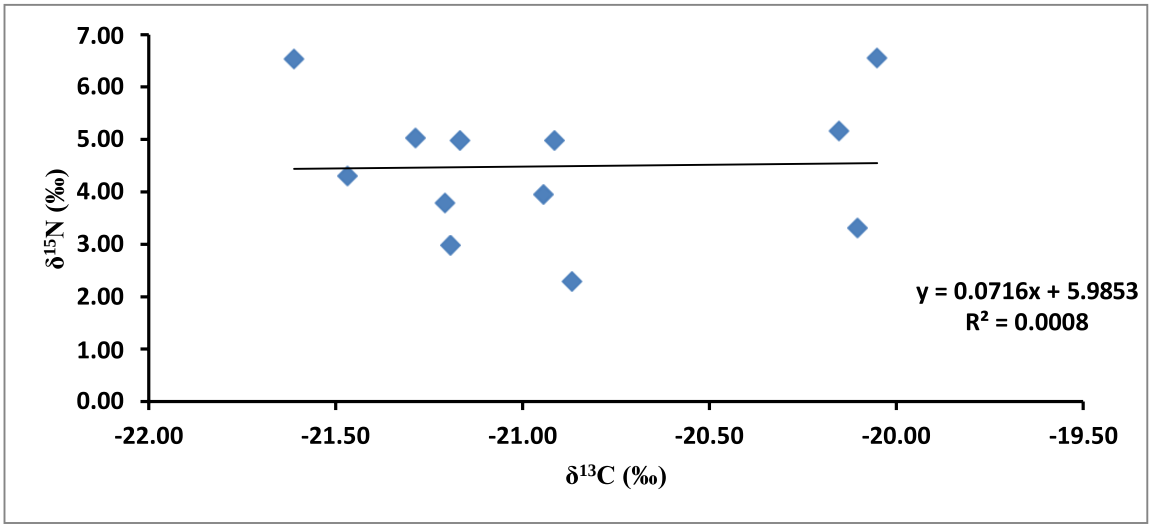


Fig. 4.3 The correlation between $\delta^{15}N$ and $\delta^{13}C$ in copepod orders at continental slope.

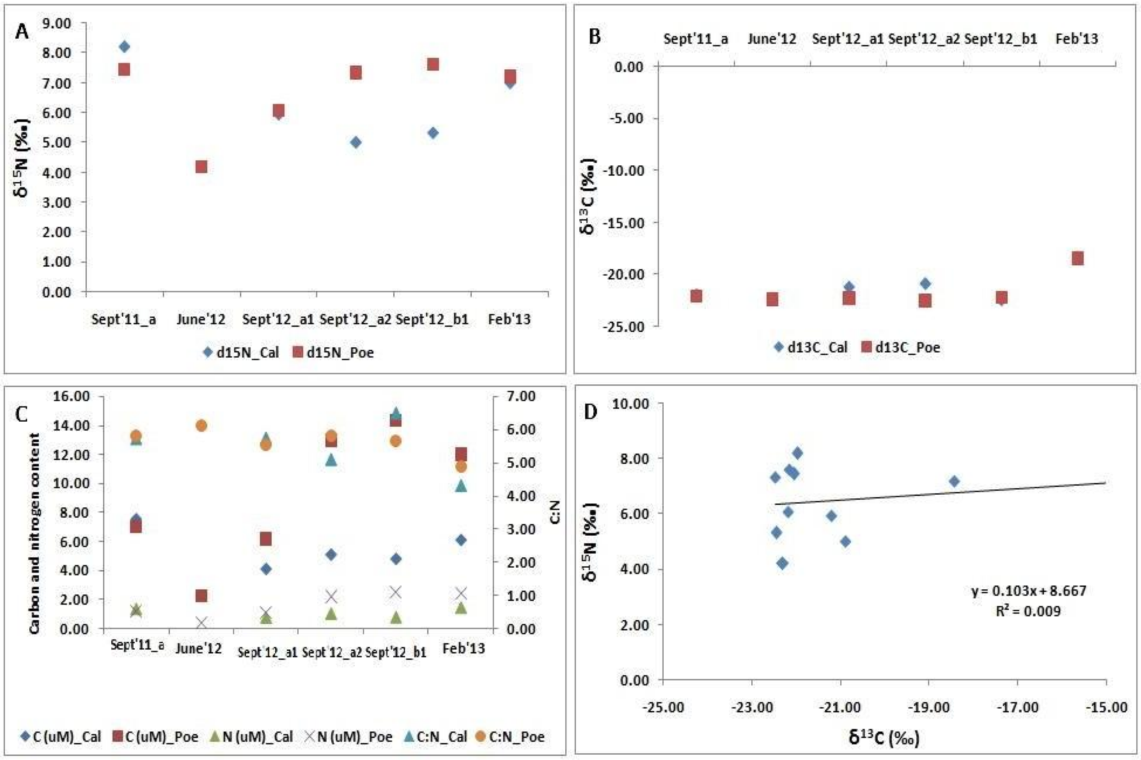


Fig. 4.4 The variations of (A) $\delta^{15}N$, (B) $\delta^{13}C$, (C) carbon and nitrogen content and (D) correlation between $\delta^{15}N$ and $\delta^{13}C$ in copepod orders at open ocean station (ASTS)

4.4 DISCUSSION

Calanoida and Poecilostomatoida are the most dominant orders in the Arabian Sea (Smith and Madhupratap 2005) and other parts of marine ecosystems (Paffenhofer 1993; Gonzalez and Smetacek 1994). The calanoids considered in this study, are reported as herbivores or omnivores while, poecilostomatoids as carnivores (Timonin 1971; Madhupratap et al. 1999). Most tropical calanoids and poecilostomatoids do not hoard extensive lipid stores (Lee et al. 2006). Also, they stay active throughout the year with the constant food supply, which does not require provisions for diapause (Lee and Hirota 1973). These small copepods may have flexible trophic niches that fluctuate with habitat and season (Turner 2004). Besides, these copepods have been characterized as a suspension feeder mostly consuming immobile prey (Peters et al. 2013). Nevertheless, heterotrophic prey may replace the diet of these species during less autotrophic biomass (Loder et al. 2011).

At continental shelf, seasonal variation in δ^{13}C values were observed. A common trend of least δ^{13}C values in pre-monsoon, with a gradual increase in a monsoon to post-monsoon was observed in copepod orders. In general, elevated ratios of δ^{13}C obtained during post-monsoon compared to other seasons gives an indication that the diet of the copepods during the post-monsoon must have been derived from heavier isotopic food sources. Since diatoms can utilize heavy-isotopic bicarbonate ion as a carbon source, they are often heavier in δ^{13}C than flagellates (Fry and Wainright 1991; Laws et al. 1995). Gut fluorescence analysis of the copepod orders also showed the dominance of autotrophic forms in the gut during monsoon and post-monsoon as compared to the pre-monsoon (D’souza and Gauns 2016). Phytoplankton abundance and composition in the study area are reported to be influenced by the seasons (Parab et al. 2006). Also, pre-monsoon season is known to be characterized by lower chlorophyll *a* concentration in the water column (D’souza and Gauns 2016). Microzooplankton that are abundant during the pre-monsoon season along with bacteria (Smith and Madhupratap 2005mayserve as substitute food source for the copepods during the pre-monsoon season when there are limited autotrophic forms.

Continental slope was conspicuous with a narrow range of variation in $\delta^{13}C$ for copepods. Spatially, the $\delta^{13}C$ and community of phytoplankton is known to vary similarly Mediterranean waters (Vizzini et al. 2005). Typically, the ^{13}C abundance relative to ^{12}C was depleted in slope water when compared with shelf waters. Similar to the present study, Sydeman et al. (1997) and Miller et al. (2008) reported that slope-oriented marine organisms had more negative $\delta^{13}C$ values compared to near-shore off northern California. Such relative distinction between the continental shelf and slope species is probably due to the more structured waters from upwelling zone (Lentz 1992; Miller et al. 2008). However, other systems, such as the Georges Bank (Fry 1988) and Scotian Shelf (Mills et al. 1984) exhibited no apparent $\delta^{13}C$ discrimination between near-shore and offshore species. This may be due to the well-mixed waters that undergo benthic–pelagic coupling that structure the pelagic ecosystems.

Open waters of Arabian Sea are known to harbor different phytoplankton than the continental shelf region, mostly dominated by picoplankton. However, the $\delta^{13}C$ values are similar to shelf copepod orders (−22.45 to −18.45 ‰). It is difficult to pinpoint the exact cause; however such inconsistency in primary producers’ $\delta^{13}C$ must be reflected onto the changes in baseline $\delta^{13}C$. Moreover, isotopic fractionation in phytoplankton is subjective to its growth rate and cell dimension (Laws et al. 1995). Graham et al. (2010) speculated more negative $\delta^{13}C$ in the open ocean of warmer seas as compared to colder regions.Further, these spatial trends were coupled with lower photosynthetic rates linked to the lower latitudes. A similar relationship between $\delta^{13}C$ and geographic region interpolated higher values of carbon isotope closer to shore and in the mid-Atlantic region (Oczkowski et al. 2016).In the present study region, the isotopic composition of carbon in copepod orders differ significantly with time and space across continental margins and open waters of this tropical sea and these differences may be reflected in top predators. There could be several reasons for variation in the $\delta^{15}N$ for copepods, apart from changes in their trophic position. The baseline $\delta^{15}N$ value will modify considerably based on nutrient supply to the phytoplankton (Hannides et al. 2009). Certainly, variations in $\delta^{15}N$ of phytoplankton or the microbial loop components are tightly coupled to the source of nitrogen (Leggett et al. 2000; O'Reilly et al. 2002; Rau et al. 2003). In coastal waters, large variations are predictable both in terms of absolute supply and the nitrogen form, either as nitrate or as ammonium. There is also the possibility that the fractionation could be altering on the basis of food quality and availability (Vander Zanden and Rasmussen 2001; Robbins et al. 2010). The $\delta^{15}N$ in copepod orders seems to vary less as compared to $\delta^{13}C$with respect to geographic variations. In general, relatively stable $\delta^{15}N$ values in tropical waters have been previously reported (Fry and Quinones 1994; Hannides et al. 2009), whereas more variable values have been found in coastal and boreal waters (Rolff 2000; Bode et al. 2007). In continental shelf waters, the $\delta^{15}N$ of copepod orders revealed seasonal variation with a wide range of fluctuation during pre-monsoon as compared to monsoon and post-monsoon. Conspicuously, heavier values were observed in Calanoida as compared to Poecilostomatoida. The copepods exhibited highly enriched $\delta^{15}N$ values in pre-monsoon season imply the strong influence of decreased phytoplankton biomass and increased water column temperatures. As the stepwise increase of δ^{15}N in marine food webs is usually 3–4‰ per trophic level (Michener and Schell 1994) is considered, therefore, baseline mean δ^{15}N value is assumed to be 3.4‰. Hence, the enrichment pattern revealed omnivorous feeding habit favored by animal based diet when compared to δ^{15}N–SPOM (3.4‰). As the δ^{15}N of plankton reflect the nitrogen supporting production and the biological processes that may alter the isotopic abundances in the ecosystem (Montoya et al. 2002). In this regards, pre-monsoon is characterized by the dominance of picoplankton (Parab et al. 2006) and blooms of *Trichodesmium* (Devassy 1979; Nair et al. 1992) that are known to promote lighter isotopic nitrogen. Additionally, mostly these *Trichodesmium* bloom are not grazed by the marine fauna (Nair et al. 1992). This suggests that copepods present in this study region might have utilized heterotrophic feed along with phytoplankton to cater their energy requirement.

Comparatively, intermediate values of enriched stable nitrogen were recorded in monsoon from shelf region, suggesting a strong influence of increased phytoplankton biomass. Therefore, seasonal shifts in δ^{15}N–copepodscorresponding to switch in diet imply assimilation of a new δ^{15}N baseline instead of a change in trophic position (Dale et al. 2011; Reid et al. 2013). Conspicuously, Poecilostomatoida attained the least enrichment of δ^{15}N (6.53 ‰). This seems to be inclined with reports on their autotrophic feeding habit (Metz 1998; D'souza and Gauns 2016). However, Poecilostomatoida are reported to feed on larvacean houses (Ohtsuka et al. 1996) as well and thus suggest a need of further investigation on their feeding ecology. Relatively, lighter δ^{15}N was observed in copepods in post-monsoon as compared to other seasons. Consumption of nutritionally deprived phytoplankton as compared to nitrate-replete phytoplankton of monsoon (Malzahn et al. 2007; El-Sabaawi et al. 2013) may be responsible to such variability. Alternatively, a shift in phytoplankton from diatom to dinoflagellates (Parab et al. 2006) might have contributed to depleted $\delta^{15}N$.It is well recognized that the $\delta^{15}N$ of dinoflagellates are less enriched as compared to diatoms (Kurten et al. 2016). Seasonal variability in Poecilostomatoida revealed less $\delta^{15}N$ enrichment in post-monsoon (3.76 ‰) than that of monsoon and pre-monsoon. The lower $\delta^{15}N$ for Poecilostomatoida corresponds with the observation from Red Sea (Kurten et al. 2016) and Gulf of Aqaba (Aberle et al. 2010). Such low values of $\delta^{15}N$ confer the ability of Poecilostomatoida to utilize the tiny heterotrophic nanoflagellates and dinoflagellates to bridge their energy requirement (Ohlendieck et al. 2000).

Concurrently in continental slope waters, the $\delta^{15}N$ of copepod orders varied from 2.29 (Poecilostomatoida) to 6.55 ‰ (Calanoida). Phytoplankton during this period seem to be dominated by isotopically depleted forms such as flagellates and cyanobacteria compared to large phytoplankton and detritus (Fry and Wainwright 1991; del Giorgio and France 1996; Fawcett et al. 2010). The selective feeding on this prey may have resulted in the low isotopic signatures in calanoids and poecilostomatoids.

Consecutively, the $\delta^{15}N$ of copepods varied from 4.21 to 8.20 ‰ and the low and high values were observed in Poecilostomatoida (June 2012) and Calanoida (September 2011) in open waters of the Arabian Sea. The baseline $\delta^{15}N$ of POM dominated by phytoplankton alter depending upon the nitrogen source and its isotopic fractionation during uptake and assimilation (Montoya and McCarthy 1995; Schmidt et al. 2003). Additionally, it is influenced by seasonal and regional variations in phytoplankton, light intensity and temperature (Waser et al. 1998). The $\delta^{15}N$ of POM revealed seasonal variability in the eastern Arabian Sea (Maya et al. 2011) and in Baltic Sea (Rolff 2000). As such copepods isotopic values are not comparable to other zooplankton, however, *Pyrosomaspinosum* (tunicates) encountered in open waters of the Arabian Sea exhibited similar δ^{15}N (7.43 ‰; Gauns et al. 2015).

Although the enrichment in δ^{15}N between trophic levels can be inconsistent (McCutchan et al. 2003), a mean trophic fractionation of 3.4‰ is widely applicable (Post 2002). Due to variations in tissue composition and metabolic pathways the fractionation factor will differ for different species and tissues (DeNiro and Epstein 1981; Pinnegar and Polunin 1999; Schmidt et al. 2004) and thus the isotopic enrichment for individual trophic transfers is variable. The application of a fixed average enrichment factor could thus lead to errors in estimated trophic level. Nevertheless, for consistency and comparability with other similar studies, considering enrichment factor that has been averaged across numerous studies and species (Minagawa and Wada 1984; Post 2002; Stowasser et al. 2012; Kurten et al. 2016) revealed typically omnivorous feeding habit of Calanoida and Poecilostomatoida. Few values referring to either depleted or enriched isotopic contents require further work to conclude on the selectivity of baseline δ^{15}N.

Quality and quantity of feed play fundamental role in the chemical composition of copepods (Cataletto and Umani 1994). In Continental shelf waters, Calanoida attained highest carbon (14.91 μM) and nitrogen (3.44 μM) content during pre-monsoon. Variations in C/N–copepod orders during pre-monsoon (4.32–5.28) and monsoon (4.20–5.91) were comparable, unlike post-monsoon (5.01–5.62). Calanoida mostly composed of *Paracalanus* spp. revealed C/N ratio similar to the previous report by Checkley (1980). In Continental Slope realm, the highest values of carbon (11.02 μM) and nitrogen (1.75 μM) content for copepods order was observed in Calanoida that was depleted as compared to the continental shelf. Unlike other region, C/N ratio for copepod order (4.19–7.13) in continental slope waters showed high variation and the highest value was observed in post-monsoon in Calanoida. In Open waters, Copepod orders affirmed highest carbon (14.30 μM) and nitrogen (2.53 μM) in Poecilostomatoida. Similar toδ^{13}C values, the carbon content of copepod orders from open waters showed similarity with continental shelf. Copepod orders–C/N ratio (4.31–6.49) in open waters markedly differed from the continental shelf and slope waters. Omori (1969) noted that the high percent of carbon content could coincide to spring bloom of diatoms and increase in nitrogen content. Collectively, the high carbon content of copepod orders from the study region implies copepods seem to attain proper nutritional requirement from various food resources.

Coupling between δ^{13}C and δ^{15}N indicated possible contributions of multiple carbon or nitrogen sources to zooplankton diets in each ecological zone (William 2013). The linear relation between carbon and nitrogen isotope ratio is attributed to kinetic isotope effects inherent to amino acid synthesis (Macko et al. 1986; Minagawa et al. 1992; Aita et al. 2011). Copepods in continental margins and oceanic realm depicting positive coupling between δ^{13}C and δ^{15}N pin points that they meet their carbon or nitrogen requirement by feeding on a matter that originated from different sources. Association among copepod–δ^{13}C and δ^{15}N is affected by the buildup of material originating from either different carbon fixation pathways or from changes in nitrogen sources. In view of the fact that δ^{13}C and δ^{15}N values get enriched with each trophic level, δ^{13}C and δ^{15}N would be significantly related if the baseline isotopic composition was consequent of single carbon and nitrogen source (Polunin et al. 2001; Fanelli et al. 2009; William 2013). Weak correlation observed between $\delta^{15}N$ and $\delta^{13}C$ in Calanoida and Poecilostomatoida at continental shelf ($r^2 = 0.21$; Fig. 4.1D), slope ($r^2 = 0.00$; Fig.4.3) and open waters ($r^2 = 0.01$; Fig. 4.4D) of the Arabian Sea implies a multiple carbon source.

In conclusion, the present study revealed site-specific strategies on feeding preferences in tropical copepod orders from the continental shelf, continental slope and open waters of the Arabian Sea. Based on the $\delta^{15}N$ enrichment of calanoids and poecilostomatoids, overlapping feeding modes were detected depending upon prey availability and individual metabolic requirements. Nonetheless, omnivory was the prevailing feeding mode, demonstrating a high degree of opportunistic feeding in tropical copepods. In addition, distinct spatial patterns in $\delta^{13}C$ of copepods were found showing elevated values in the dynamic continental shelf, which was more pronounced in poecilostomatoids. In general, feeding modes of omnivores appeared rather unselective, and relative contributions of heterotrophic protists and degraded material in the diets of copepods is presumed. Studies on copepod feeding strategies and dietary preferences are decisive to understand the transfer of energy to other trophic levels in marine food webs. Studies of this nature will enhance the knowledge of energy fluxes from the continental margins to the open ocean in tropical pelagic food webs.

Chapter 5

FEEDING OF COPEPODS IN ARABIAN SEA, AS DETERMINED BY GUT FLUORESCENCE TECHNIQUE

5.1 INTRODUCTION

Copepods are the dominant members of the mesozooplankton community in the Arabian Sea (Madhupratap et al. 1990) and in the other parts of the world oceans (Roman and Gauzen, 1997; Lo et al. 2004). Moreover, copepods are the key link between the phytoplankton and economically important fishes (Madhupratap et al. 2001). Therefore, food consumed by copepods has a deterministic influence on the transfer of energy to the higher trophic organisms. Copepod grazing is influenced by different aspects like copepod abundance (Atkinson 1996), seasonal variation (Tseng et al. 2008) and type and quantity of feed (Atkinson 1996; Tseng et al. 2009). As a result of grazing, copepod generates carbon-rich fecal pellets. Furthermore, copepods persuade the energy transfer to the different trophic levels across the marine food web. Being a notable contributor to the marine biological pump, it is crucial to understand copepods' feeding strategies. Although, copepods are known to feed on wide range of food (Turner 2004), their tendency to switch its diet on the locale-basis, makes it vital to understand their feeding in every habitat (Stern 1986; Peters et al. 2013).

In common, the feeding habit of copepods was deduced on the morphological basis of mouthparts (Madhupratap 1999). Also, experimental studies with bottle incubations have been used to study diets of calanoid copepods (Jansen et al. 2006). But the experimental pressure on organisms may lead to varied feeding habit than the *in situ* feeding type. Moreover, the strategies of copepods feeding might be selective (Go et al. 1998) or non-selective (Tseng et al. 2008) depending upon the mixed dietary type, algal-make and toxicity (Atkinson 1996; Jansen et al. 2006). Copepods are known to impact the microbial assemblages (Schnetzer and Caron 2005) by grazing the bacterial biomass (Gowing and Wishner 1998). Studies on copepod feeding habits were mostly addressed with either direct gut examination (Gowing and Wishner 1998) or fecal pellets study (Turner et al. 2002), but these methods seem to be unpredictable to determine the diet composition as lots of feed could go unclaimed with swift digestion.

Gut fluorescence technique is extensively used to reveal the *in situ* feeding habits of copepods by numerous researchers (Mackas and Bohrer 1976; Kleppel and Pieper 1984; Rodriguez and Durbin 1992; Tsuda and Sugisaki 1994; Saito and Taguchi 1996; Takatsuji et al. 1997; Tseng et al. 2009). Gut pigment contents analyzed using fluorometer analysis gives a quantification of only chlorophyll *a* and its derivatives, and HPLC gives the composition of gut pigments (Kleppel and Pieper 1984). The gut pigments, chiefly canthaxanthin and astaxanthin remains stable in copepod gut (Lotocka and Styczynska-Jurewicz 2001) and suitably gets eluted by chromatography (Jeffrey 1981) which are the bio-indicators of feed (Lewin 1974).

Sole producers of carotenoids *de novo* are the autotrophs (Lotocka and Styczynska-Jurewicz, 2001; Matsuno 2001), which is grazed by heterotrophs as β-carotene and further metabolically transformed as astaxanthin and canthaxanthin (Kleppel et al. 1985; Matsuno 2001; Nieuwerburg et al. 2005). The exploitation of precursor carotenoids and consecutive production of astaxanthin by herbivorous mesozooplankton thus signifies a crucial doorway of astaxanthin into marine food webs.

This is the first *in situ* study of copepod gut pigments from different topographic regions of the Arabian Sea. I intended to study the copepod gut pigments (quantitatively) on a seasonal scale from representative stations covering continental shelf, slope and oceanic realm to understand copepod feeding behavior. To gain better insights on copepod feeding types, monthly observations were carried out on the continental shelf station that is situated in the vicinity of the coast. The gut pigments of copepods orders were studied quantitatively (fluorometric) as well qualitatively (pigment composition) using gut fluorescence method at the monthly sampled station (G5). This objective is complementary to the stable isotope technique. It provides a supportive data on feeding habits of copepod Orders over different seasons across a transect covering continental shelf, slope and the oceanic realm of the Arabian Sea.

5.2 MATERIALS AND METHODS.

5.2.1 Sampling

The continental shelf station (G5) located at 15°31.17N and 73°44.200E off Candolim, Goa, on the central west coast of India (Fig. 1.2) was sampled on the monthly basis. A single representative station at continental shelf (G7; 15°28.92N and 73°29.9E), slope (G11; 15°20.47N and 73°0.04E) and oceanic stations (ASTS; 17 °N and 68 °E) was selected for seasonal collections. The collection was done either from entire water column i.e., surface to bottom or from the epipelagic realm (0–200 m) from deeper depth stations. The monthly sampling at G5 was carried out in daytime from November'11 to October'13. However, due to rough weather samples were not collected for gut fluorescence analysis during December'11–February'12, April–May'12, June–July'12, September'12 and June'13. The seasonal sampling was carried out onboard research vessels during June'12 (SK- 294), September'12 (SSK-38), February'13 (SSK-46) and October'13 (SSK-56). It covered monsoon (June–September), post-monsoon (October–January) and pre-monsoon (February–May) seasons.

Mesozooplankton samples collection is mentioned in the methodology section of chapter 2. Chlorophyll estimation (Chl *a*) from the ambient water was carried out only at G5. Water samples for water Chl *a* were collected using a 5 L Niskin sampler coupled with a reversible thermometer mounted on nylon rope enabling temperature measurement. To obtain adequate vertical resolution of the water column, a vertical sampling of water Chl *a* was done in four depths (0 m, 9 m, 18 m and 27 m) by collecting a known volume of water sample (0.5 L) in the amber colored bottle. All the samples were stored in the icebox until transferred to the laboratory for further processing. The data on salinity was obtained using CTD (Conductivity–temperature–depth; Sea-Bird electronics). The seasons covered include monsoon (June–September), post-monsoon (October–January) and pre-monsoon (February–May).

5.2.2 Fluorometric estimation of water Chl *a*

The Chl *a* concentrations in ambient water were estimated using JGOFS protocol (UNESCO 1994) with slight modification. Water samples of 0.5 L were filtered using GF/F polycarbonate filters (47 mm) and extracted in 90 % acetone at −20 °C overnight in dark. The acetone extract was analyzed by Turner Designs-10 fluorometer before and after acidification with 1.2 M HCl under scanty light condition.

Water column Chl *a* (mg/m^2) was obtained after integrating the four depths sampled for water chlorophyll analyses and was used as ambient water Chl *a* to the mesozooplankton.

5.2.3 Copepod sorting and fluorometric estimation of gut pigments

Mesozooplankton were stored at −20 ºC for the gut pigments analyses were thawed, rinsed with filtered seawater and sorted under a microscope for different copepod orders with minimum light and then the gut pigments were analyzed using fluorometer.

Gut fluorescence method was followed as described by Mackas and Bohrer (1976) with slight variation proposed by Wong et al. (1998), Islam et al. (2005) and Tseng et al.

(2008) for the current study. A known measure of individuals (ranged 20–40) were selected and set aside for extraction in 6 ml of 90 % acetone in dark under −20 ºC (Islam et al. 2005) for 24 hr without homogenization (Wong et al. 1998; Tseng et al. 2008). Once the pigments were extracted, the upper clear solution was then analyzed by Turner Design-10 Fluorometer in low illumination before and after acidification. Acidification was performed using 1.2 M HCl. Literature suggests phaeopigment loss during estimation using the gut fluorescence technique (Dagg and Wyman 1983; Tseng et al. 2008), hence, all the phaeopigment values were multiplied by a factor of 1.51 (Dagg and Wyman 1983). Gut pigment contents were expressed as ng/copepod for Chl *a*, phaeopigment and total pigment (obtained from the addition of Chl *a* and corrected phaeopigment) concentrations in the copepod gut (Dam and Peterson 1988).

5.2.4 Gut pigment composition by HPLC

Due to the requirement of a high number of individuals per copepod order (~300) for HPLC analyses, only Calanoida and Poecilostomatoida were considered for qualitative pigment assessment sampled at the continental shelf on a seasonal scale.

The individual copepods were sorted and placed in a vial containing 2ml of HPLC grade methanol. The samples were not sonicated as previously analyzed samples did not show much variation in the pigment extracted with or without sonication. Further, the samples were placed at −20 ºC for 24 hrs in dark for pigment extraction. The clear extract was then sampled in 3 ml amber colored glass vial and passed straight into the sampler tray for analyses (Gasparini et al. 2000).

Eclipse XDB C8 HPLC column (4.6 x 150 mm) manufactured by Agilent Technologies was used to carry out the analysis. Two solvents used for elution were methanol and mixture of (70:30) methanol and 1 M ammonium acetate (pH 7.2). The eluting pigments were detected at 450 and 665 nm (excitation and emission) by the diode array detector. All the chemicals used were of HPLC grade (E. Merck, Germany).

5.2.5 Statistical analysis

Spearman's non-parametric correlation was executed to examine the pattern of variation of gut Chl *a* and gut phaeopigments in copepods orders. Two-way analysis of variance (ANOVA) was performed to observe the significant seasonal and depth-wise variation in water Chl *a* and phaeopigment. Similarly, ANOVA was carried out to check significant seasonal variations of total gut pigments in different copepods orders. Subsequently, Tukey's Post Hoc test was used to reveal the significant variation within the different seasons. Values were considered significant at 95% level of confidence (Statsoft, Statistica 6.0).

5.3 RESULTS

5.3.1 Environment

The results on salinity and dissolved oxygen have been adopted from the previously published article by Naqvi et al. (2006) that depicted a decadal variation of these parameters from the study region. This work reports distinct variations during monsoon with lower values in temperature and salinity. The minimum salinity value of 34.8 and maximum of 36.0 was reported during monsoon and pre-monsoon.

The minimum and maximum temperature recorded during the present study ranged 23.5–29.4 °C during monsoon (August'12) and pre-monsoon season (March'12; Fig. 5.1). The highest (August'12) and lowest (April'13) concentration of surface water chlorophyll *a* ranged between 0.69 and 4.29 ng/mL. While the lowest (March'13) and highest (July'13) concentration of water phaeopigment ranged 0.05–4.59 ng/mL.

5.3.2 Seasonal variation in copepods

As mentioned in chapter 2, copepods, the dominant mesozooplankton group comprised 72–99 % of the abundance. Seasonally, monsoon observed low copepod abundance (93600 ± 30399 individuals/100 m^3; Fig. 5.2) with the dominance of species *Oncaea venusta*. Highest copepod density was observed during post-monsoon (133062 ± 76342 individuals/100 m^3), dominated by *Acrocalanus* spp. Amongst, Calanoida dominated the copepod community throughout the year with an occasional dominance of Poecilostomatoida (46543 ± 28178 individuals/100 m^3) during pre-monsoon. The dominant Calanoida and Poecilostomatoida families represented annually were Paracalanidae and Oncaeidae, respectively.

The species occurring continuously throughout the year were considered for studying feeding habits. So, *Acrocalanus* spp., *Paracalanus* spp., *Subeucalanus* spp., *Temora* spp. and *Acartia* spp. of order Calanoida, *Euterpina* sp. of Harpacticoida, *Oncaea* spp. and *Corycaeus* spp. of Poecilostomatoida and *Oithona* spp. of Cyclopoida were considered for this study. Among the given Calanoida, only the dominant species which were potentially herbivores according to the existing knowledge of their feeding biology by literature review were taken into account.

5.3.3 Variation in water column Chlorophyll *a* and phaeopigment

The water Chl *a* content in the surface water ranged 1.69–2.96 ng/mL; minimum and maximum concentration recorded during post-monsoon and monsoon (Fig. 5.3A). The minimum (0.59 ng/mL) and maximum (1.93 ng/mL) concentration of phaeopigment content in the surface water was recorded during pre-monsoon and monsoon season (Fig. 5.3B). The water Chl *a* content at 9 m depth ranged 1.14–3.50 ng/mL, at 18 m 2.47–6.52 ng/mL and at 27 m 1.73–6.60 ng/mL. While, the phaeopigment concentration ranged 0.20–0.54 ng/mL at 9 m, 0.35–1.58 ng/mL at 18 m and1.11–2.15 ng/mL at 27 m depth. On the contrary to the surface water Chl *a*, the other depth zones (9 m, 18 m and 26 m), showed highest water Chl *a* values during pre-monsoon. Besides, highest phaeopigment concentration for 9 m and 26 m deep waters was observed during post-monsoon. Seasonally, the Chl *a* variation differed significantly ($p < 0.001$; Table 5.1), nevertheless no significant variation was observed within the depths and the interaction between the season–depth. Further, post hoc test revealed significantly high Chl *a* in monsoon ($p < 0.001$).

5.3.4 Temporal variation in gut copepod Chlorophyll *a* and phaeopigment content at the continental shelf

Quantitative analysis of gut pigment content of Calanoida, Poecilostomatoida, Harpacticoida and Cyclopoida was carried out on a monthly basis from November 2011 to October 2013 at G5. A lapse in data for few months is owed to either difficulty in sampling during the rough weather or absence of a sufficient number of individual species required for analysis. Also, samples analyses were carried out in duplicates wherever an adequate number of organisms of copepod orders were available.

The gut Chl *a* (Fig. 5.4) and phaeopigment (Fig. 5.5) in copepods showed distinct variation. Estimates of gut Chl *a* and phaeopigment content for the Calanoida copepods were highest during monsoon (July'13; Fig. 5.4A, 5.5A). However, the least value for gut Chl *a* and phaeopigment content was observed during pre-monsoon (April'13) and post-monsoon (November'12), respectively. Also, their gut pigments showed the highest variability for gut Chl *a* (0.02–1.02 ng/copepod) and gut phaeopigment (0.11–3.26 ng/copepod) as compared to Poecilostomatoida, Harpacticoida and Cyclopoida. Calanoida exhibited comparatively larger variability in body size (0.93–2.6 mm).

In Poecilostomatoida, the gut Chl *a* content ranged between 0.013 and 0.548 ng/copepod (Fig. 5.4B) and gut phaeopigment ranged from 0.07 to 1.23 ng/copepod (Fig. 5.5B). The highest copepod gut Chl *a* was observed in the month of October'12 and least in August'13. Consecutively, highest (1.11 ng/copepod) and least (0.07 ng/copepod) gut phaeopigment content was observed in the month of August'12 and December'12, respectively. Furthermore, the total body size of poecilostomatoids in the study region varied between 1.00 and 1.27 mm.

Although Harpacticoida comprised of minimal body size (0.35–0.66 mm), it secured second highest gut Chl *a* pigment (0.03 to 0.693 ng/ copepod; Fig. 5.4C). The highest concentration of harpacticoid gut Chl *a* was observed in August'12 and the lowest in July'13. Consecutively, phaeopigment content was in the range of 0.098–1.712 ng/copepod (Fig. 5.5C) with least value recorded in November'12 and highest during March'12.

Cyclopoida had the most slender body and their size ranged from 0.75 to 1.50 mm. Comparatively, this order was recorded to have the least content of gut Chl *a* pigment and phaeopigment content that ranged from 0.014–0.42 ng/copepod (Fig. 5.4D) and 0.06–1.45 ng/copepod (Fig. 5.5D), respectively. The high and low value for copepod gut Chl *a* was observed in October'12 and March'12, respectively. Successively, gut phaeopigment concentration was least during December'12 and highest in July'13.

Overall, inter-annual and seasonal variability was observed in gut Chl *a* pigment and gut phaeopigment content of copepods. Equally, the pattern of variation of gut Chl *a* and phaeopigment differed. Consecutively, Chl *a* was always less copious than phaeopigment in the gut of copepods; however, no significant statistical relation was observed. A peculiar feature was noted in March'13 in all copepod orders that gut Chl *a* was more compared to gut phaeopigment.

The integrated water column Chl *a* recorded highest during monsoon (86.08 mg/m^2) followed by post-monsoon (46.26 mg/m^2) and the least during pre-monsoon (42.80 mg/m^2). When integrated water column Chl *a* was correlated with gut Chl *a* of all the four copepod orders, no significant correlation was observed. The lack of correlation was more obvious in Calanoida (n= 21; r^2= 0.06; Fig. 5.6A), Poecilostomatoida (n= 20; r^2= <0.01; Fig. 5.6B), and Cyclopoida (n= 15; r^2= 0.06; Fig. 5.6D) than in Harpacticoida (n= 15; r^2= 0.28; Fig. 5.6C)

5.3.5 Seasonal variations in copepod gut chlorophyll *a* and phaeopigment across the transect

Seasonal variations of gut pigments of copepods studied across the transect had three representatives of varied topographic structures. Due to lesser sample size, limited analyses of copepod Orders were possible.

The copepods gut Chl *a* (Fig. 5.7) and phaeopigment (Fig. 5.8) showed a distinct variation on the spatial and seasonal scale. Highest estimates of gut Chl *a* (1.02 ng/copepod; Fig. 5.7A) and phaeopigment content (3.26 ng/copepod; Fig.5.8A) for the Calanoida copepods were observed during a monsoon on the continental shelf. However, the least value for gut Chl *a* (0.03 ng/copepod) was noticed during post-monsoon at the oceanic site. Consecutively, the lowest phaeopigment content (0.05 ng/copepod) was observed during pre-monsoon at the continental slope.

Being the most dominant order at the slope and oceanic realm, Poecilostomatoida attained the gut Chl *a* content in the range of 0.02–0.25 ng/copepod (Fig. 5.7) and gut phaeopigment 0.15–0.84 ng/copepod (Fig. 5.8). The highest copepod gut Chl *a* was observed in pre-monsoon at the continental shelf and least in a monsoon at the oceanic site. Consecutively, highest and least gut phaeopigment content was observed in monsoon (continental shelf) and pre-monsoon (continental slope), respectively.

Although Harpacticoida were merely found at continental slope and oceanic site, it showed comparatively high gut Chl *a* pigment (2.00 ng/ copepod) and phaeopigment (1.50 ng/copepod) content at the continental slope during monsoon. Conspicuously, harpacticoid gut Chl *a* was below detectable limit at the continental shelf in post-monsoon. The phaeopigment content in harpacticoids was detected in less concentration for the most part of the year except in monsoon.

Cyclopoida recorded gut Chl *a* pigment and phaeopigment content in the range <0.01–1.32 ng/copepod and <0.01–1.45 ng/copepod (Fig. 5.7 and 5.8), respectively. A common trend of high gut Chl *a* and phaeopigment concentration was observed during monsoon. But the highest gut Chl *a* was observed at the continental slope realm. The low gut Chl *a* and phaeopigment value was recorded in pre-monsoon (at the oceanic site) and post-monsoon (continental slope), respectively.

Overall, geographic and seasonal variability was observed in gut Chl *a* pigment and phaeopigment content of copepods. Evenly, the pattern of variation of gut Chl *a* and phaeopigment fluctuated. Simultaneously, no peculiar feature of low Chl *a* compared to phaeopigment in the gut of copepods was observed.

5.3.6 Seasonal variation in total gut pigment in copepod orders at the continental shelf

The data are presented on a seasonal scale; specifically, monsoon (June–September), post-monsoon (October–January) and pre-monsoon (February–May). Further, qualitative analysis of gut pigment content was carried out following HPLC technique on a seasonal basis for the copepod orders: Calanoida and Poecilostomatoida. Due to unavailability of a required number of individual species of Harpacticoida and Cyclopoida, these orders were not taken into consideration for analyses.

Estimates of total gut pigment contents for the copepod orders showed higher concentration during monsoon than during pre-monsoon and post-monsoon (Fig. 5.9). The total gut pigment (Chl *a* and corrected phaeopigments) in Calanoida varied 0.27–5.93 ng/copepod (Fig.5.9A) more than that of Poecilostomatoida, Cyclopoida and Harpacticoida. Seasonally, monsoon depicted the highest gut pigment content (2.02 ± 2.15 ng/copepod). Further, the qualitative analysis revealed the predominance of astaxanthin, canthaxanthin and alloxanthin pigment (Table 5.2). However, alloxanthin, marker pigment of Cryptophyta was conspicuous by its absence in pre-monsoon suggesting seasonality in gut pigment composition of Calanoida. Consecutively, total gut pigments ranged between 0.12 and 2.01 ng/copepod (Fig. 5.9B) for Poecilostomatoida. Again, the highest gut pigment content, 1.15 ± 0.79 ng/copepod was noticed in monsoon. Successively, qualitative gut pigment composition revealed predominantly canthaxanthin and astaxanthin (Table 5.2). HPLC absorbance chromatogram depicted the peaks of gut pigments in Calanoida and Poecilostomatoida composition during post-monsoon. Few tiny peaks eluted were at lower limits of detection hence confirmation of their identity was critical. Amongst, harpacticoids attained the second highest total gut pigment values that ranged from 0.20–2.75 ng/copepod (Fig. 5.9C). However, a decline in total gut pigment was prominent in post-monsoon although gradual elevation was observed during pre-monsoon season. Furthermore, the seasonal variation showed a similar trend as observed in Calanoida copepods. Similarly, total gut pigment content in Cyclopoida varied from 0.17 to 2.41

ng/ copepod (Fig. 5.9D) with highest values noticed in monsoon (1.12 ± 0.82 ng/ copepod). Further, the variation of gut pigment concentration was almost similar to that of Poecilostomatoida, with descending concentration from monsoon to post-monsoon and pre-monsoon.

The total gut pigment content of copepods observed major contribution of phaeopigment than chlorophyll. Copepods were found to contain photosynthetic pigments in their gut throughout the year. However, gut pigment concentration was maximum during monsoon indicating significant variability ($p < 0.01$; Table 5.3). Further Post-Hoc test revealed high value during post-monsoon ($p < 0.01$).

5.3.7 Seasonal variation in total gut pigment in copepods across the transect

Overall, the total gut pigment content in Calanoida was more than that of Poecilostomatoida, Cyclopoida and Harpacticoida (Fig. 5.10). In particular, monsoon depicted the highest gut pigment content; the highest value was recorded at continental shelf (5.93 ng/copepod) and least at the oceanic site (0.23 ng/copepod). During pre-monsoon the total gut pigments in calanoid varied in the range of 0.23–3.13 ng/copepod and post-monsoon 0.15–0.70 ng/copepod. Conspicuously, the highest value of total pigment content during post-monsoon was attained at the oceanic site.

Consecutively, total gut pigments ranged between 0.07 and 1.53 ng/copepod for Poecilostomatoida (Fig. 5.10). The highest and least pigment content was attained during pre-monsoon at the shelf and slope realm, respectively. During monsoon the total pigment varied in the range of 0.26–1.30 ng/copepod and post-monsoon 0.14–0.34 ng/copepod.

Harpacticoida attained total gut pigment values that ranged from below detectable limit to 4.25 ng/ copepod (Fig. 5.10). During monsoon, harpacticoids were second highest order and attained total pigment content in the range 1.95–4.25 ng/copepod. In post-monsoon, total pigment content was detectable only at the oceanic site (0.68 ng/copepod). The highest value was recorded at shelf during pre-monsoon (0.96 ng/copepod). Similarly, total gut pigment content in Cyclopoida varied from 0.03 to 3.04 ng/ copepod (Fig. 5.10) with highest values noticed in a monsoon at the continental shelf realm. Further, the gut pigment concentration declined in post-monsoon (0.03–0.22 ng/copepod) and successively inclined during pre-monsoon (0.06–2.24 ng/copepod).

Generally, the total gut pigment content of copepods received major input of phaeopigment than chlorophyll. Although spatial-seasonal variations were observed, all the copepod Orders showed the presence of photosynthetic pigments. Moreover, significant variability ($p < 0.01$; Table 5.4) in gut pigment concentration was observed during monsoon and post-hoc test revealed high value during post-monsoon ($p < 0.01$).

Table 5.1. Two-way ANOVA comparing the seasonal and depth-wise variation of water chlorophyll *a* and phaeopigment

Effect	**SS**	***Df***	**MS**	**F**	***p***
Chlorophyll *a*					
Season	58.74	2	29.37	6.86	0.004*
Depth	4.14	3	1.38	0.32	0.81
Season x Depth	14.24	6	2.37	0.55	0.76
Phaeopigment					
Season	9.47	2	4.74	1.57	0.23
Depth	18.17	3	6.06	2.01	0.14
Season x Depth	27.97	6	4.66	1.55	0.20

The variables that were significant are represented with ‘*’ mark.

Table 5.2. Seasonal variation of gut pigment composition in copepods

Seasons	Orders	Dominant Pigments	RT (min)
Monsoon	Calanoida	Astaxanthin	15.9
		Alloxanthin	17.7
Monsoon	Poecilostomatoida	Astaxanthin	15.9
		Canthaxanthin	18.2
Post -monsoon	Calanoida	Astaxanthin	15.9
		Alloxanthin	17.7
Post -monsoon	Poecilostomatoida	Astaxanthin	15.9
		Canthaxanthin	18.2
Pre-monsoon	Calanoida	Astaxanthin	15.9
		Canthaxanthin	18.2
Pre-monsoon	Poecilostomatoida	Astaxanthin	15.9
		Canthaxanthin	18.2

RT is the retention time

Table 5.3. Two-way ANOVA comparing the seasonal variation of total gut pigments for copepod orders at G5

Effect	SS	*Df*	MS	F	*p*	Post hoc test
Order	0.02	3	0.01	0.30	0.83	
Season	0.33	2	0.17	6.99	0.01*	Post-monsoon
Order x Season	0.05	6	0.01	0.34	0.90	

The variables that were significant are represented with '*' mark. The season showing significantly highest mean values from the Turkey's post hoc test is shown.

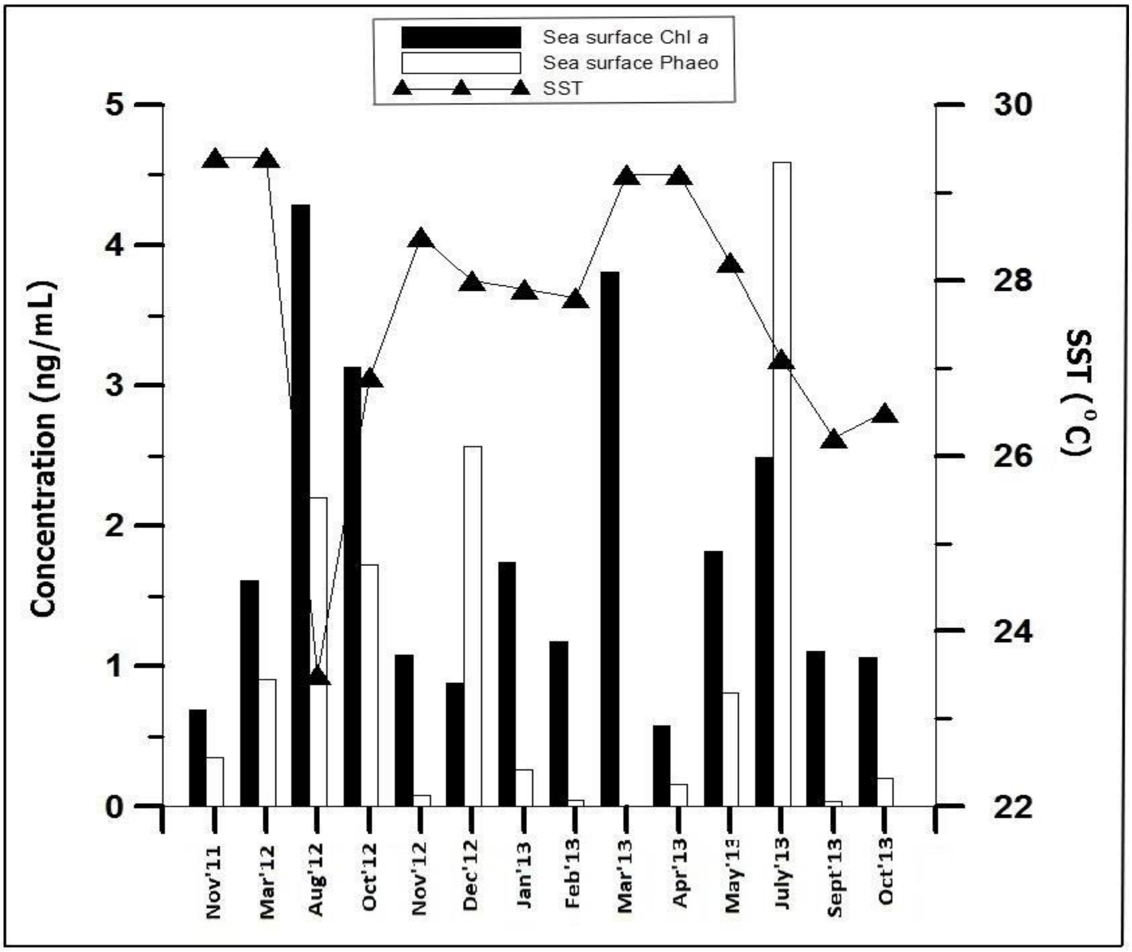


Fig. 5.1 Temporal variation in the surface physical parameters recorded at the coastal station (G5). (The legend shows *Surface chl*- surface chlorophyll *a*; *surface phaeo*- surface phaeopigment; *SST* - Sea Surface Temperature)

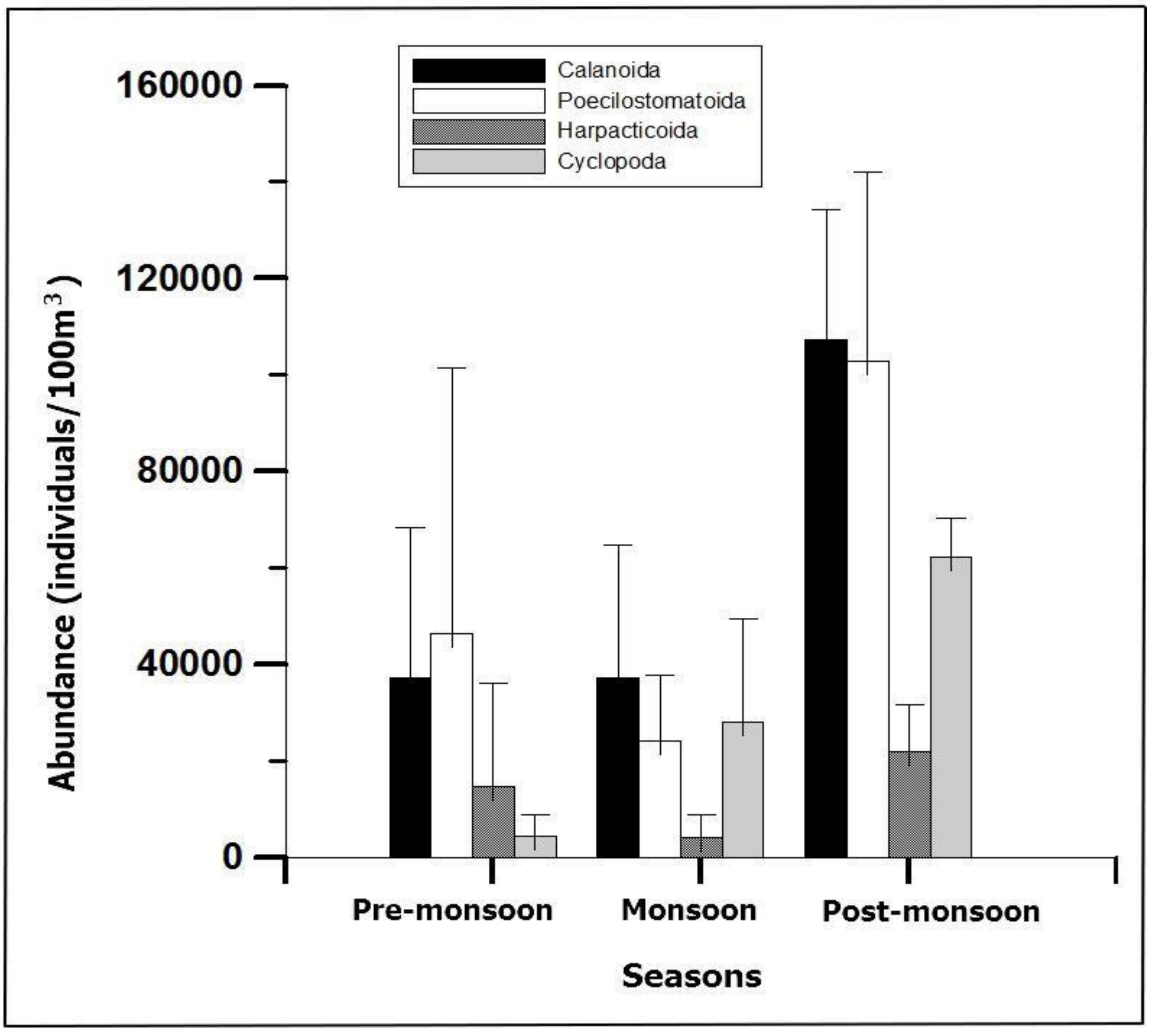


Fig. 5.2 Seasonal variation of abundance (mean value ±SD) for different copepod orders for at a coastal station (G5).

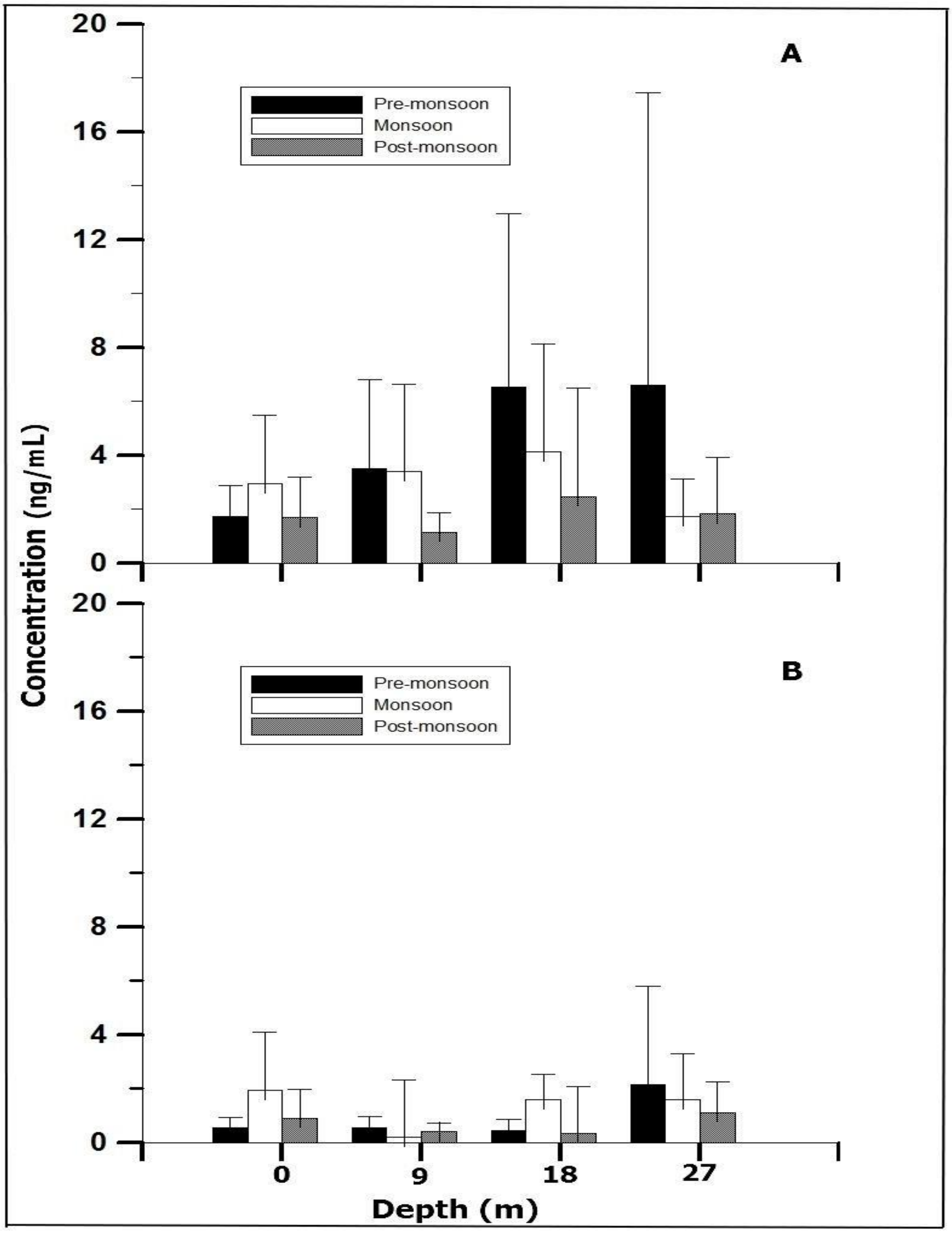


Fig. 5.3 Seasonal variation of water pigments (A) Chlorophyll *a* and (B) Phaeopigments (mean value ±SD) at different depths at a coastal station (G5).

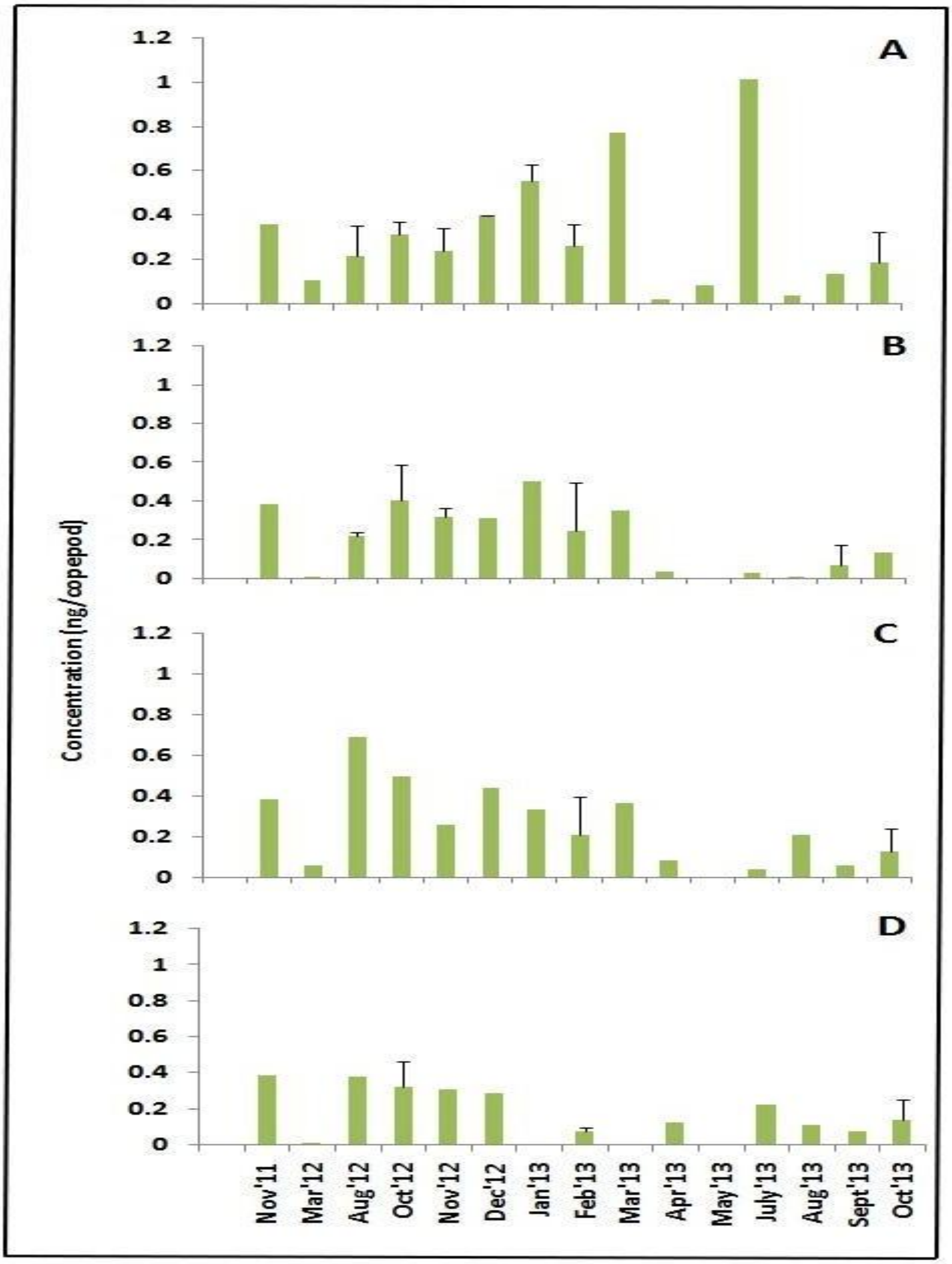


Fig. 5.4 Gut chlorophyll *a* contents (±SD) in copepod orders (A) Calanoida (B) Poecilostomatoida (C) Harpacticoida and (D) Cyclopoida at a coastal station (G5)

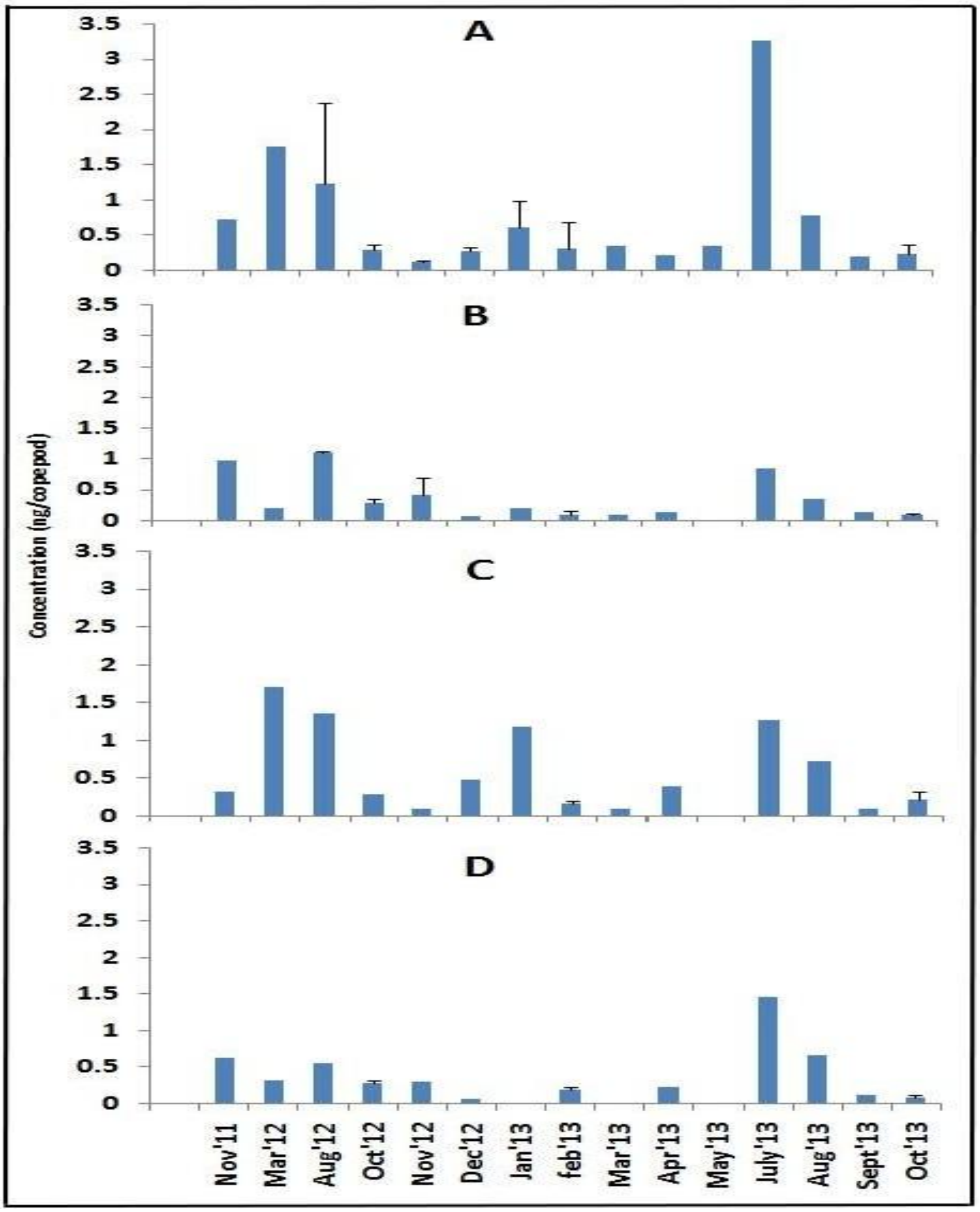


Fig. 5.5 Gut phaeopigment contents (±SD) in copepod orders (A) Calanoida (B) Poecilostomatoida (C) Harpacticoida and (D) Cyclopoida at a coastal station (G5)

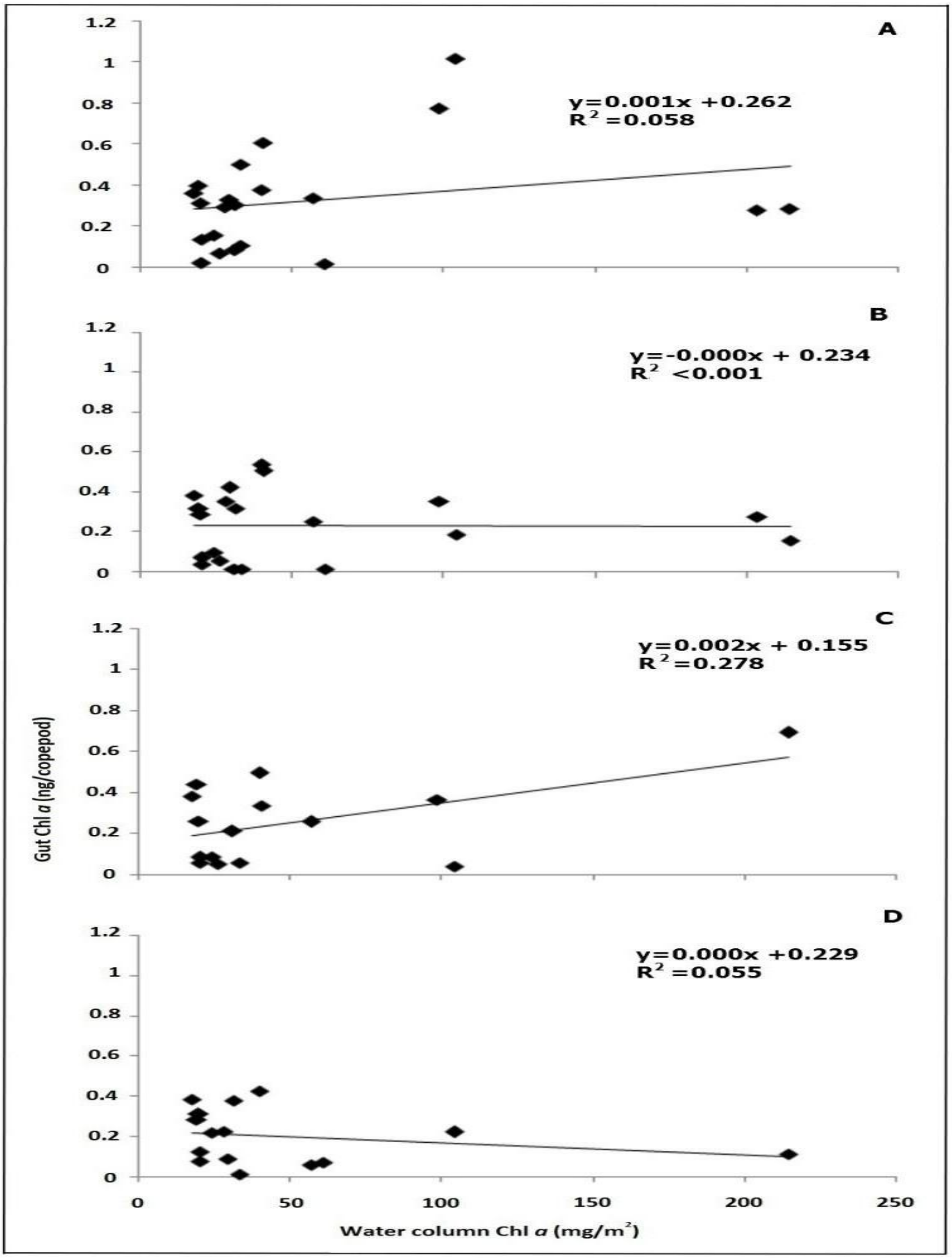


Fig. 5.6 Correlation between water column Chl *a* and copepod gut Chl *a* content for (A) Calanoida (B) Poecilostomatoida (C) Harpacticoida and (D) Cyclopoida from November 2011 to October 2013 at G5. (*Gut Chl* a- gut chlorophyll *a*; *water column Chl* a- water column chlorophyll *a*)

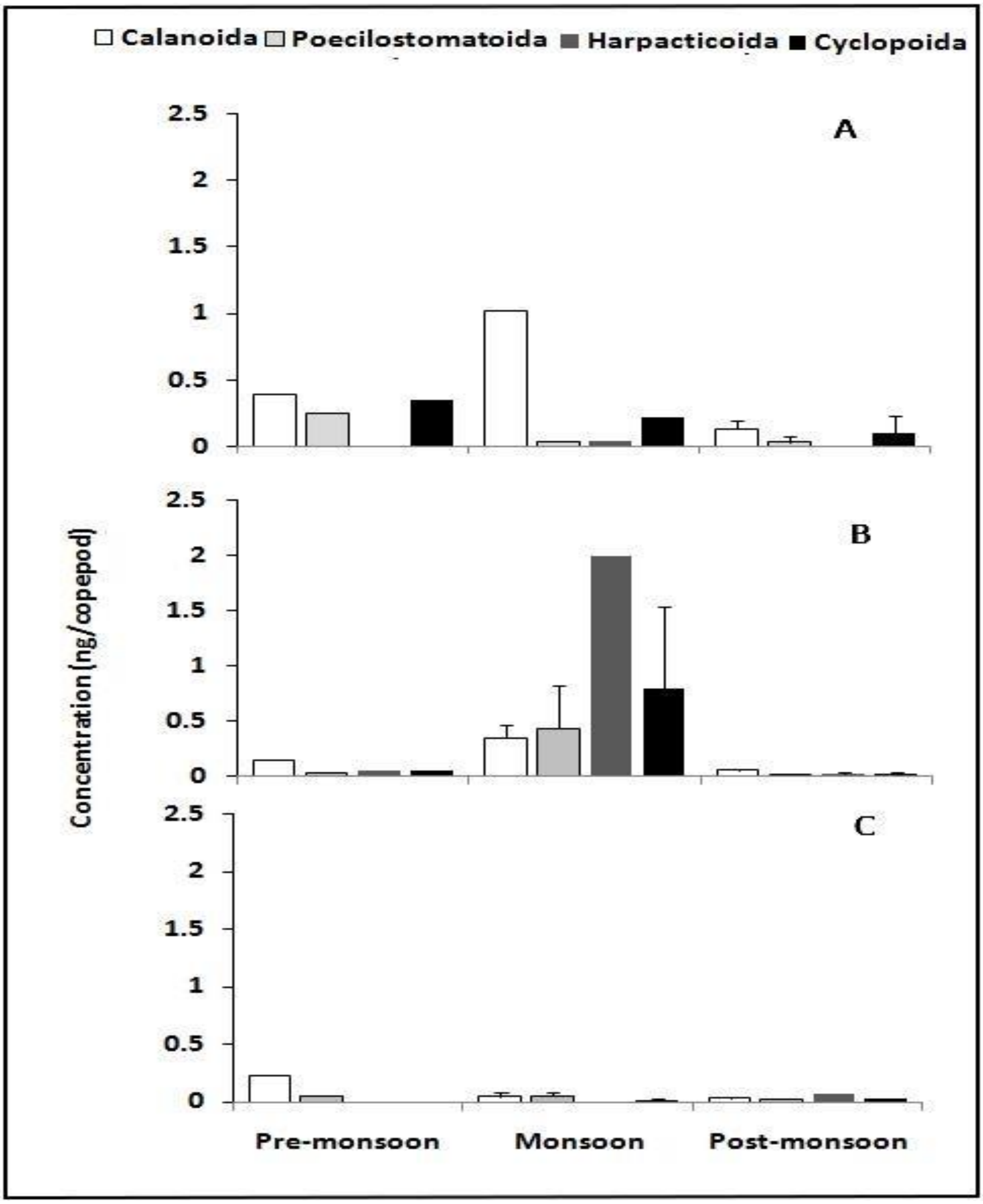


Fig. 5.7 Gut chlorophyll a contents (±SD) in copepod orders at (A) continental shelf, (B) slope and (C) oceanic stations.

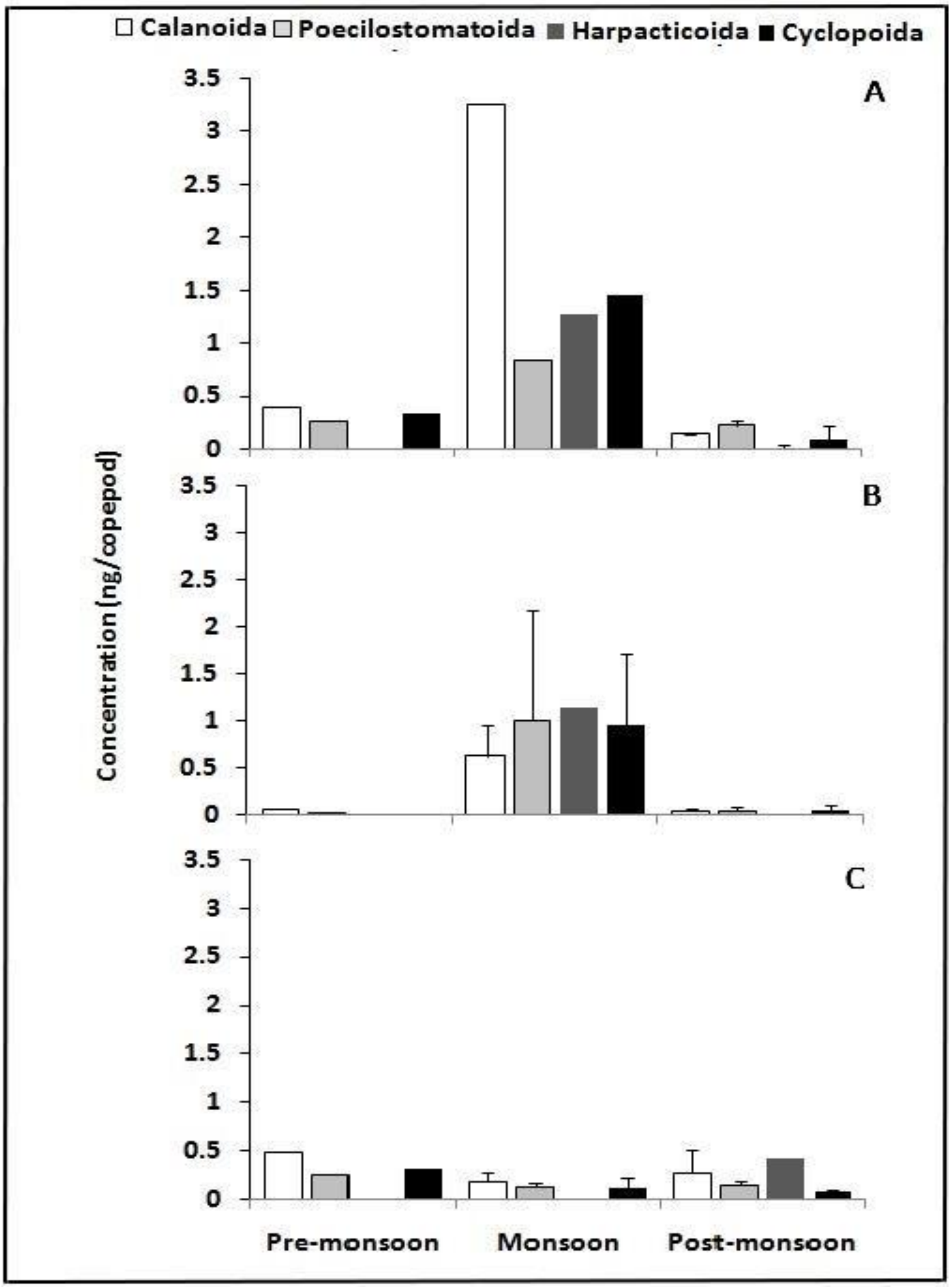


Fig. 5.8 Gut phaeopigment contents (±SD) in copepod orders at (A) continental shelf, (B) slope and (C) oceanic stations.

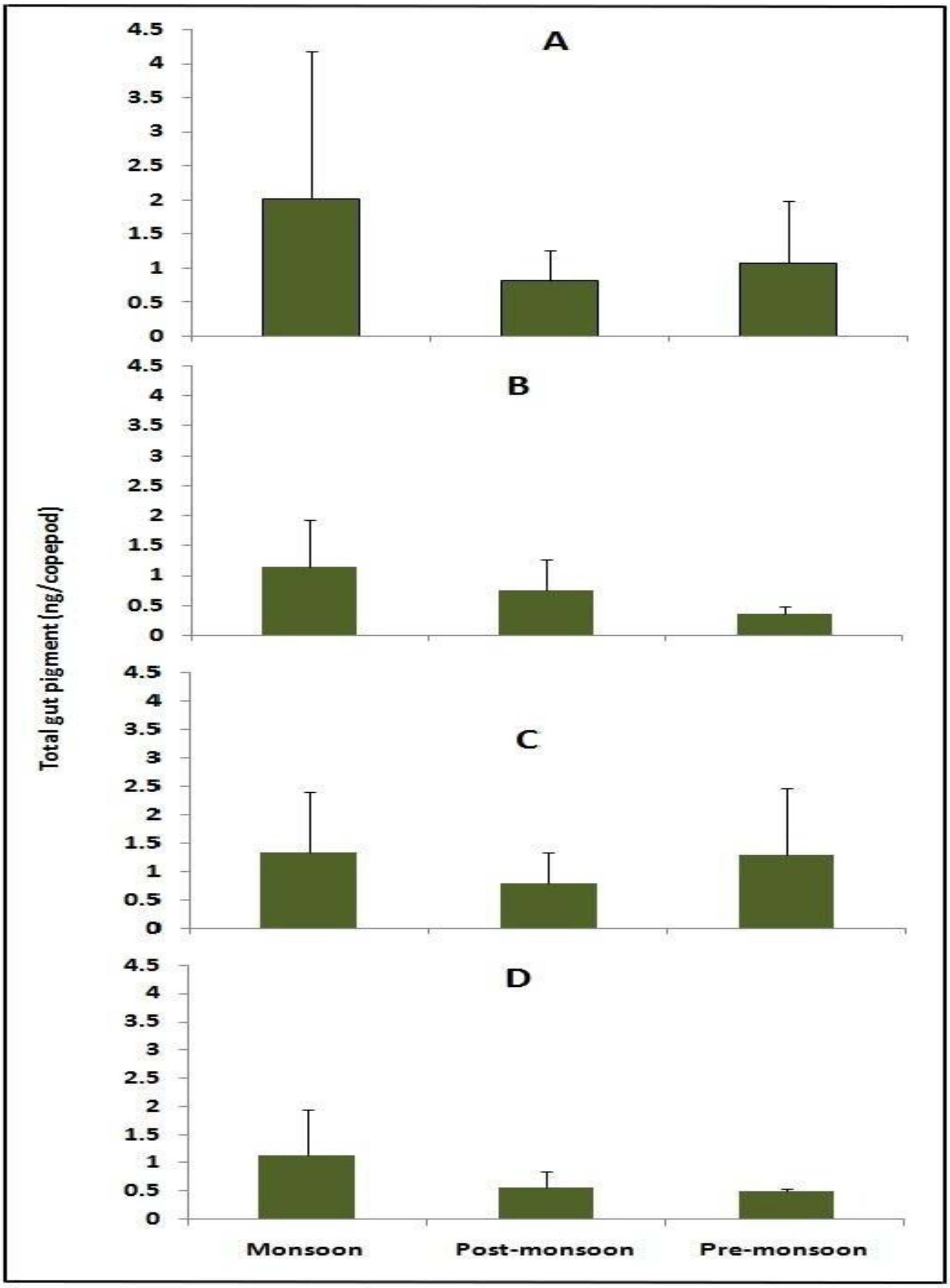


Fig. 5.9 Seasonal variation in total pigments content (± SD) of (A) Calanoida (B) Poecilostomatoida (C) Harpacticoida and (D) Cyclopoida at a coastal station (G5).

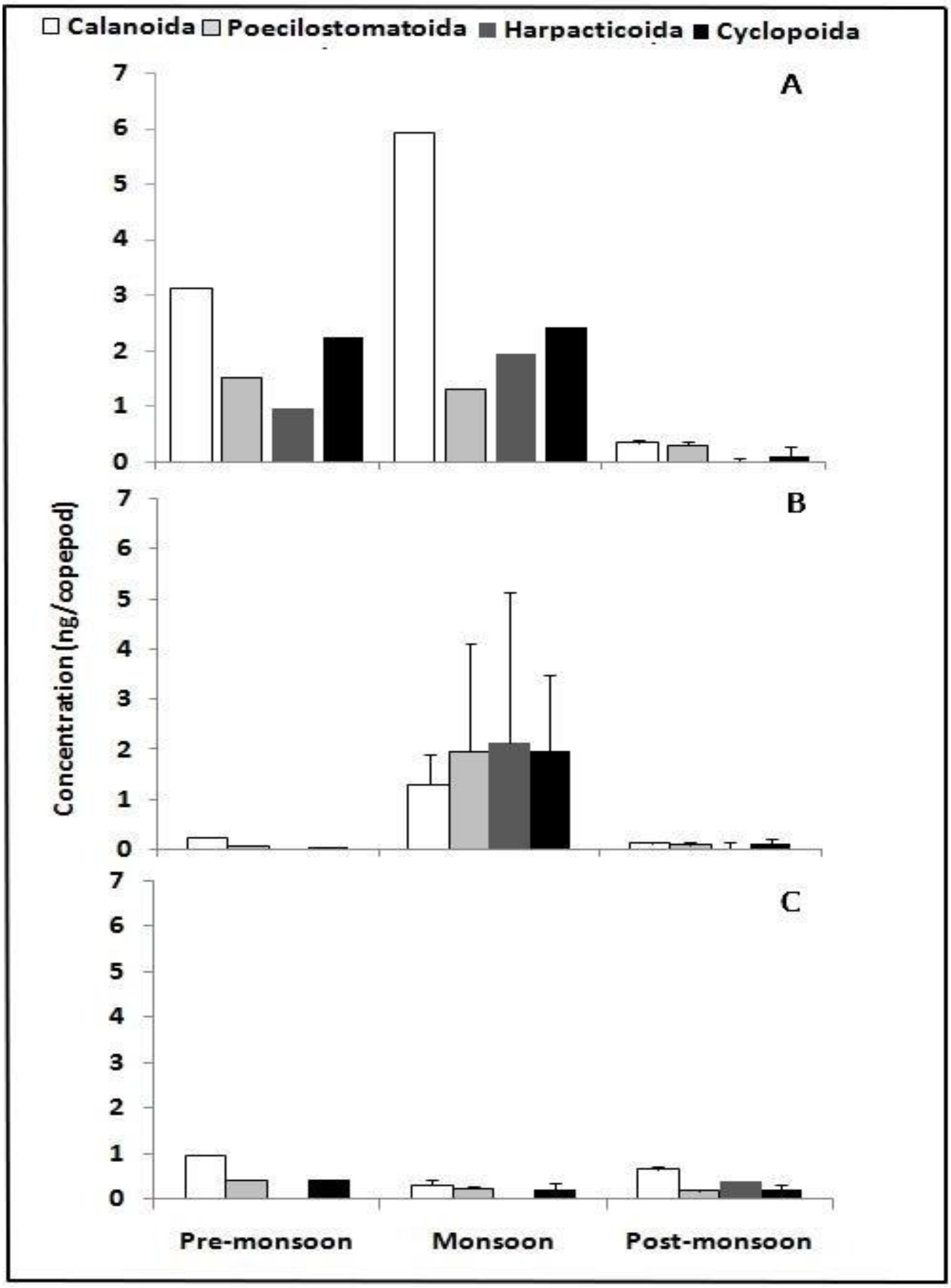


Fig. 5.10 Seasonal variations of total pigments (± SD) in copepod orders at (A) continental shelf, (B) slope and (C) oceanic station.

5.4 DISCUSSION

The Arabian Sea is controlled by the monsoonal regime with the occurrence of varied biochemistry that modulates copepod ecology. The Arabian Sea is one of the productive systems (Banse et al. 2014; Pratihary et al. 2014). Seasonal anoxia is a distinctive feature of the continental shelf realm of the Arabian Sea (Naqvi et al. 2006); however, it remains concise only to the near-shore region of the shelf (Pratihary et al. 2014). Open oceanic realm of the Arabian Sea harbors a permanent oxygen minimum zone below ~150–1000 m. In addition, seasonal fluctuations in phytoplankton composition occur in the Arabian Sea as reported by Parab et al. (2006). Additionally, the pigment study from continental shelf realm reported a plethora of tiny phytoplankton groups dominated by prymnesiophytes and green algae during monsoon (Roy et al. 2006). Also, blooms of *Trichodesmium* during pre-monsoon have continued to occur from a long time in Indian coastal waters (Devassy et al. 1978; Parab et al. 2006; Roy et al. 2006).

The copepod feeding ecology is mostly constraint to its mouth part morphology from the Arabian Sea (Madhupratap 1999). During the present study, ambient Chl *a* concentration was > 1 $\mu g\ L^{-1}$ throughout the water column (Fig. 5.3) in the continental shelf realm. It is an indication of productive waters and therefore, feeding preference for herbivorous/omnivorous copepod would be autotrophic prey. The important observation of the present study revealed undegraded chlorophyll in the gut of all the copepod Orders (Calanoida, Poecilostomatoida, Harpacticoida and Cyclopoida). This signified non-diapausing copepods which actively grazed the abundant autotrophic biomass throughout the year.

Higher gut pigment contents were observed in Calanoida which were relatively of bigger body size (0.93–2.6 mm). Such observation must have occurred as a result of biased consideration of only herbivores calanoids. Secondly, the bigger organisms are known to hoard more gut pigments (Morales et al. 1990, Tseng et al. 2008; Tseng et al. 2009), due to more gut volume, as a consequence, high gut Chl *a* was observed with escalating body sizes. Further, studies on phytoplankton ingestion by copepods posed minimal size limit of 2 μm as feed (Roman and Gauzens, 1997). Another study in Tolo Harbor by Lie et al. (2013) proposed that large phytoplankton were inadequately grazed by the small copepods as the transfer efficiency was less (1.4%) among primary production and secondary production. Collectively, it appears that copepod feed has a critical size range that acts as an important component governing the gut estimates. Also, the gut pigments in copepods revealed a decreasing trend from the continental shelf, slope to the oceanic realm. This pattern of spatial distribution clearly indicates the strong coupling with the biochemistry of geographic variation.

The dissimilar pattern of variations for Chl *a* and phaeopigment in copepod gut is an indication of governance of diverse processes for their distribution. Among these, photo-degradation of Chl *a* to phaeopigment could be one of the probable reason as the organisms were exposed to light in natural habitat and in the laboratory while sorting under a microscope (Islam et al. 2005). Variation in the Chl *a* concentration can also be coupled with the growth phase and size of the phytoplankton cell consumed by the copepods (Uye 1986; Bautista and Harris 1992; Tan et al. 2004). Likewise, the estimate of degradation and pigment loss in the copepod guts could fluctuate under varied conditions such as the quantity of feed in ambience, digestion of the chlorophyll biomass and the past record of the feed by organism (Dagg and Walser 1987; Penry and Frost 1991; Head 1992; Head and Harris 1996). To a certain extent, it might get affected by ingestion of detritus and coporophagy (Goes et al. 1999).

Commonly, phaeopigment concentration was higher than Chl *a* values in copepods gut during the present study is a common observation of other researchers (Shuman and Lorenzen, 1975; Hallegraeff, 1981; Dagg and Wyman, 1983; Islam et al. 2005; Tseng et al. 2008). This might be because of the rapid degradation of ingested chlorophyll to phaeopigments that eventually remains unaffected (Shuman and Lorenzen, 1975). Moreover, variable phaeopigment: Chl *a* ratio in gut signifies the amount of chlorophyll recently ingested. Goes et al. (1999) hypothesize that the high phaeopigment concentration is due to the reingestion of the previously evacuated particulate organic matter. An interesting result was noticed during March'13 at G5 when gut Chl *a* was higher than gut phaeopigment in all copepods and the water phaeopigments were below detectable limit. The inter-annual, seasonal and spatial variability in the gut pigments of copepods necessitates long-term monitoring to understand the pigment dynamics.

Bioconversion of Chl *a* into the measurable phaeopigment is controversial. Certain researchers like Shuman and Lorenzen (1975) supported the complete degradation of chlorophyll into phaeophorbide. Simultaneously, Hallegraeff (1981) suggested that Chl *a* undergo alteration ranging 20–50% of phaeophorbide and remaining to phaeophytin. Besides, Bustillos-Guzman et al. (2002) suggested that phaeopigments can be produced at different rates based on the chemical/enzymatic reaction acting differently upon the gut chlorophylls. Nevertheless, a deficit of information on Chl *a* conversion and turnover rates is the primary limitation of this technique. In addition, we did not assess the pigment loss and chose to use an average estimate value of 33% to correct the pigment damage (Dam and Peterson 1988).

The monthly sampling on continental shelf was carried out during the daytime; therefore, the observed estimates of copepod gut Chl *a* and phaeopigments were comparably low i.e. within a range of 0.013–2.6 ng/copepod. However, the values were comparable to those reported by Tseng et al. (2008; 2009) and Li et al. (2004) from tropical waters. The total gut pigments across the transect covering the continental shelf, slope and oceanic site during different seasons ranged <0.01–5.93 ng/copepod. Low copepod gut pigment content at the oceanic site was obvious due to the low primary productivity and primary producers are dominated by picoplankton (Jain et al. 2014). Previous studies (Mackas and Bohrer 1976; Saito and Taguchi 1996; Lee 1998; Islam et al. 2005; and Tseng et al. 2008; Wu et al. 2013) revealed high gut pigment contents in copepods during the nocturnal hours and low at daylight hours. Apart, quicker gut evacuation and pigment destruction in the gut was assumed to the observed underestimation as reported elsewhere (Morales et al. 1991; Bollen and Landry 2000).

Although copious autotrophic biomass was available at the continental shelf realm, copepod species might prefer selective size fraction to prey upon. Thus, no significant correlation between total water Chl *a* and gut Chl *a* of Calanoida, Poecilostomatoida, Cyclopoida and Harpacticoida were observed. Additionally, the diel feeding rhythms, individual variance and/or feeding synchronization could result in this type of surveillance (Uye and Yamamoto 1995; Li et al. 2004). Such observation was also reported by Dagg and Wyman (1983), Dam and Peterson (1993) and Li et al. (2004). On the contrary, a significant positive correlation between copepods gut Chl *a* and ambient water Chl *a* is known to be an indication of less productive waters (Tseng et al. 2009).

The gut pigment estimates were scrutinized to be higher in the monsoon at continental shelf, slope and the oceanic habitat. One of the reasons for such variability could be the discrepancy of the accessible autotrophic feed. The complexity of phytoplankton variation with respect to seasons has been studied in the Arabian Sea (Parab et al. 2006; Gomes et al. 2014). Precisely, during pre-monsoon, blooms of cyanobacteria specially

Trichodesmium sp. dominates the phytoplankton followed by diatoms in monsoon and dinoflagellates in post-monsoon (Parab et al. 2006; Pratihary et al. 2014). Additionally, *Noctiluca scintillans* bloom was reported in pre-monsoon which was considered to be undesired food by copepods (Gomes et al. 2014). Thus, a shift in phytoplankton community seems to be an important cause for the seasonal variability in feeding habits. Also, gut pigment study in barnacle larvae from neighboring waters of the studied region (Gaonkar and Anil 2012) reported seasonal variability with higher pigment content in post-monsoon as compared to pre-monsoon. Interestingly, a report on the fishery of the Arabian Sea by Madhupratap et al. (2001) pointed out elevated fish abundance, especially planktonivorous ones during October–March. Combining this information at the trophic levels imply that the copepods may play a vital role in the maintenance of fishery in this realm.

Pigment compositions of copepod gut require a lot of individual numbers for HPLC estimation. The need of a high number of individual from continental slope and oceanic site restricted the analyses. Hence, the pigment compositions were studied only from continental shelf realm on a seasonal scale. Copepod gut composition revealed the dominance of astaxanthin. Most of the researchers considered astaxanthin to be derived from canthaxanthin; which is produced from β-carotene via echninenone in herbivores (Goodwin 1971; Lotocka and Styczynska-Jurewicz 2001; Caramujo et al. 2012). But a few researchers considered astaxanthin as an animal pigment (Gasparini et al. 2000), due to its presence even in starved copepods. Conversely, according to the available literature, it is more appealing to judge astaxanthin as marker pigment for omnivory (see Juhl et al. 1996). Present observation portrays occurrence of astaxanthin and canthaxanthin in Calanoida this is in accordance with Lotocka and Styczynska-Jurewicz (2001) and Holeton et al. (2009). Fascinatingly, astaxanthin plays an epochal role in copepods by being a potent antioxidant for lipids protection, photo-protector against photosynthetically active radiation and UV light (Hairston 1980; Terao 1989; Holeton et al. 2009; Hansson, 2004). Additionally, astaxanthin acts as precursors of vitamin A and retinoid compounds (Schiedt et al. 1985; Holeton et al. 2009). Pisces, especially Salmon needs astaxanthin for their characteristic red color (Olsen et al. 2005) and definite facets of resistance (Thompson et al. 1995) but cannot manufacture it *de novo*. Therefore, copepod-astaxanthin can be transferred to the fish stock by preying on copepods.

The occurrence of alloxanthin in calanoids was studied to show seasonal variation in feeding habit during the present study (at G5). During monsoon and post-monsoon, alloxanthin was noticed in calanoid gut probably due to the selective feeding on Cryptophycaea from ambient water. This was evident from the previous record on seasonal variations in alloxanthin concentration from the water column with trace amounts reported during pre-monsoon (Maya et al. 2011). Supporting the preceding statement, during pre-monsoon, the dominance of *Trichodesmium* sp. (devoid of alloxanthin) was reported (Parab et al. 2006). Collectively, our finding is inclining towards the common viewpoint of selective grazing by calanoid. On the contrary, alloxanthin is sometimes considered as an alloxanthin-like animal pigment (Pandolfini et al. 2000). However, our consideration of alloxanthin as marker pigment for Cryptophytes is favored by other studies (Breton et al. 1999; Cotonnec et al. 2001). Also, a study by Juhl et al. (1996) reported the occurrence of astaxanthin and alloxanthin in copepod guts that were experimentally fed on *Rhodomonas* sp. Conjointly, *Temora longicornis* (Calanoida) showed the presence of high alloxanthin contents (Antajan and Gasparini 2004). Consequently, alloxanthin in copepod gut should be used with prudence and more investigation needs to be carried out to provide an informative view to this controversy.

In this study, the presence of fucoxanthin, a marker pigment for diatom (Jeffrey 1981) and chlorophyll went undetected. Most probably the pigment fucoxanthin may be degraded in the gut passage (Head and Harris 1994). Also, it is reported that fucoxanthin gets degraded faster than chlorophyll derivatives into undetectable compounds (Antajan and Gasparini 2004). Although the obvious reason is unknown, one probable reason is pigment decomposition while sorting of copepods which may be due to the longtime exposure of the species to light. In addition, it could be due to the low concentration of fucoxanthin eluted on chromatogram as less intensity peak could not be identified. Recent studies revealed that the thick siliceous diatoms are less favored by copepods (Nieuwerburgh et al. 2005) probably due to aldehydes content that may act as a defense against the predatory pressure (Ianora et al. 2003). There is a possibility that copepods must have lured on other phytoplankton and restricted grazing on diatom in the natural habitat of Arabian Sea.

Studies on microscopic gut assessment in Poecilostomatoida revealed the presence of phyto- as well as zooplankters (Ohtsuka et al. 1996; Metz 1998). Precisely, Ohtsuka et al. (1996) noticed chains of diatom and appendicularian houses in *Oncaea* sp. (Poecilostomatoida) gut. Further investigation by Metz (1998) revealed diatoms as preferred food in *Oncaea curvata* (Poecilostomatoida). On the contrary, in the Arabian Sea, Poecilostomatoida and Cyclopoida have been cited as carnivorous (Timonin 1971; Smith and Madhupratap 2005) on the basis of mouthpart morphology. Current study shows that species of Poecilostomatoida and Cyclopoida feed on autotrophs as evident by the presence of Chl *a*, although in trace quantity. Poecilostomatoida and Cyclopoida may prey upon animal-based diet to suffice their nutritional constraint. It is convincing to suggest omnivorous feeding habit by these tiny organisms in the waters of the Arabian Sea. Further, due to their small size (<1 mm), in accordance with Atkinson (1996) and Roman and Gauzens (1997), these mesozooplankton might be exerting more grazing pressure on the nominal-sized primary producers. Alternatively, copepod of Order Harpacticoida accumulated gut Chl *a* considerably without significant correlation with ambient water Chl *a* which may be due to ingestion of benthic Chl *a* to meet its dietary quota.

It is apparent that the copepods across the continental shelf, slope and oceanic realm of the Arabian Sea essentially graze upon the chlorophyll-bearing material and probably can act as astaxanthin source to the fish stock. This study highlights the spatial-seasonal variability in copepod gut pigment contents with highest values recorded during monsoon that corresponds to breeding season of fishes.

SUMMARY

Biogeochemistry of the eastern Arabian Sea is very unique with its landlocked nature, monsoonal cycles and intense oxygen minimum zone. As evident from the literature survey, no much work is devoted to understanding the feeding behavior of copepods from this sea. It is important to known the feeding habits of copepods are imperative in order to understand the carbon cycle in the marine ecosystem. Hence, the present study was aimed at knowing trophic segregation between copepod genders, species and orders from this region by stable isotope technique. An effort was made to study gut pigment contents in copepod orders using gut fluorescence to compliment the results gained using stable isotope techniques. The present thesis is divided into six chapters. Ecological roles of the zooplankton particularly copepods forms the major part of **Chapter 1**. Relevant literature on copepod ecology and its feeding studies using gut fluorescence and stable isotope technique across the world is reviewed in the first chapter. Characteristics of the study area (continental shelf, continental slope, open ocean waters) and objectives of the present work are given at the end.

Spatio-temporal variations in copepod community of the eastern Arabian Sea are discussed in **Chapter 2**. A monthly sampling of mesozooplankton was carried out at the continental shelf station (G5) and seasonal sampling for pre-monsoon (February to May), monsoon (June to September) and post-monsoon (October to January) was restricted on the continental shelf (G5, G6 and G7), slope (G9, G11 and G13) and open-ocean stations (ASTS). Copepods were predominant in all the stations and seasons; Calanoida and Poecilostomatoida were the dominant copepod orders in the study area. The hydrographic conditions prevailing in the study region showed seasonal variations strongly coupled with the monsoon. Overall, copepod species showed strong spatial variability, however, seasonal variability was not significant statistically. Clusters of the stations–association revealed by Bray–Curtis analysis and nMDS plot illustrated relationships with topography based on copepods identified by SIMPER test. Copepods namely *Euterpina acutifrons*, *Centropages furcatus*, *Temora turbinata* and *Pseudodiaptomus serricaudatus* were responsible for clustering the months at the continental shelf station (G5) whereas *Pleuromamma robusta*, *Mormonilla phasma*, *Euchaeta concinna* and *Macrosetella* spp. comprehended for the cluster formation at the open water station (ASTS). Copepod diversity, varied from the continental shelf (H': 1.90–3.71), transect (H': 3.56–4.63) and oceanic realm (H': 2.48–3.93) of the Arabian Sea. High species richness and diversity of copepods seem to be strongly coupled to seasons supporting the rich secondary productivity in the Arabian waters.

The stable isotope content for copepod species and gender specific are detailed in **Chapter 3.** Seasonal variations in $\delta^{13}C$ and $\delta^{15}N$ for genders of *Subeucalanus* spp. on the continental shelf (G5) were deciphered mostly due to the enriched $\delta^{13}C$ (−19.97 to −17.18 ‰) and depleted $\delta^{15}N$ (4.91 ‰) in post-monsoon. Similarly, the copepod genera *Acartia* spp. and *Temora* spp. decoded seasonal variation in $\delta^{13}C$ and $\delta^{15}N$ with enriched values of both $\delta^{13}C$ (−18.25 to −17.61 ‰) and $\delta^{15}N$ (7.95 to 9.70 ‰)in the monsoon period.

Overall, the $\delta^{13}C$ of copepods genders of *Subeucalanus* spp. and *Euchaeta* spp. was in the range of −21.16 to −20.01 ‰, $\delta^{15}N$ ranged from 6.56 to 8.96 ‰ and C/N ratio at the continental slope (4.23–5.53) was consistent with the copepods in shelf waters. Conspicuously, $\delta^{13}C$ (−21.96 to −20.33 ‰) and $\delta^{15}N$ (8.36 ‰) of copepod species were depleted as compared to shelf copepods, however, the C/N ratio (4.09–5.45) was similar to shelf copepods. *Euchaeta*, *Pleuromamma* and *Subeucalanus* revealed gender–wise segregation in δ^{13}C (−22.19 to −19.52 ‰) and δ^{15}N (5.82–10.47 ‰) with enriched values in male counterpart, particularly in the oceanic waters (ASTS). Briefly, *Pleuromamma* spp. and *Subeucalanus* spp. exhibited omnivory while, *Euchaeta* spp. found to be carnivorous throughout the study.

Overall, the most depleted δ^{13}C (−24.36 to −21.46 ‰) and δ^{15}N (2.31 to 7.22 ‰) were observed in copepod species in oceanic waters. Significant variations were found in δ^{13}C and δ^{15}N of copepod species and genders between three study sites. It is clear that variations in phytoplankton community and different nitrogen source at all the three sites govern the isotope composition. This is because of the seasonal shift in phytoplankton community; especially in the continental shelf waters, in particular, the dominance of diatoms during monsoon, which are capable of utilizing isotopically heavier bicarbonates. A poor correlation between δ^{15}N and δ^{13}C of copepods at the continental shelf, slope and oceanic waters was noteworthy. Such weak correlations suggest utilization of multiple carbon sources contributed to the trophic food web.

Copepod orders from the continental shelf, slope and open waters with respect to stable isotopes of nitrogen and carbon studies is dealt in **Chapter 4.** The dominant copepod orders, Calanoida and Poecilostomatoida were considered in the feeding studies to get a broad outlook of copepod feeding from the study region. The common trend of least δ^{13}C values in pre-monsoon (−21.35 to −18.46 ‰) with a gradual increase in monsoon (−21.24 to −17.64 ‰) and most enriched values during post-monsoon (−22.01 to −15.76 ‰) was observed at continental shelf. On the other hand, high enrichment of δ^{15}N was noticed in pre-monsoon (1.97 to 10.05 ‰) followed by post-monsoon (3.76 to 9.56 ‰) and monsoon (6.88 to 9.23 ‰). In copepod orders, the δ^{13}C (−21. 61 to −20.05) was conspicuous by low enrichment in continental slope waters, indicating different carbon source as that of the shelf and open water copepods. Typically, δ^{15}N (6.55 ‰) also showed low enrichment indicating omnivorous feeding habits. In oceanic waters, δ^{13}C content (−22.45–−18.45 ‰) and δ^{15}N (4.21 to 8.20 ‰) in copepod orders was similar to shelf waters. The isotopic composition of carbon in Calanoida and Poecilostomatoida differs significantly with time and space across continental margins and open waters of this tropical sea and these differences may be transported onto their predators. On the other hand, the isotopic content of nitrogen varied on a narrow scale thereby revealing omnivorous feeding habit.

Gut content in copepod orders using gut fluorescence method is mentioned in **Chapter 5**. In particular, quantitative analysis of the copepod gut pigments was carried out on a seasonal scale from representative stations covering continental shelf, slope and oceanic realm. Also, on a seasonal scale, gut pigment composition using HPLC was studied for Calanoida and Poecilostomatoida, which reside in continental shelf region. This is the first *in situ* study of copepod gut pigments from different topographic regions of the Arabian Sea. Calanoida, Poecilostomatoida, Harpacticoida and Cyclopoida revealed the presence of gut Chl *a* in copepods, which were sampled from the continental shelf, slope and open waters of the Arabian Sea in all three season (pre-monsoon, monsoon and post-monsoon). Monthly variation in gut Chl *a* in copepods at continental shelf (G5) showed a distinct pattern of highest concentration during monsoon. Amongst the orders, Calanoida attained highest gut Chl *a* (0.02–1.02 ng/copepod) and phaeopigment (0.11–3.26 ng/copepod) content. Overall, inter-annual and seasonal variability was observed in copepods gut Chl *a* pigment and phaeopigment content. Equally, the pattern of variation of gut Chl *a* and phaeopigment differed, and consecutively, Chl *a* was always less copious than phaeopigment; however, no significant statistical relation was observed between the two. It is apparent that the copepods across the continental shelf, slope and the oceanic realm of the Arabian Sea essentially graze upon the chlorophyll bearing material and probably can act as the astaxanthin source in fish stock.

The summary includes abstract of the thesis and salient findings of the study.

For the first time, this study points out some of the salient findings:

- The monsoon season was conspicuous with less enriched δ^{15}N (7.34–9.27 ‰) and high gut pigment content in copepods along with minimum copepod counts at the continental shelf.
- Poecilostomatoida and Cyclopoida which were previously assumed to be carnivorous revealed gut Chlorophyll and depleted δ^{15}N content, indicating an omnivorous feeding habit in the Arabian Sea.
- Male copepods of *Subeucalanus*, *Euchaeta* and *Pleuromamma* showed segregation in feeding behavior than their female counterpart, particularly the male copepods always accumulated enriched values of carbon and nitrogen isotopes.
- As affirmed with stable isotope technique, *Euchaeta concinna* constantly exhibited carnivorous feeding behavior in the continental shelf, slope and open waters of the Arabian Sea. Other copepods like *Acartia* spp. and *Temora* spp. revealed omnivorous feeding behavior in continental shelf waters with seasonal variations in a stable isotope of carbon and nitrogen.
- In general, the copepod carbon isotopic values were always enriched at the continental shelf as compared to the slope and open water realms. Also, seasonal variation of isotopic carbon in copepods at continental shelf was coupled with the

phytoplankton fluctuations. On the other hand, the isotopic values of nitrogen in copepods varied in narrow scale indicating predominantly omnivorous feeding habits.

- Although, water chlorophyll had been always above 1 ng/mL in continental shelf waters, seasonal variation in gut pigment in Calanoida, Poecilostomatoida, Harpacticoida and Cyclopoida were noticed. Asthaxanthin and canthaxanthin were the dominant pigments in Calanoida and Poecilostomatoida sampled from shelf waters.
- Typically, copepods dominated the mesozooplankton (72–99 %) in the study region, however on few occasions, Poecilostomatoida was the dominant orders and a minor contribution from Harpacticoida, Cyclopoida and Mormonilloida was accounted during this study. Copepod species distribution revealed spatial and temporal variation in abundance and diversity indices.

Suggestions for further study:

- Quantification of copepod nauplii, their pigment compositions and stable isotope ratio are needed to better understand the community structure of copepods.
- Stable isotope studies are needed to address isotope fractionation at a food-web level to better understand the trophic positions. Also, a study of isotope contents in microbial loop components and its effects on copepods will provide comprehensive knowledge on food-web interactions.
- Future studies should examine the significance of nitrogen fixation and low oxygen on deep-sea copepod stable isotope contents.

- Use of lower mesh size like 100 to 150 µ along with 200 µ is needed to judge if there are underestimations of early developmental stages of copepods and small copepod genera.
- Laboratory experiments using gut fluorescence and stable isotope techniques on copepod cultures from juveniles to adults will provide better insights into trophic fractionations and pigment transfers to different trophic levels of the marine food web.

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Temporal variability in copepod gut pigments over the central western continental shelf of India

ANALIZA MARIA D´SOUZA AND MANGESH UTTAM GAUNS
CSIR – National Institute of Oceanography, Dona Paula, Goa, India

The Indian Western continental shelf (IWCS) is amongst the most productive regions of the world, being noteworthy for upwelling (south-west monsoon) and downwelling (north-east monsoon) that tunes the water biogeochemistry. The present study provides baseline information on temporal variation of in situ *copepod gut pigments from IWCS. The copepods were collected between November 2011 and October 2013 and gut pigment contents and composition were estimated using the gut fluorescence method. Results revealed that copepods procured high gut pigment content in monsoon that coincided with ambient water pigment credited to discrete upwelling. Fluorometric analyses of copepod orders revealed presence of gut chlorophyll* a *(Chl* a*) throughout the study with highest gut Chl* a *(0.31 ± 0.25 ng copepod^{-1}; $N = 21$) and total gut pigments (2.01 ± 2.15 ng copepod^{-1}; $N = 21$) recorded in Calanoida. Consecutively, Calanoida and Poecilostomatoida chiefly consumed autotrophic biomass that was evident from presence of canthaxanthin and astaxanthin as dominant gut pigments. Interestingly, the marker pigment of Cryptophyceae was present only in Calanoida during monsoon and post-monsoon. Collectively these results conclude that copepods predominantly showed omnivory with discrete temporal variability by grazing upon autotrophic biomass that in turn probably supports the fishery.*

Keywords: Copepoda, gut fluorescence, monsoon, omnivory, astaxanthin

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INTRODUCTION

Copepods constitute a major part of the mesozooplankton community in the coastal as well as oceanic habitat of the Arabian Sea (Madhupratap *et al.*, 1990) and in the other parts of the world oceans (Roman & Gauzens, 1997; Lo *et al.*, 2004). Being a crucial prey, they support secondary consumers of the marine food web (Madhupratap *et al.*, 2001). Also, copepods generate carbon rich faecal pellets as a result of their grazing. Collectively, copepods greatly influence the transfer of energy and carbon compounds to the different trophic levels throughout the marine food web. Being noteworthy contributors to the marine biological pump, it is crucial to understand copepods' feeding habits. Copepods are known to feed on a wide range of food (Turner, 2004) but their tendency to switch diet based on the locale makes it vital to understand their feeding in every habitat (Stern, 1986; Peters *et al.*, 2013).

The common method to establish copepod feeding types is based on morphology of mouth parts (Madhupratap 1999). However, copepod feeding behaviour might be selective (Go *et al.*, 1998) or non-selective (Tseng *et al.*, 2008) based on assorted dietary type, algal type and toxicity (Atkinson, 1996; Jansen *et al.*, 2006). Copepods impact microbial assemblages (Schnetzer & Caron, 2005) by consuming the bacterial biomass (Gowing & Wishner, 1998). Copepod feeding studies have been mostly conducted with either direct gut examination (Gowing & Wishner, 1998) or faecal pellets study (Turner, 2002). However, these techniques may not be practical to determine the diet composition as lots of feed could go unclaimed with swift digestion. Also, bottle incubations have been used to study diets of calanoid copepods (Jansen *et al.*, 2006), but the experimental pressure on organisms may lead to a feeding habit different from an *in situ* feeding type.

While *in situ* studies on natural feeding observation of copepods are difficult, gut fluorescence method is widely used for this purpose by numerous researchers (Mackas & Bohrer, 1976; Kleppel & Pieper, 1984; Rodriguez & Durbin, 1992; Tsuda & Sugisaki, 1994; Saito & Taguchi, 1996; Takatsuji *et al.*, 1997; Tseng *et al.*, 2009). Fluorometric analysis gives quantitative estimates of only Chl a and its derivatives and HPLC proves qualitative composition of gut pigments (Kleppel & Pieper, 1984). These gut pigments, chiefly canthaxanthin and astaxanthin, remain stable in copepod gut (Lotocka & Styczynska-Jurewicz, 2001), also conveniently are eluted by chromatography (Jeffrey, 1974) and act as indicators of feed (Lewin, 1974).

Only autotrophs can manufacture carotenoids *de novo* (Lotocka & Styczynska-Jurewicz, 2001; Van Nieuwerburgh *et al.*, 2005), which are grazed by primary consumers as β-carotene and processed as astaxanthin and canthaxanthin via metabolic pathway (Kleppel *et al.*, 1985; Van Nieuwerburgh *et al.*, 2005). The exploitation of precursors and successive

Corresponding author:
A.M. D'souza
Email: dsouzaa@nio.org

synthesis of astaxanthin by herbivorous zooplankton thus represents a vital entry point of astaxanthin into marine food webs.

This is the first study on *in situ* copepod gut pigments from the continental shelf of the eastern Arabian Sea. To understand the copepod feeding types, we studied the gut pigments of copepod orders quantitatively (fluorometric) as well qualitatively (pigment composition) using the gut fluorescence method. This paper presents copepod feeding habits and gut pigment contents over different seasons at the coastal time series station along the central western coast of India.

MATERIALS AND METHODS

Sampling

The sampling site was located at 15°31.17′N 73°44.200′E (G5) off Candolim, Goa, on the continental shelf of the central western coast of India (Figure 1) with depth of ~28 m. The sampling was carried out in daytime during November 2011, March 2012, August 2012, October 2012, November 2012, December 2012, January 2013, February 2013, April 2013, May 2013, July 2013, August 2013, September 2013 and October 2013. It covered monsoon (June–September), post-monsoon (October–January) and pre-monsoon (February–May) seasons. A single mesozooplankton sample, representative of each month, was collected by vertically towing a Heron Tranter net (0.25 m^2 mouth area; 200 μm mesh size) from ~26 m to the surface. Sampling of water Chl *a* was carried out from four depths (0, 9, 18 and 27 m) using a 5 l Niskin sampler coupled with reversible thermometer enabling temperature measurement. A sub-sample of known volume (0.5 l) was collected for each depth in an amber-coloured bottle during each month.

All the samples were stored in an icebox until transferred to the laboratory for further processing. The data on salinity were obtained using CTD (Conductivity-temperature-depth; Sea-Bird electronics).

Fluorometric estimation of water Chl *a*

Chl *a* levels in ambient water were measured using JGOFS protocol (UNESCO, 1994) with slight modification. Water samples of 0.5 l were filtered using 47 mm GF/F polycarbonate filters and extracted in 90% acetone at −20°C overnight in the dark. The acetone extract was then analysed on a Turner Designs-10 fluorometer before and after acidification with 1.2 M HCl under poorly lit conditions.

All the four depths sampled for water chlorophyll analyses were integrated to get water column Chl *a*. Further, the depth integrated Chl *a* was used as ambient water Chl *a* to the copepods.

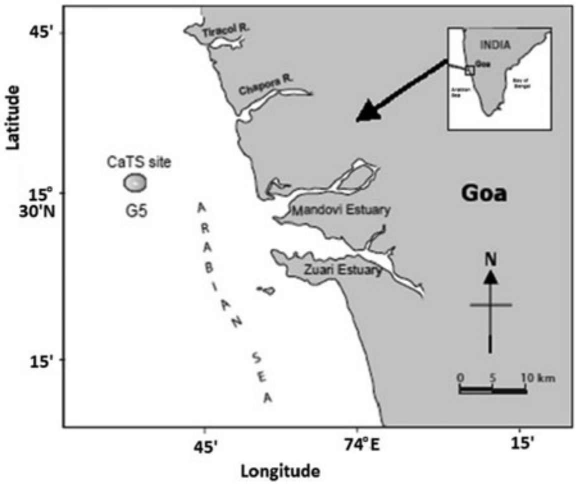

Fig. 1. Location of sampling site (G5) off Goa, in the Arabian Sea.

Copepod taxonomy and sorting

In the laboratory, the mesozooplankton samples were split into four parts using a Folsom splitter. Two sub-samples were preserved in buffered formalin (4%) for further taxonomic analysis and the remaining two were stored at −20°C until analysed for the gut pigment contents.

Taxonomic identification and enumeration of copepods was carried out from the formalin-preserved sub-samples, placed in Bogorow's chamber under stereoscopic microscope (Olympus SZX 16) using the standard identification keys of Kasturirangan (1963) and Conway *et al.* (2003). The copepod abundance was expressed as individual 100 m^{-3}. The other two sub-samples were thawed, rinsed with filtered seawater and sorted under microscope with minimum light and then the gut pigments were analysed using a fluorometer and HPLC.

Fluorometric estimation of gut pigments

The gut fluorescence technique described by Mackas & Bohrer (1976) with modifications proposed by Morales *et al.* (1990) and followed by Tseng *et al.* (2008) was carried out. For each group, known number of individuals (ranged from 20–40) were picked and kept for extraction in 6 ml of 90% acetone in dark under −20°C (Islam *et al.*, 2005) for 24 h with no homogenization (Wong *et al.*, 1998; Tseng *et al.*, 2008). Once the pigments were extracted, the upper clear solution was analysed on a Turner Design-10 Fluorometer in low illumination before and after acidification. Acidification was performed using 1.2 M hydrochloric acid. Literature suggested phaeopigment loss when using the gut fluorescence technique (Dagg & Wyman, 1983; Tseng *et al.*, 2008), hence, all the phaeopigment values was multiplied by a factor of 1.51 (Dagg & Wyman, 1983). Gut pigment contents were then expressed as ng/copepod for Chl *a*, phaeopigment and total pigment (obtained from the addition of Chl *a* and corrected phaeopigment concentrations in the copepod gut; Dam & Peterson, 1988).

Gut pigment analysis by HPLC

Approximately 300 individuals per copepod order were required for sample analysis using HPLC; the dominant orders such as Calanoida and Poecilostomatoida were analysed for qualitative pigment assessment. The required numbers of copepods were sorted and placed in 2 ml of HPLC grade methanol. The samples were not macerated because previously analysed samples did not show much variation in the pigment extracted with or without sonication. The samples were kept in a refrigerator at −20°C for 24 h in the dark for pigment extraction. The clear extract was then collected in 3 ml amber coloured glass vial and passed directly into the sampler tray for analysis (Gasparini *et al.*, 2000).

Eclipse XDB C8 HPLC column (4.6 × 150 mm) manufactured by Agilent Technologies was used to carry out the analysis. Methanol and mixture of (70:30) methanol and 1 M ammonium acetate (pH 7.2) were the solvents used for elution. The eluting pigments were detected at 450 and 665 nm (excitation and emission) by the diode array detector. All the chemicals used were of HPLC grade (E. Merck, Germany).

Statistical analysis

Spearman's non-parametric correlation was performed to observe the pattern of variation of gut Chl *a* and gut phaeopigments in different copepods orders. Further, two-way analysis of variance (ANOVA) was performed to examine the significant seasonal and depth-wise variation in water Chl *a* and phaeopigment. Similarly, ANOVA was carried out to check significant seasonal variations of total gut pigments in different copepod orders. ANOVA was followed by Tukey's *post hoc* test to reveal the significant variation within the different seasons. Values were considered significant at 95% level of confidence (Statistica 6.0, Statsoft, OK, USA).

RESULTS

Hydrography

The results on salinity have been adopted from the previously published article by Naqvi *et al.* (2006) that depicted a decadal variation of this parameter from the study region. This work reports distinct variations during monsoon with lower values in salinity. The minimum salinity value of 34.8 and maximum of 36.0 were examined during monsoon and pre-monsoon.

The minimum and maximum temperature recorded during the present study ranged 23.5–29.4°C during monsoon (August 2012) and pre-monsoon season (March 2012; Figure 2). The highest ($4.29\ \mathrm{ng\,l^{-1}}$) and lowest ($0.69\ \mathrm{ng\,l^{-1}}$) concentration of surface water Chl *a* was observed during monsoon (August 2012) and pre-monsoon (April 2013). The lowest ($0.05\ \mathrm{ng\,l^{-1}}$) and highest ($4.59\ \mathrm{ng\,l^{-1}}$) concentration of water phaeopigment was recorded during pre-monsoon (March 2013) and monsoon (July 2013), respectively.

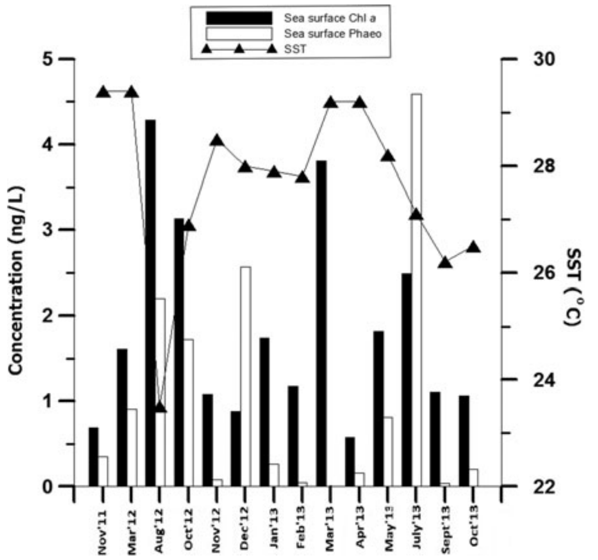

Fig. 2. Temporal variation in the sea surface physical parameters (chlorophyll *a*, phaeopigment, temperature) recorded at coastal station (G5).

Seasonal variation in Copepoda

Copepods, the dominant mesozooplankton group, comprised >80% of the abundance. Seasonally, low copepod abundance accounted for 93,600 ± 30,399 ind. $100\ \mathrm{m^{-3}}$ (Figure 3) with dominance of species *Oncaea venusta* during monsoon. Highest copepod density was observed in post-monsoon (133,062 ± 76,342 ind. $100\ \mathrm{m^{-3}}$), dominated by *Acrocalanus* spp. Amongst the copepod orders, Calanoida dominated the copepod community throughout the year with an occasional dominance of Poecilostomatoida (46,543 ± 28,178 ind. $100\ \mathrm{m^{-3}}$; during pre-monsoon). The dominant Calanoida and Poecilostomatoida families represented annually were Paracalanidae and Oncaeidae, respectively.

The species best represented continuously throughout the year were considered for studying feeding habits. Therefore gut pigment analyses on the following species were undertaken. Calanoida comprised *Acrocalanus* spp., *Paracalanus* spp., *Subeucalanus* spp., *Temora* spp. and *Acartia* spp.; Harpacticoida was represented by *Euterpina* sp.; Poecilostomatoida by *Oncaea* spp. and *Corycaeus* spp.; Cyclopoida was represented by *Oithona* spp. Dominant Calanoida species which were potentially herbivores according to the existing knowledge of their feeding biology through literature review were taken into account.

Variation in water column Chl *a* and phaeopigment

The water Chl *a* content in the surface water ranged 1.69–$2.96\ \mathrm{ng\,l^{-1}}$; minimum and maximum concentration recorded during post-monsoon and monsoon (Figure 4A). The minimum ($0.59\ \mathrm{ng\,l^{-1}}$) and maximum ($1.93\ \mathrm{ng\,l^{-1}}$) concentration of phaeopigment content in the surface water was recorded during pre-monsoon and monsoon season (Figure 4B). The

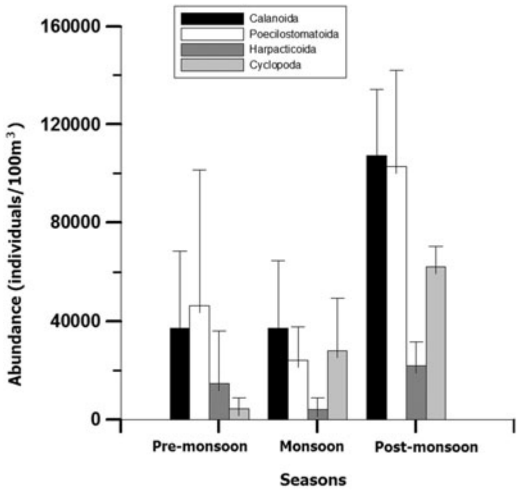

Fig. 3. Seasonal variation of abundance (mean value ± SD) for different copepod orders at coastal station (G5).

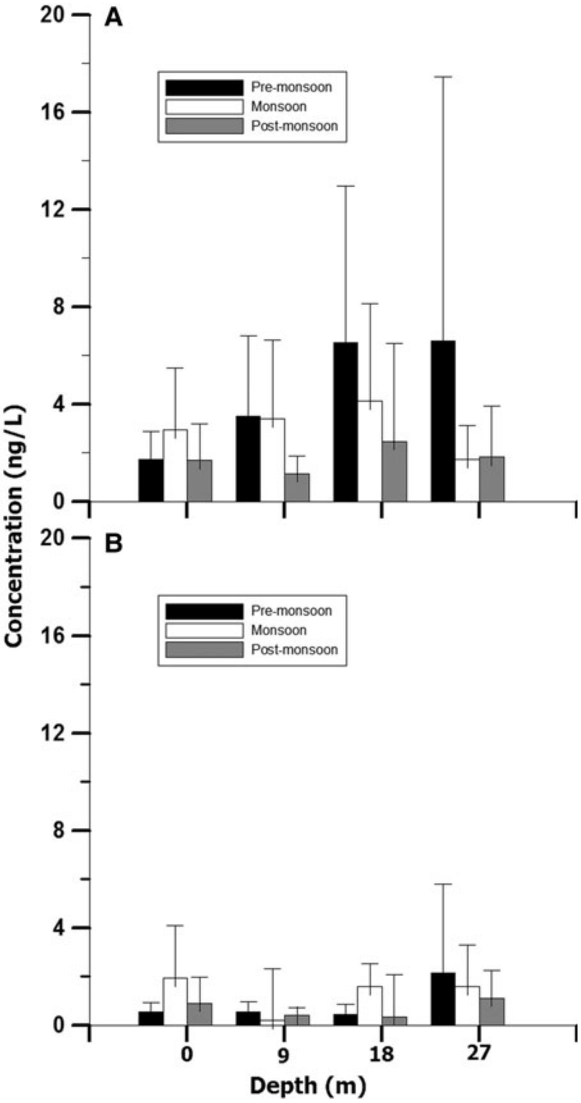

Fig. 4. Seasonal variation of water pigments (A) chlorophyll *a* and (B) phaeopigments (mean value ± SD) at different depths at coastal station (G5).

Table 1. Results of two-way ANOVA comparing seasonal and depth-wise variation of water chlorophyll *a* and phaeopigment.

Effect	SS	df	MS	*F*	*P*
Chlorophyll *a*					
Season	58.74	2	29.37	6.86	0.004*
Depth	4.14	3	1.38	0.32	0.81
Season × Depth	14.24	6	2.37	0.55	0.76
Phaeopigment					
Season	9.47	2	4.74	1.57	0.23
Depth	18.17	3	6.06	2.01	0.14
Season × Depth	27.97	6	4.66	1.55	0.20

*Indicates variables that were significant.

water Chl *a* content at 9 m depth ranged 1.14–3.50 ng l^{-1}, at 18 m 2.47–6.52 ng l^{-1} and at 27 m 1.73–6.60 ng l^{-1}. The phaeopigment concentration ranged 0.20–0.54 ng l^{-1} at 9 m, 0.35–1.58 ng l^{-1} at 18 m and 1.11–2.15 ng l^{-1} at 27 m depth. On the contrary to the surface water Chl *a*, the other depth zones (9, 18 and 26 m) showed highest water Chl *a* values during pre-monsoon. Besides, highest phaeopigment concentrations for 9 and 26 m deep waters were observed during post-monsoon. Seasonally, the Chl *a* variation differed significantly ($P < 0.001$; Table 1), nevertheless no significant variation was observed within the depths and the interaction between the season–depth. Further, *post hoc* test revealed significantly high Chl *a* in monsoon ($P < 0.001$).

Temporal variation in gut Chlorophyll *a* and phaeopigment content in Copepoda

Quantitative analysis of gut pigment content of Calanoida, Poecilostomatoida, Harpacticoida and Cyclopoida was carried out on a monthly basis from November 2011 to October 2013. Lapse in data for a few months is due to either difficulty in sampling during the rough weather or absence of sufficient number of individual species required for analysis. Also, duplicate samples analysis was carried out wherever adequate numbers of organisms of copepod orders were available.

The gut Chl *a* and phaeopigment in copepods showed distinct variation (Figure 5). Estimates of gut Chl *a* and phaeopigment content for the Calanoida copepods were highest during monsoon (July 2013; Figure 5A). However, the lowest value for gut Chl *a* and phaeopigment content was observed during pre-monsoon (April 2013) and post-monsoon (November 2012), respectively. Also, their gut pigments showed the highest variability for gut Chl *a* (0.02–1.02 ng copepod^{-1}) and gut phaeopigment (0.11–3.26 ng copepod^{-1}; Figure 5A) amongst Poecilostomatoida, Harpacticoida and Cyclopoida. Calanoida exhibited comparatively larger variability in body size (0.93–2.6 mm). In Poecilostomatoida, the gut Chl *a* content ranged between 0.013–0.548 ng copepod^{-1} and gut phaeopigment ranged from 0.07–1.23 ng copepod^{-1} (Figure 5B). The highest copepod gut Chl *a* was observed in the month of October 2012 and least in August 2013.The highest (1.11 ng copepod^{-1}) and lowest (0.07 ng copepod^{-1}) gut phaeopigment content was observed in August 2012 and December 2012, respectively. Furthermore, its total body size ranged from 1.00–1.27 mm.

Although Harpacticoida comprised minimal body size (0.35–0.66 mm), it yielded the second highest gut Chl *a* pigment range (0.03–0.693 ng copepod^{-1}; Figure 5C). The highest concentration of harpacticoid gut Chl *a* was observed in August 2012 and the lowest was recorded in July 2013. The phaeopigment content was in the range of 0.098–1.712 ng copepod^{-1} (Figure 5C) with least value recorded in November 2012 and highest during March 2012. Cyclopoida had the most slender body and their size ranged from 0.75–1.50 mm. Comparatively, this order yielded the least content of gut Chl *a* pigment and phaeopigment content that ranged from 0.014–0.42 and 0.06–1.45 ng copepod^{-1} (Figure 5D), respectively. The highest and lowest values for copepod gut Chl *a* were observed in October 2012 and March 2012, respectively. The gut phaeopigment concentration was least during December 2012 and highest in July 2013.

Overall, inter-annual and temporal variability were observed in gut Chl *a* pigment and gut phaeopigment content of copepods. Equally, the pattern of variation of gut Chl *a* and phaeopigment differed. The Chl *a* was always less copious than phaeopigment in the gut of copepods; however, no significant statistical relation was observed. An exception was noted in March 2013, when all copepod orders had gut Chl *a* higher compared with gut phaeopigment.

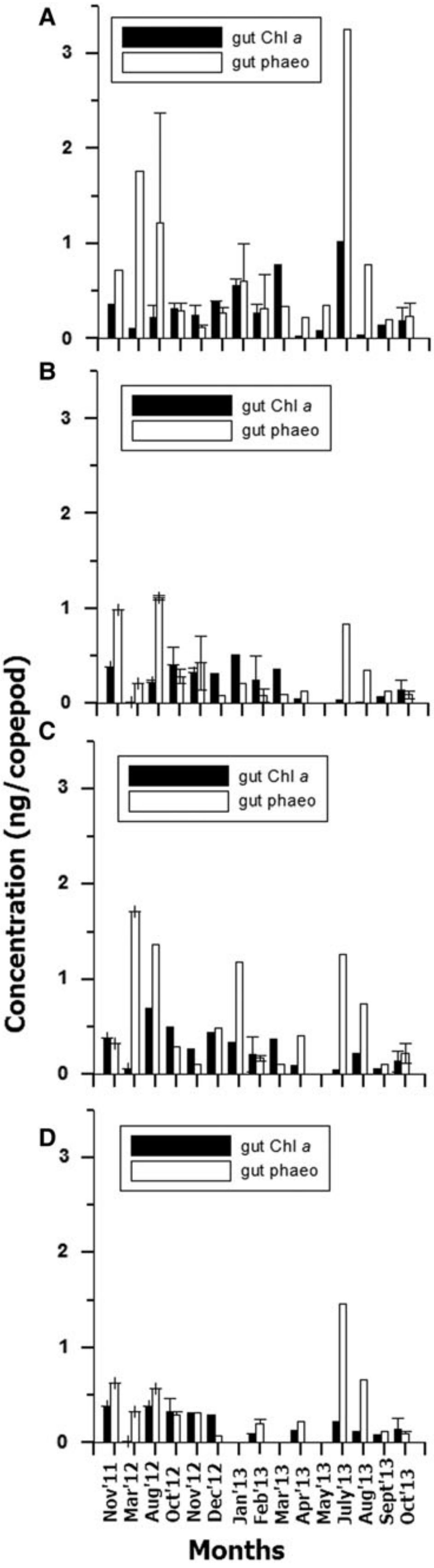

Fig. 5. Temporal variation of gut chlorophyll *a* and gut phaeopigment contents (mean value ± SD) in copepod orders (A) Calanoida, (B) Poecilostomatoida, (C) Harpacticoida and (D) Cyclopoida at coastal station (G5).

The integrated water column Chl *a* recorded highest during monsoon (86.08 mg m^{-2}) followed by post-monsoon (46.26 mg m^{-2}) and the least during pre-monsoon (42.80 mg m^{-2}). When integrated water column Chl *a* was correlated with gut Chl *a* of all the four copepod orders, no significant correlation was observed. The lack of correlation apprehended for Calanoida ($N = 21$, $r^2 = 0.06$; Figure 6A), Poecilostomatoida ($N = 20$, $r^2 \leq 0.01$; Figure 6B), Harpacticoida ($N = 15$, $r^2 = 0.28$; Figure 6C) and Cyclopoida ($N = 15$, $r^2 = 0.06$; Figure 6D).

Seasonal variation in total gut pigment in Copepoda

The data were presented on a seasonal scale; specifically, monsoon (June–September), post-monsoon (October–January) and pre-monsoon (February–May). Further, qualitative analysis of gut pigment content was carried out following HPLC technique on a seasonal basis for the copepod orders Calanoida and Poecilostomatoida. Due to unavailability of the required number of individual species of Harpacticoida and Cyclopoida, those orders were not taken into consideration for analysis.

Estimates of total gut pigment contents for the copepod orders showed higher concentration during monsoon than during pre-monsoon and post-monsoon. The total gut pigment (Chl *a* and corrected phaeopigments) in Calanoida varied from 0.27–5.93 ng $copepod^{-1}$ (Figure 7A) more than that of Poecilostomatoida, Cyclopoida and Harpacticoida. Seasonally, monsoon depicted the highest gut pigment content (2.02 ± 2.15 ng $copepod^{-1}$). Further, qualitative analysis revealed predominantly astaxanthin, canthaxanthin and alloxanthin pigments (Table 2). However, alloxanthin, the marker pigment of Cryptophyta, was conspicuous by its absence in pre-monsoon suggesting seasonality in gut pigment composition of Calanoida. The total gut pigments ranged between 0.12 and 2.01 ng $copepod^{-1}$ (Figure 7B) for Poecilostomatoida. Again, the highest gut pigment content, 1.15 ± 0.79 ng $copepod^{-1}$ was noticed in monsoon. The qualitative gut pigment composition revealed predominantly canthaxanthin and astaxanthin (Table 2). In addition, an HPLC absorbance chromatogram depicted a few tiny peaks that were eluted at lower limits of detection hence confirmation of their identity was critical.

Harpacticoids attained the second highest total gut pigment values that ranged from 0.20–2.75 ng $copepod^{-1}$ (Figure 7C). However, a decline in total gut pigment was prominent in post-monsoon although gradual elevation was observed during the pre-monsoon season. Furthermore, the seasonal variation showed a similar trend to that observed in Calanoida copepods. Similarly, total gut pigment content in Cyclopoida varied from 0.17–2.41 ng $copepod^{-1}$ (Figure 7D) with highest values noticed in monsoon (1.12 ± 0.82 ng $copepod^{-1}$). Further, the variation of gut pigment concentration was similar to that of Poecilostomatoida, with descending concentration from monsoon to post-monsoon and pre-monsoon.

Total gut pigment content of copepods revealed a greater contribution of phaeopigment than chlorophyll. Also, copepods were found to contain photosynthetic pigments in their gut throughout the year. However, gut pigment concentrations were at a maximum during monsoon indicating

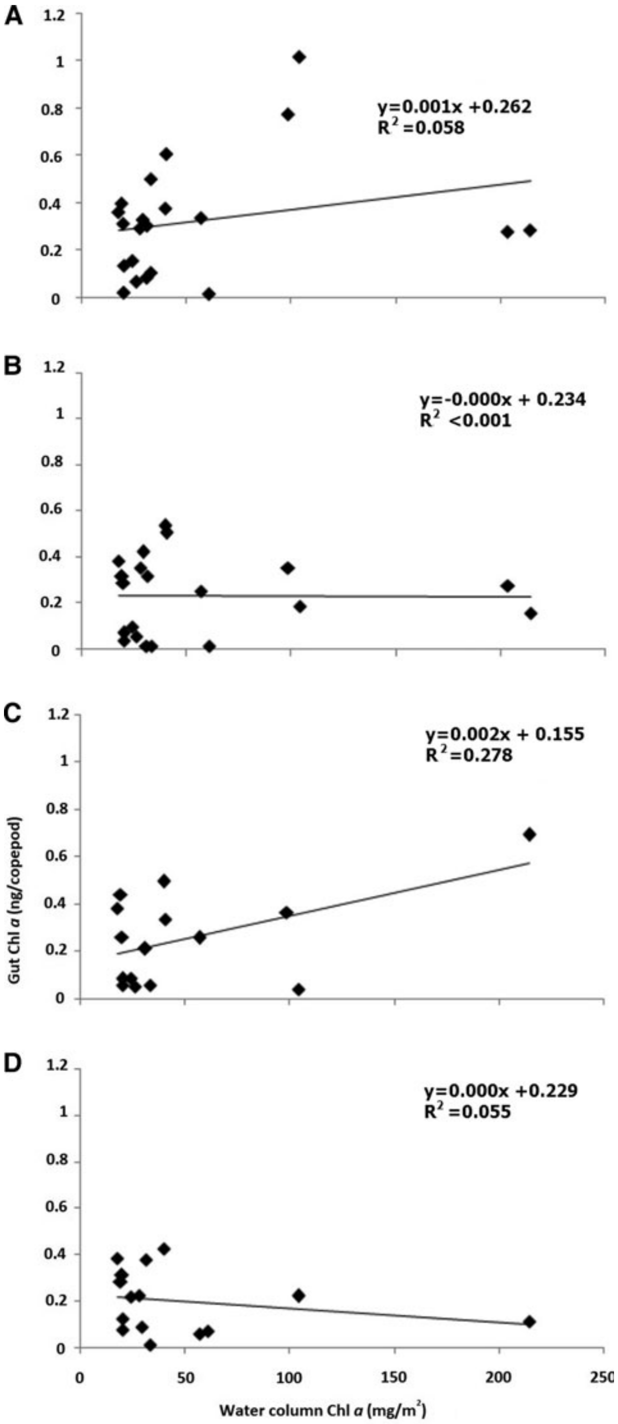

Fig. 6. Correlation between integrated water column chlorophyll *a* and copepod gut chlorophyll *a* content for copepod orders (A) Calanoida, (B) Poecilostomatoida, (C) Harpacticoida and (D) Cyclopoida from November 2011 to October 2013. The water column Chl *a* has been integrated for four depths viz., 0, 9, 18 and 27 m.

significant variability ($P < 0.01$; Table 3). Further *post hoc* tests revealed high value during post-monsoon ($P < 0.01$).

DISCUSSION

The IWCS is governed by the monsoon regime and experiences diverse biochemical phenomena that appear to modulate copepod distribution as well as their feeding habits. The cusp of biochemical phenomena occurring in the region is the reciprocal action of upwelling (from July/August to October/November) and downwelling (during the

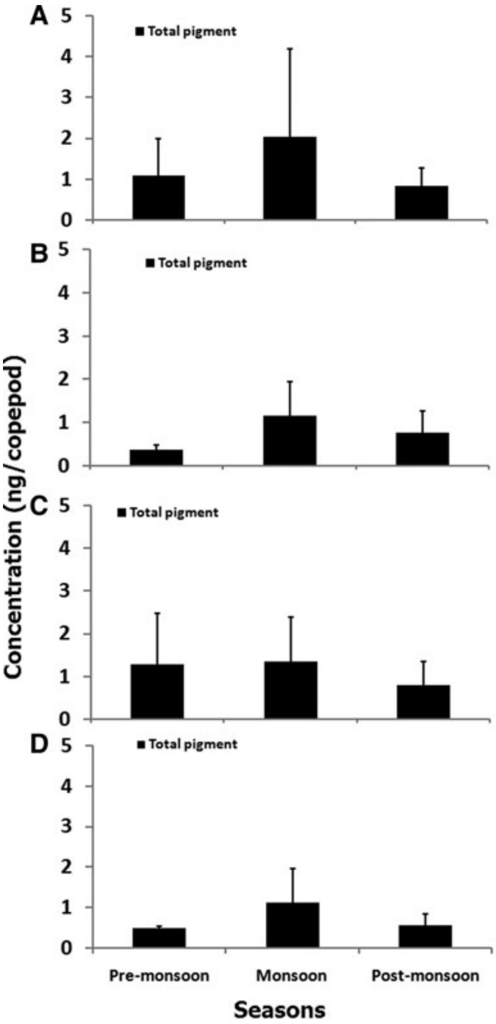

Fig. 7. Seasonal variation of total pigment (±SD) in orders of copepods: (A) Calanoida, (B) Poecilostomatoida, (C) Harpacticoida and (D) Cyclopoida at coastal station (G5). Total gut pigment is summation of gut chlorophyll *a* and corrected gut phaeopigment (gut phaeopigment × 1.51) content.

Table 2. Seasonal variation of gut pigment composition in copepods.

Seasons	Orders	Dominant pigments	RT (min)
Monsoon	Calanoida	Astaxanthin	15.9
		Alloxanthin	17.7
Monsoon	Poecilostomatoida	Astaxanthin	15.9
		Canthaxanthin	18.2
Post-monsoon	Calanoida	Astaxanthin	15.9
		Alloxanthin	17.7
Post-monsoon	Poecilostomatoida	Astaxanthin	15.9
		Canthaxanthin	18.2
Pre-monsoon	Calanoida	Astaxanthin	15.9
		Canthaxanthin	18.2
Pre-monsoon	Poecilostomatoida	Astaxanthin	15.9
		Canthaxanthin	18.2

RT is the retention time.

Table 3. Two-way ANOVA comparing seasonal variation of total gut pigments for copepod orders.

Effect	SS	df	MS	*F*	*P*	*Post hoc* test
Order	0.02	3	0.01	0.30	0.83	
Season	0.33	2	0.17	6.99	0.01*	Post-monsoon
Order × Season	0.05	6	0.01	0.34	0.90	

*Indicates variables that were significant. The season showing significantly highest mean values from the Tukey's *post hoc* test is shown.

rest of the year) that hold in check the oxygen conditions in benthic waters (Maya *et al*., 2011). Moreover, IWCS is a productive system due to nutrient enrichment owing to coastal upwelling and riverine run-off due to monsoonal flushing (Pratihary *et al*., 2014). In addition, freshening of coastal surface waters is known to occur during the monsoon due to freshwater supply from rivers along the Indian west coast (Jayakumar *et al*., 2001; Suprit & Shankar, 2008). A distinctive feature of the IWCS is seasonal anoxia (Naqvi *et al*., 2006), although this is confined to the near-shore region of the shelf (Pratihary *et al*., 2014). Eventually, the monsoonal effects result in intense anoxia during the early post-monsoon period (October–November). Another crucial event of seasonal fluctuation in phytoplankton composition occurs in the study region as described previously by Parab *et al.* (2006). A pigment study from this region reported a plethora of tiny phytoplankton groups dominated by prymnesiophytes and green algae during monsoon (Roy *et al*., 2006). Likewise, blooms of nitrogen fixers, *Trichodesmium* have long been known to occur in Indian coastal waters during pre-monsoon (Devassy *et al*., 1978; Parab *et al*., 2006; Roy *et al*., 2006).

Although mesozooplankton are considered to be an important component of the marine food chain, information on copepod feeding types was based on morphology of mouth parts (Madhupratap, 1999). In the present study, copepod abundance and taxonomy are in close agreement with prior data reported from the Arabian Sea by Madhupratap *et al.* (1996), Padmavati *et al.* (1998) and Smith & Madhupratap (2005). Four dominant copepod orders, namely Calanoida, Poecilostomatoida, Harpacticoida and Cyclopoida, were consistently recorded from this study. Interestingly, the low copepod abundance during monsoon may be attributed to factors such as freshening of the system and coastal upwelling. The highest copepod abundance during post-monsoon corresponds to the breeding season of organisms. Also, ambient Chl *a* concentration was $>1\ \mu g\ l^{-1}$ throughout the water column (Figure 3). It is an indicator of productive waters and therefore, feeding preference for herbivorous/omnivorous copepod would be autotrophic prey. All the copepod orders (Calanoida, Poecilostomatoida, Harpacticoida and Cyclopoida) showed presence of undegraded chlorophyll. This indicated that copepods were non-diapausing and were actively grazing on the abundantly available autotrophic biomass throughout the year.

The standard 200 μm mesh used to collect mesozooplankton would obtain samples that are comparable to previous studies (Madhupratap *et al*., 1996; Padmavati *et al*., 1998; Smith & Madhupratap, 2005) albeit absolute values of small copepods may be biased. Therefore, present data on copepod abundance might inefficiently capture small-sized poecilostomatoids, cyclopoids, copepodites and their nauplii. In addition, the seasonal patterns of copepod assemblage require adjustments in fine and coarse mesh size according to the temporal change in diversity. The breeding season for most of the copepods in the Indian waters was during the post-monsoon period, although a few species breed continuously throughout the year (Ummerkutty, 1965). Consequently, in monsoon, copepod nauplii would seldom be encountered and the underestimation would be preferably negligible. From the experience of the present study, for future research it will be best to use a smaller mesh size along with 200 μm.

The findings of the present study showed higher gut pigment contents in Calanoida that belong to the comparatively larger body size (0.93–2.6 mm). First, it may be the result of consideration of only herbivores belonging to Calanoida from the studied region. Second, the larger forms are known to accumulate more gut pigments (Morales *et al*., 1990; Tseng *et al*., 2008, 2009), as they have larger gut volume and metabolic expenditures. The value of Chl *a* thus seems to increase in copepod gut with escalating body sizes. Additionally, studies on ingestion of phytoplankton by copepods revealed that the minimal size limit of feed was 2 μm (Roman & Gauzens, 1997). In this view, Lie *et al.* (2013) suggested that the large phytoplankton was inadequately grazed by the small copepods in Tolo Harbour as the transfer efficiency was low (1.4%) among phytoplankton (primary production) and copepods (secondary production). Thus, it appears that size range of copepod feed is another important component governing the gut content estimates.

The dissimilar pattern of variation for Chl *a* and phaeopigment in copepod gut is indicative of governance of diverse processes for their distribution. Among these, photodegradation of Chl *a* to phaeopigment could be one of the probable reasons as the organisms are exposed to light in the natural habitat and during sorting of samples under the microscope (Islam *et al*., 2005). Furthermore, the growth phase and size of the phytoplankton cell consumed by the copepods also portray the variation in Chl *a* concentration (Uye, 1986; Bautista & Harris, 1992; Tan *et al*., 2004). On the other hand, the degree of degradation and pigment loss in the copepod guts could fluctuate under diverse circumstances such as the concentration of feed in ambience, digestion of the chlorophyll-bearing material and history of feed of the organism (Dagg & Walser, 1987; Penry & Frost, 1991; Head, 1992; Head & Harris, 1994). It might have also been affected by ingestion of detritus and coprophagy resulting in varied distribution (Goes *et al*., 1999).

In our study, phaeopigment concentration in copepod guts was mostly found to be higher than Chl *a* values. This might be because of rapid degradation of ingested chlorophyll to phaeopigments that eventually remains unaffected (Shuman & Lorenzen, 1975). Also, variable phaeopigment:chlorophyll ratio in gut signifies the amount of recently ingested chlorophyll but phaeopigments (phaeophorbide and phaeophytin) generally make up the major part of the total pigments assessed (Shuman & Lorenzen, 1975; Hallegraeff, 1981; Dagg & Wyman, 1983; Islam *et al*., 2005; Tseng *et al*., 2008). Goes *et al.* (1999) speculate that the higher per cent of phaeopigment is due to the reingestion of the already evacuated particulate organic matter. Conspicuously, in March 2013, gut Chl *a* was higher than gut phaeopigment in all copepod orders and water phaeopigments were below the detectable limit. Such inter-annual variability between the water pigments and the copepods gut pigments needs to be monitored for longer duration to understand the pigment dynamics.

However, bioconversion of Chl *a* to detectable phaeopigment is controversial; Shuman & Lorenzen (1975) supported complete degradation of chlorophyll into phaeophorbide, while Hallegraeff (1981) suggested up to 20–50% conversion of Chl *a* into phaeophorbide and the rest to phaeophytin takes place. Further, Bustillos-Guzman *et al.* (2002) suggested that individual phaeopigments could be produced at different rates in accordance with the chemical/enzymatic reaction acting differently on the chlorophylls in the copepod gut. Besides, lack of information on Chl *a* degradation and turnover rates is the major shortcoming of the present method. Furthermore, we did not evaluate the pigment loss during this study and opted to correct for pigment damage using an average estimate value of 33% (Dam & Peterson, 1988).

The total gut pigments content of copepods were 0.16–4.13 ng copepod^{-1} (Figure 7); the values were lower than those documented in Dabob Bay, Washington (0.23–8.35 ng copepod^{-1}; Dagg *et al.*, 1989). Sampling in daytime might have recorded the comparably low copepod gut content estimates. Prior studies (Mackas & Bohrer, 1976; Saito & Taguchi, 1996; Islam *et al.*, 2005; Tseng *et al.*, 2008; Wu *et al.*, 2013) suggest that gut pigment contents in copepods were usually higher during the nocturnal hours and minimal at daylight hours. Besides this, faster gut evacuation rate and occurrence of gut pigment destruction also possibly led to underestimation of the observed values (Morales *et al.*, 1991; Bollens & Landry, 2000). However, the values were comparable to those estimated by Tseng *et al.* (2008, 2009) and higher compared with those reported by Islam *et al.* (2005).

Although copious autotrophic biomass was available in the studied region, particular copepod species may prefer different size fractions to prey upon. This may be why no significant correlation was observed between total water Chl *a* and gut Chl *a* of Calanoida, Poecilostomatoida, Cyclopoida and Harpacticoida (Figure 6). The present observations are consistent with the views of Dagg & Wyman (1983), Dam & Peterson (1988) and Li *et al.* (2004). Such surveillances are also suggestive of diel feeding rhythms, individual variance and/or feeding synchronization (Uye & Yamamoto, 1995; Li *et al.*, 2004). On the other hand, significant positive correlation of copepod gut Chl *a* and ambient water Chl *a* has been reported from less productive waters (Tseng *et al.*, 2009).

Gut pigment contents in copepods were observed to be higher in the monsoon (Figure 7) that coincided with low copepod abundance (Figure 2). It implies less inter-species competitive stress on copepods for favoured feed. At the same time, copepods may be facing predation pressure for efficient energy transfer to the higher consumers. The shift in community structure of phytoplankton seems to be a crucial factor leading to seasonality in feeding habits. Existence of cyanobacterial dominance, especially *Trichodesmium* sp. in pre-monsoon followed by a diatom-rich community in monsoon and dinoflagellates in post-monsoon have been reported from the Arabian Sea (Parab *et al.*, 2006; Pratihary *et al.*, 2014). Additionally, in pre-monsoon, *Noctiluca scintillans* bloom that is considered to be an undesired food by copepods was recorded (Gomes *et al.*, 2014). Gaonkar & Anil (2012) revealed gut pigment content in barnacle larvae from neighbouring waters of the study region. Although our data cannot be directly compared with barnacle larvae, it is interesting to note that the observed seasonality in the gut pigment content were higher in post-monsoon as compared with pre-monsoon season. A report on fishery of the Arabian Sea by Madhupratap *et al.* (2001) pointed out abundances of planktonivorous fishes in the region with highest catches observed between October and March. Interestingly, in this study high abundance of copepods was noted during post-monsoon. Combining this information in view of trophic levels suggests that the copepods play a vital role in the sustenance of fishery in this realm.

Predominance of astaxanthin in copepod gut is eminent. Most researchers considered astaxanthin to be derivative of canthaxanthin, which is produced from β- carotene via echinenone in herbivores (Goodwin, 1971; Lotocka & Styczynska-Jurewicz, 2001; Caramujo *et al.*, 2012). Such a mode of bioconversion of dietary carotenoid is generally considered the pathway in aquatic organisms (Goodwin, 1971; Caramujo *et al.*, 2012), but a few researchers have considered astaxanthin as an animal pigment (Gasparini *et al.*, 2000) due to its presence even in starved copepods. However, with the available literature, it is reasonable to consider astaxanthin as a marker pigment for omnivory (see Juhl *et al.*, 1996). Hence, presence of canthaxanthin in Calanoida and Poecilostomatoida gut (Table 2) is suggestive of herbivorous and astaxanthin of omnivorous feeding habits. The current study portrays presence of astaxanthin and canthaxanthin in Calanoida that is in accordance with Lotocka & Styczynska-Jurewicz (2001) and Holeton *et al.* (2009). The pigment, astaxanthin, plays an important role in copepods by being a potent antioxidant for protecting lipids, photo-protection against photosynthetically active radiation and UV light (Hairston, 1980; Terao, 1989; Holeton *et al.*, 2009; Hansson, 2004). Additionally, astaxanthin is suggested to act as a precursor of vitamin A and retinoid compounds (Schiedt *et al.*, 1985; Holeton *et al.*, 2009). Also, fishes such as salmon require astaxanthin for their characteristic red colour (Olsen *et al.*, 2005) and for certain aspects of immunity (Thompson *et al.*, 1995) but cannot produce it *de novo*. Hence, copepods with astaxanthin pigment can be a source of astaxanthin for the fish stock.

A notable observation is the presence of alloxanthin in calanoids that varied at seasonal scale (Table 2). The gut alloxanthin recorded during monsoon and post-monsoon could be due to the feeding on Cryptophyceae from ambient water. This theory is based on previous work of Maya *et al.* (2011) that reported seasonal variations in water alloxanthin concentration, with trace quantities during pre-monsoon. Also, dominance of *Trichodesmium* sp. (devoid of alloxanthin) was reported during pre-monsoon (Parab *et al.*, 2006). Thus, our finding roughly conforms to the universal assumption of selective grazing of calanoids. At the same time, consideration of alloxanthin as marker pigment of cryptophytes is a sensitive statement as sometimes it is considered as an alloxanthin-like animal pigment (Pandolfini *et al.*, 2000). Nevertheless, our observation of alloxanthin as a cryptophytes marker pigment is favoured by other studies (Breton *et al.*, 1999; Cotonnec *et al.*, 2001), and there are reports on presence of astaxanthin and alloxanthin in copepods (Juhl *et al.*, 1996) in particular *Temora longicornis* (Calanoida) (Antajan & Gasparini, 2004). These facts imply caution while considering alloxanthin to be a marker pigment in copepod gut.

In this study, the presence of fucoxanthin, a marker pigment for diatoms (Jeffrey, 1974) was not detected, probably due to pigment degradation in the gut passage (Head & Harris, 1994). It has been reported that fucoxanthin degrades faster than chlorophyll derivatives into undetectable compounds (Antajan & Gasparini, 2004). In addition, it could be due to the low concentration of fucoxanthin eluted on chromatogram as low intensity peaks went unidentified. It is noteworthy that chlorophyll pigments went undetected by HPLC for no known reason. One possibility could be that pigment decomposition occurred during gut passage in copepods. Similarly, Kleppel & Pieper (1984) and Kleppel *et al.* (1985) considered carotenoids to be more conserved compared with chlorophylls in copepod guts. Further investigation on pigment dynamics is required on this aspect on copepod feeding behaviour for better understanding.

Previous documentation on microscopic gut examination of Poecilostomatoida species revealed presence of phyto- as well as zooplankter (Ohtsuka *et al.*, 1996; Metz, 1998). Ohtsuka *et al.* (1996) explained the presence of diatom chains and appendicularian houses in *Oncaea* sp. (Poecilostomatoida) gut in detail. Also, an experimental study by Metz (1998) found diatoms to be a preferred food in *Oncaea curvata*. Conversely, it has been reported that Poecilostomatoida and Cyclopoida undertake carnivorous feeding behaviour in the Arabian Sea (Timonin, 1971; Smith & Madhupratap, 2005). It is interesting that in the current study, both Poecilostomatoida and Cyclopoida reflected presence of Chl *a*. Poecilostomatoida and Cyclopoida may compensate for their nutritional need mostly from an animal-based diet. This suggests that these tiny organisms exhibit omnivory in the natural habitat of the Arabian Sea. Also, as their sizes are low (<1 mm), based on the observation by Atkinson (1996) and Roman & Gauzens (1997), these copepods might exert more grazing pressure on the nominal-sized primary producers. On the other hand, Harpacticoida had a considerable amount of gut Chl *a* with no significant relation with ambient water Chl *a*, which suggested a blend of water and benthic Chl *a* source for its dietary quota.

It is apparent that the copepods from coastal waters of Arabian Sea essentially graze upon the chlorophyll-bearing material and probably can act as an astaxanthin source to the fish stock. This study highlights the temporal variability in copepod gut pigment contents with highest values recorded during monsoon, corresponding to the breeding season of fishes.

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Correspondence should be addressed to:

A.M. D'souza
CSIR–National Institute of Oceanography, Dona Paula,
Goa, India
email: dsouzaa@nio.org

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Spatial variability of copepod species distribution in the eastern Arabian Sea in pre-monsoon conditions

Analiza Maria D'souza, Mangesh Gauns*

Biological Oceanography Division, CSIR-National Institute of Oceanography, Dona Paula 403004, Goa, India

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ABSTRACT

This work examines the spatial variability among mesozooplankton abundance and copepod species diversity along the continental margin prior to the onset of southwest monsoon in the eastern Arabian Sea during the year 2011. The eastern Arabian Sea experiences seasonal hypoxia during the receding phase of monsoon that corresponds to low copepod abundance in the slope region. Collectively, fifty copepod species were identified over the continental margin where the diversity index (H′) ranged between 2.59 and 3.73. Bray–Curtis cluster analysis clustered the stations into three groups that corresponded to the continental shelf, slope and break reaches of the eastern Arabian Sea. This spatial variability among the groups is mainly ascribed to changes in the relative contributions of the prevailing species. The distinct genera of the continental shelf were *Microsetella* spp. and *Temora turbinata*; at the slope region, *Oncaea* spp. and at shelf-break, *Pleuromamma indica*. Overall, herbivorous copepods were numerically abundant at the continental shelf and carnivores at the slope. The discrepancy between the distributions of herbivorous versus carnivorous copepod assemblages may be attributed to environmental factors such as ambient water dissolved oxygen and phytoplankton biomass.

1. Introduction

The Arabian Sea houses a dynamic and productive bionetwork (Madhupratap et al., 1996; Barimalala et al., 2013) and its biology is distinguished by sharp seasonal variability in organism abundance coupled with monsoonal cycles. The Arabian Sea harbors niches with depleted oxygen, particularly, on the continental shelf in bottom-waters during the southwest monsoon (Naqvi et al., 2006; Cowie et al., 2014) whereas the continental slope and shelf break embraces a permanent oxygen minimum zone (from ~ 250 to 1300 m depth range; Naqvi et al., 2010). There are studies on mesozooplankton in relation to the dissolved oxygen dynamics from coastal as well as open-ocean waters from the Arabian Sea (Sewell and Fage, 1948; Vinogradov and Voronina, 1962; Smith, 1982; Madhupratap et al., 1990, 1996, 2001; Padmavati et al., 1998; Wishner et al., 2008; Banse et al., 2014). Sewell and Fage (1948) and Vinogradov and Voronina (1962) provided the preliminary information of presence of mesozooplankton in the oxygen minimum zone. Madhupratap et al. (1990), Madhupratap et al. (1996) and Padmavati et al. (1998) all characterized vertical gradients of mesozooplankton distribution including in the low oxygen waters. Madhupratap et al. (2001) reported the mesozooplankton community with respect to low oxygen waters during fall inter-monsoon. Banse et al. (2014) laid emphasis on the oxygen and nitrite variation on daily to decadal scales and related the animal life such as zooplankton to the environmental conditions.

Mesozooplankton are the critical primary consumers, and therefore these organisms are an essential link for the nourishment of fisheries (Madhupratap et al., 1994; Srichandan et al., 2015). Thus, studies on mesozooplankton and their diversity, occurrences and their life stages have been undertaken using microscopy methods (Nair et al., 1981; Achuthankutty et al., 1980; Madhupratap and Haridas, 1990; Smith et al., 1998; Smith and Madhupradap, 2005; Jagadeesan et al., 2013; Gauns et al., 2015). These studies show that the mesozooplankton community is chiefly dominated by copepods in the Arabian Sea.

Although, spatial heterogeneity of mesozooplankton is a familiar feature in the marine environment, which that is a result of many interacting physicochemical and biological processes (Pinel-Alloul, 1995), there is little information on mesozooplankton biogeography from Indian waters. Also, the seasonal variability of hydrography necessitates a high intensity of sampling in different seasons from neritic and oceanic habitats of the Arabian waters. Therefore, the present study was conducted prior to southwest monsoon to investigate the distribution of epipelagic copepods across the continental shelf, slope and break, and to discover correlations between geography and species composition.

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* Corresponding author.
E-mail address: gmangesh@nio.og (M. Gauns).

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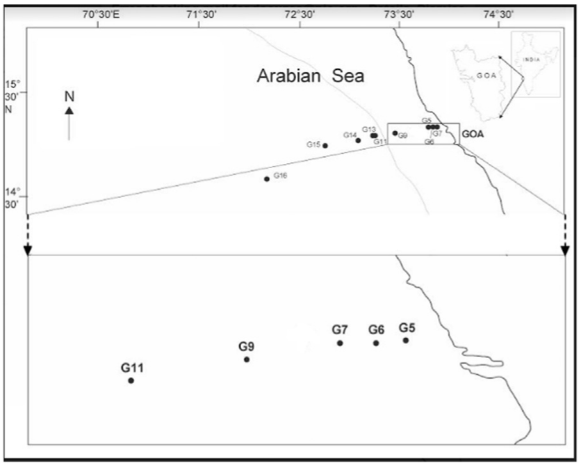

Fig. 1. Location of sampling transect in the eastern Arabian Sea.

2. Materials and methods

2.1. Sampling site and sample collection

Samples were collected on one cruise aboard RV *Sindhu Sankalp* (SSK-16) during May 2011 across a transect perpendicular to the Goan coast, which covered the stations across the continental shelf, break and slope. Sampling and profiling of the water-column were carried out at nine stations (Fig. 1) using a conductivity-temperature-depth (CTD; Sea-Bird electronics) rosette system fitted with Niskin samplers. Temperature and salinity values were recorded for the water column where subsequently mesozooplankton were sampled. In addition, water samples for chlorophyll *a* were collected from the 10 L Niskin samplers from surface to 150 m and analyzed using JGOFS protocol (Knap et al., 1996). The dissolved oxygen data were obtained from by Cowie et al. (2014) wherein the samples were analyzed using the titrimetric Winkler method. In Cowie et al. (2014), the G16 location was not taken into consideration. Overall, it is important to note that the use of one time sampling data cannot provide a complete picture of the system.

Mesozooplankton were collected using a Heron Tranter net (200 µm mesh size and mouth area of 0.25 m^2) equipped with a calibrated digital flowmeter (Hydrobios) to quantify the volume of filtered seawater. Vertical hauls were conducted from the epipelagic realm (0–200 m) and the entire water column was sampled for the stations with shallower depth (G5: 26 m; G6: 35 m; G7: 40 m; G8: 55 m; G9: 70 m; G11: 120 m).

2.2. Sample processing and analysis

Onboard, samples were concentrated through a 200 µm nylon mesh and split using a Folsom splitter to get a sub-sample (50%) containing around 300 individuals. These sub-samples were preserved in 4% buffered (sodium borate) formalin in seawater for further analyses.

In the laboratory, an individual sample was placed in Bogorow's chamber and enumeration and morphological identification were done under a stereoscopic microscope (Olympus SZX 09). The sample was sorted to the group level, and the abundance of each group was calculated following standard procedure (Goswami, 2004). All the samples were identified at broad taxonomic groups (Harris et al., 2000; Conway et al., 2003) and only Copepods were characterized at the generic level and wherever possible to species level using taxonomic keys (Kasturirangan, 1963; Bradford-Grieve, 1994; Conway et al., 2003). Identification of the occasionally occurring calanoid species was confirmed mostly by 5th leg dissection.

2.3. Statistical analysis

The species diversity indices i.e., Margalef's species richness (*d*), Shannon–Wiener diversity (*H′*) and Peilou's evenness (*J′*) were calculated on copepods species abundance. Species diversity (*H′*) was calculated using the following equation:

$$H' = -\sum (P_i \log_2(P_i)),$$

where $P_i = ni/n$ (proportion of the sample belonging to i^{th} species). *S* is the number of species and *N* is the total number of individuals of all the species in a sample as given by Shannon and Weaver (1963).

The square root transformation was performed on copepod abundance data for non-multidimensional scaling (nMDS) and Bray–Curtis cluster analyses. The square root transformation of data was used to obtain a more nearly normal distribution prior to statistical analyses. nMDS analysis was performed on the clusters and the species having the peak contribution was recognized using SIMPER (PRIMER 5).

Canonical correspondence analysis (CCA) is represented in an ordination plot with stations and plankton variables represented by points and the environmental factors by arrows (Ter Braak, 1986). CCA jointly displays the dominant patterns in the copepod community based on the environmental parameters. CCA was analyzed using the Multivariate statistical package (MV step) 3.1.

3. Results

Among the sampling stations represented in Fig. 1, the stations G5, G6 and G7 lie on the continental shelf while, G9 at shelf break and G11, G13, G14, G15 and G16 are on the continental slope. The results presented below derive from samples taken at a single time of collection from the aforementioned sites during pre-monsoon period.

3.1. Hydrographic conditions prevailing at the study region

The published results on dissolved oxygen from the same cruise (SSK-16) are briefly described from Cowie et al. (2014). The dissolved oxygen (DO) was averaged for the entire water column. Therefore, chlorophyll concentrations, temperature and salinity are also reported as the water column average for the same stations. In addition, sea-surface temperature (SST) and sea-surface salinity (SSS) are reported from the stations.

At the continental shelf, the SST ranged between 28.56 and 28.98 °C, column averaged temperature from 27.52 to 27.83 °C, SSS from 35.41 to 35.60 and column averaged salinity from 35.59 to 35.69 (Fig. 2). The averaged water column chlorophyll ranged from 0.39 to 2.00 µg/L; the highest value was recorded at G5. The reported values of DO indicate that the water column was well oxygenated (85.40–90.20 µM). The SST and SSS was 29.26 °C and 35.32, respectively at the shelf break. In addition, the averaged column temperature, salinity and chlorophyll *a* were recorded as 27.92 °C, 35.59 and 0.28 µg/L. Also, low DO (57.20 µM) as compared to the continental shelf was reported at this site. Away from the coast, the continental slope hydrography varied widely as compared to shelf and break. Higher SST (29.88–30.07 °C) occurred over continental slope. The column averaged temperature varied between 24.83 °C and 27.10 °C. The SSS ranged between 35.07 and 35.36 and column averaged salinity from 35.49 to 35.67. Water column averaged chlorophyll (0.12–0.16 µg/L) was lower as compared to shelf and break. The DO values ranged between 10 and 70 µM. As the continental slopes harbor a permanent OMZ, values of DO concentrations below the epipelagic zone were comparatively stable (< 5 µM).

To summarize, distinct spatial variability in water column characteristics was recorded in concentration of DO and chlorophyll *a*.

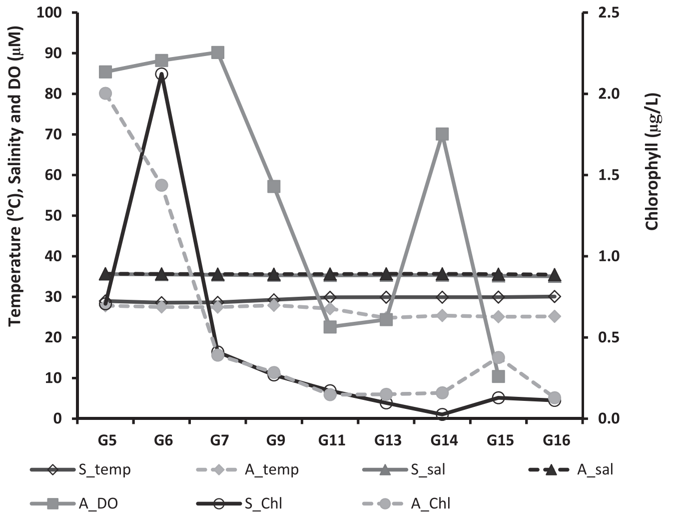

Fig. 2. Environmental factors in the eastern Arabian Sea. S_temp: sea-surface temperature; A_temp: Averaged column temperature; S_sal: sea-surface salinity; A_sal: Averaged column salinity; A_DO: averaged dissolved oxygen; A_Chl: averaged column chlorophyll *a*.

3.2. Mesozooplankton abundance, spatial distribution and composition

Mesozooplankton displayed spatial patterns along the transect (Fig. 3). Total abundance ranged between 17,922 and 5,016,216 individuals/100 m^3 (693,697 ± 1,633,758 individuals /100 m^3). The highest counts were observed at the shelf break (G9) and lowest at the continental slope (particularly at G15). Copepods, the most dominant mesozooplankton, mirrored the total mesozooplankton abundance. The highest abundance of copepods was observed at the shelf break (G9; 4,246,486 individuals/100 m^3) and lowest at the slope (G15; 13,007 individuals/100 m^3). Comparatively, continental shelf stations (G5, G6 and G7) showed higher abundance of copepods than the slope region (G11, G13, G14, G15 and G16).

The mesozooplankton community was represented by 19 taxonomic groups composed of nine groups of holoplankton and ten of meroplankton. Copepoda was the dominant holoplankton group along with Appendicularia, Ostracoda and Cladocera. Meroplankton were dominated by Decapoda, Gastropoda, Polychaeta and Fish larvae.

Altogether, Copepoda, Ostracoda, Decapoda, Appendicularia, Chaetognatha, Tunicata, Polychaeta and Gastropoda represented the bulk of the mesozooplankton community. Of these, copepods were the major contributor of the mesozooplankton community at all the three regions. Besides copepods, the other groups encountered (with their percent contribution) in the study are represented in Fig. 4. Interestingly, larval Decapoda dominated the continental shelf whereas ostracods were the dominant group of break and slope region. Mesozooplankton groups like Cladocera preferred the continental shelf, bivalve larvae were relatively more abundant at shelf break and other groups like Amphipoda, Gastropoda, Icthyplanktons and Siphonophora were relatively more abundant on the continental slope. In general, the gelatinous predators belonging to Cnidarians attained low abundance throughout the study.

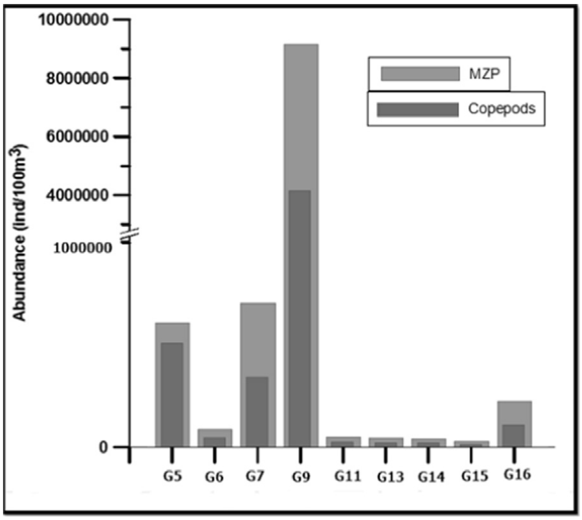

Fig. 3. Spatial variation of mesozooplankton and copepod abundance in the eastern Arabian Sea. MZP: mesozooplankton.

Doliolids dominated by *Doliolum* sp. contributed significantly to the mesozooplankton biomass because of their large body size. Comparatively high doliolid counts (9103 individuals/100 m^3) were observed over the continental shelf as compared to the continental slope (206 individuals/100 m^3) and were absent at break. The larval fishes (Icthyplanktons) occurred at most of the stations situated on the continental slope.

3.3. Spatial distribution and diversity of copepods

In total, 50 copepod species belonging to 24 families of Calanoida (16), Poecilostomatoida (3), Cyclopoida (1) and Harpacticoida (4; Table 1) were identified from the studied region. In rank order of abundance, copepod families were characterized by the dominance of Oncaeidae, Paracalanidae, Oithonidae, Centropagidae, Temoridae and Clausocalanidae. The dominant calanoid *Acrocalanus* spp. contributed 7.48% and 8.69% to the total copepod abundance from the continental shelf and slope region, respectively. Other abundant calanoids were *Acartia* spp., *Centropages tenuiremis*, *Centropages* spp., *Subeucalanus pileatus* and *Temora turbinata* at the continental shelf. Concurrently, *Pleuromamma indica*, *Metridia* spp., *Euchaeta* spp. and *Calocalanus* sp. showed dominance at the continental shelf break and slope. Equally, non-calanoid, *Oithona* spp., *Oncaea* spp. and *Farranula* spp. were abundant on all the three regions. In addition, *Oithona plumifera*, *Euterpina acutifrons*, and *Microsetella* sp. were abundant on the continental shelf. In comparison to the continental shelf break and slope, copepods community showed high abundance of calanoids over the continental shelf.

Copepod species diversity varied along the transect. Diversity (H′) for the shelf was in the range of 2.59–3.73, break 2.97 and slope 3.00–3.54 (Fig. 5). The species richness (d) was variable for the shelf in the range of 1.14–1.94, d was 1.93 at the shelf break and 1.42–2.50 at the slope stations. Evenness (J) ranged between 0.61 and 0.83 for the shelf and 0.70–0.79 for the slope whereas evenness was relatively low at shelf break (0.60). Specifically, highest value of H′ was observed at G7 (3.73) and lower values at G6 (2.59) whereas, highest and least number of species were recorded at G9 (30) and G11 (15), respectively. Species richness (d) was highest at G14 (2.50) and lowest at G5 (1.17). The copepods species were evenly distributed at G5 ($J = 0.83$) and less evenly at G9 ($J = 0.60$).

Bray–Curtis analysis was performed on the basis of abundances of copepod species and clustered the studied stations into the three groups (Fig. 6A). Station G9 did not cluster with other stations (group I). In addition, the continental slope stations G13, G14, G11 and G15 clustered together forming the group at 67% similarity (group II). However, another group was formed by continental shelf stations (G5 and G7) along with G16 at 58% similarity (group III). Further, nMDS plot showed an analogous pattern of clustering of the stations (Fig. 6B). Results of SIMPER analysis showed that the first cluster differed from the other two clusters by the dominance of *Microsetella* spp. (Fig. 6C) and *Temora turbinata* (Fig. 6D). Distinctly, the dominance of *Oncaea* spp. was present at all stations and its dominance was responsible for clustering the continental slope stations (Fig. 6E). Markedly, *Pleuromamma indica* accounted for the uniqueness at station G9 (Fig. 6F).

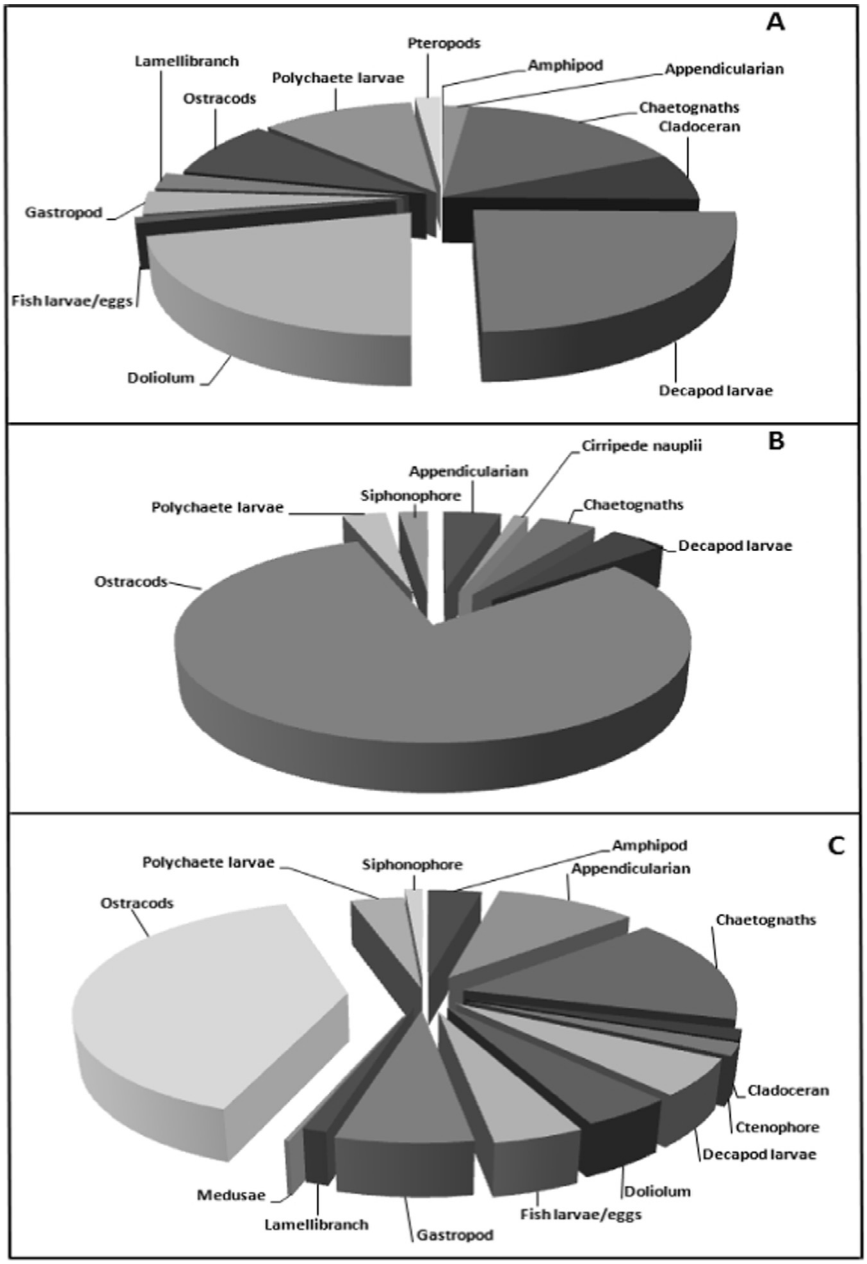

Fig. 4. Percent composition of mesozooplankton groups (copepods excluded) at (A) Continental shelf, (B) Shelf break and (C) Continental slope.

The distribution of species and stations was governed by the environment that was confirmed by the CCA plot (Fig. 7). The two ordination axes of CCA explained 71.09% and 7.68% of the relationship among the mesozooplankton and environmental factors. Chlorophyll and DO seem to have been most influencing factors for *Microsetella* spp. and *Temora turbinata*. The distribution of *Oncaea* spp., total mesozooplankton and total copepods abundance were not directly linked to the environmental factors. The CCA reproduced the spatial variability in the occurrence of copepod species as observed in the cluster analyses (Fig. 6A). We caution, however, that these relationships are based on abundance data from a single sample collection.

3.4. Feeding habits of Copepods

Feeding habits of copepods were classified based on the reports by Longhurst (1967), Timonin (1971) and Madhupratap and Haridas (1990). Geographic variability was observed in the distribution of feeding habit of dominant copepod species (Fig. 8). High percentage composition of herbivore copepods was encountered at the shelf and carnivores towards the shelf break and slope. Omnivore species were nearly 50% of the total species at the coastal station but showed no particular trend along the rest of the transect.

The most dominant herbivores recorded in this study were *Acrocalanus gibber*, *Acrocalanus* spp., *Canthocalanus pauper*, *Paracalanus* spp. and *Undinula vulgaris* (Table 2). Concurrently, the carnivorous copepods were dominated by *Oncaea* sp. and *Oithona* sp., *Euchaeta concinna* and *Candacia* spp. Correspondingly, the dominant omnivore copepods were *Acartia erythrea*, *Pleuromamma indica*, *Centopages* spp., *Euterpina acutifrons* and *Microsetella* spp. Numerically, the carnivores dominated the copepod community.

4. Discussion

4.1. Environment

Physical and chemical characteristics of the eastern Arabian Sea

Table 1
Variations of percent composition of copepods at the continental shelf and slope realm of Arabian Sea.

Zooplankton	Continental shelf (%)	Continental slope (%)
Subclass: Copepods		
Order: Calanoida		
Family: Acartiidae		
Acartia erythrae	2.05	0.56
Acartia spp.	3.91	1.52
Family: Paracalanidae		
Acrocalanus gibber	0.06	0.00
Acrocalanus gracilis	1.01	0.00
Acrocalanus longicornis	0.34	0.00
Acrocalanus spp.	6.72	8.69
Paracalanus aculeatus	3.41	0.56
Paracalanus parvus	0.00	0.49
Paracalanus spp.	.00	0.50
Family: Calanidae		
Canthocalanus pauper	0.68	0.00
Undinula vulgaris	0.17	0.00
Family: Candaciidae		
Candacia discaudata	0.00	0.24
Candacia spp.	.02	0.28
Family: Centropagidae		
Centropages furcatus	0.38	0.00
Centropages tenuiremis	4.01	0.00
Centropages spp.	7.68	0.62
Family: Clausocalanidae		
Clausocalanus spp.	3.46	0.74
Family: Eucalanidae		
Eucalanidae juv	0.51	1.01
Subeucalanus pileatus	1.09	0.00
Family: Euchaetidae		
Euchaeta concinna	0.85	0.51
Euchaeta marina	0.00	0.59
Euchaeta wolfendeni	0.00	0.01
Euchaeta spp.	1.21	3.54
Family: Augaptilidae		
Haloptilus spp.	.00	0.51
Family: Pontellidae		
Calanopia spp.	.04	0.00
Calocalanus spp.	.00	1.11
Labidocera acuta	0.00	0.24
Pontella spinipes	0.36	0.00
Pontellina spp.	.17	0.01
Family: Lucicutiidae		
Lucicutia flavicornis	0.00	0.02
Lucicutia spp.	.00	0.12
Family: Metridinidae		
Metridia spp.	.00	3.16
Pleuromamma indica	0.00	2.69
Family: Pseudodiaptomidae		
Pseudodiaptomus serricaudatus	0.21	0.00
Family: Temoridae		
Temora turbinata	3.62	0.00
Family: Aetideidae		
Undeuchaeta plumosa	0.00	0.24
Order: Cyclopoida		
Family: Oithonidae		
Oithona plumifera	1.95	0.29
Oithona spp.	8.47	11.90
Order: Harpacticoida		
Family: Euterpinidae		
Euterprina spp.	9.67	0.04
Family: Clytemnestridae		
Clytemnestra spp.	.00	0.51
Family: Miraciidae		
Macrosetella spp.	.00	0.25
Family: Ectinosomatidae		
Microsetella spp.	3.70	0.33
Order: Poecilostomoida		
Family: Sapphirinidae		
Sapphirina spp.	.17	0.50
Copilia spp.	.02	0.27
Family: Oncaeidae		
Oncea spp.	30.63	43.99
Family: Corycaeidae		
Coryaceaus spp.	2.52	1.66
Farranula spp.	.92	12.27

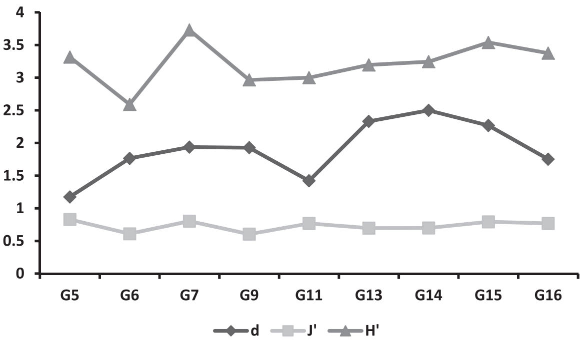

Fig. 5. Spatial variation of copepod species diversity indices in the eastern Arabian Sea.

make a favorable environment for the continued existence of mesozooplankton. These favorable features are reflected in the values of water column averaged temperature, salinity and chlorophyll *a* concentration, which vary in the region within the range of 24.83–27.92 °C, 35.49–35.69 and 0.13–2.00 μg/L, respectively. Concurrently, it is well-known that mesozooplankton from these locales show spatiotemporal variations (Madhupratap and Haridas, 1986; Madhupratap et al., 1990; Padmavati et al., 1998; Nair et al., 1999; Jagadeesan et al., 2013; Gauns et al., 2015) similar to primary production. Biological productivity of the Arabian Sea is governed by upwelling during southwest monsoon and winter cooling during northwest monsoon (Madhupratap et al., 1996).

4.2. Mesozooplankton counts and composition

Prevailing high temperature, high salinity and oxic waters during pre-monsoon is replaced by low oxygen waters and high chlorophyll *a* concentration in monsoon on the continental shelf region (Naqvi et al., 2006; D'souza and Gauns, 2016). Thus, the water column experiences cooling and freshening due to reduced temperature and salinity during monsoon period (Naqvi et al., 2006). Such seasonality in the region appears to influence the mesozooplankton community. Seasonal variation in copepod abundance and taxonomy work from the region by D'souza and Gauns (2016) showed decreased copepod abundance during monsoon and attributed it to the influence of upwelling (bringing up low oxygen waters) and freshening of the system (due to run-off). The transition period from pre-monsoon to monsoon during which extensive changes occurs in the water column is hitherto sparsely studied; thus the observations of the present study will augment the knowledge on mesozooplankton from this region. Lower counts of mesozooplankton in continental slope region than in the shelf and shelf break region were noticeable in this study. This trend of mesozooplankton abundance seems to be influenced by phytoplankton biomass, as the shelf region was characterized by high chlorophyll concentration during the present study. Similar observations that support the high mesozooplankton counts at near-shore stations were earlier reported by Rakhesh et al. (2006) and Jagadeesan et al. (2013). Conspicuously, areas with distinct bathymetry with steep incline or decline (seamounts and trenches) stand out with abruptly high abundance (Saltzman and Wishner, 1997), as observed at the continental break (G9) in this study. Some researchers (Dower et al., 1992; Dower and Mackas, 1996; Martin and Christiansen, 2009) proposed that increased biomass in such sites is caused by modifications to the current regime, which cause geographic

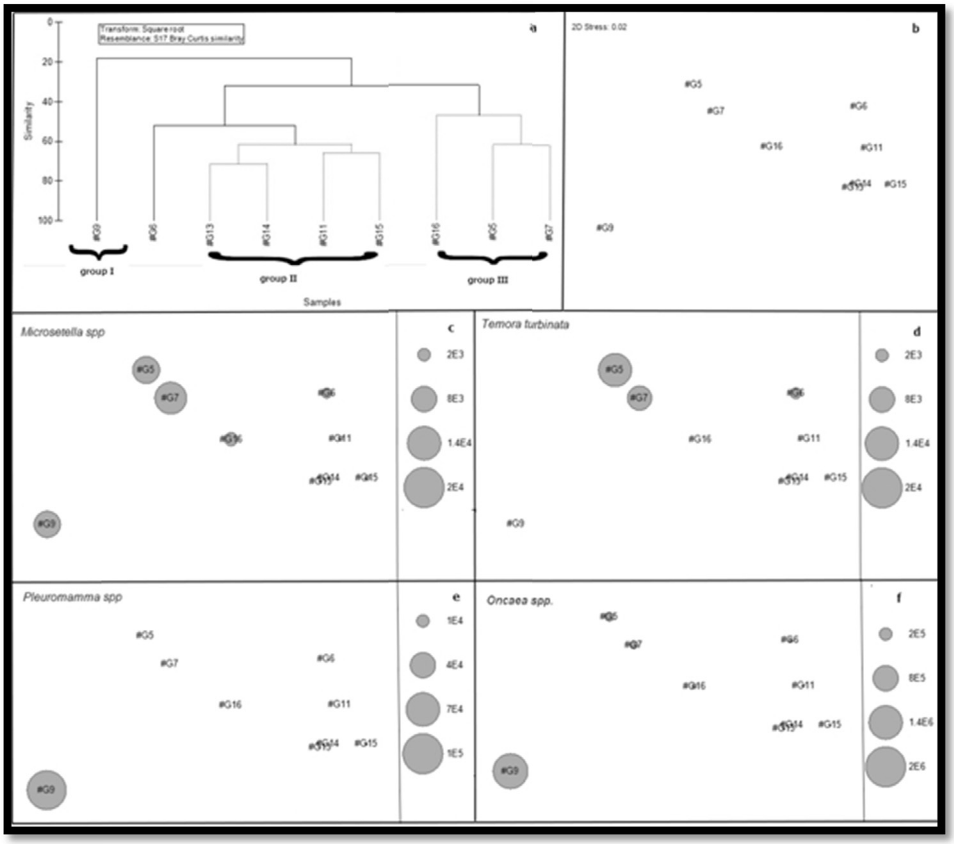

Fig. 6. (a) Bray–Curtis cluster and (b) nMDS plot based on copepod abundance. Bubble plot of dominant copepod species (c–f).

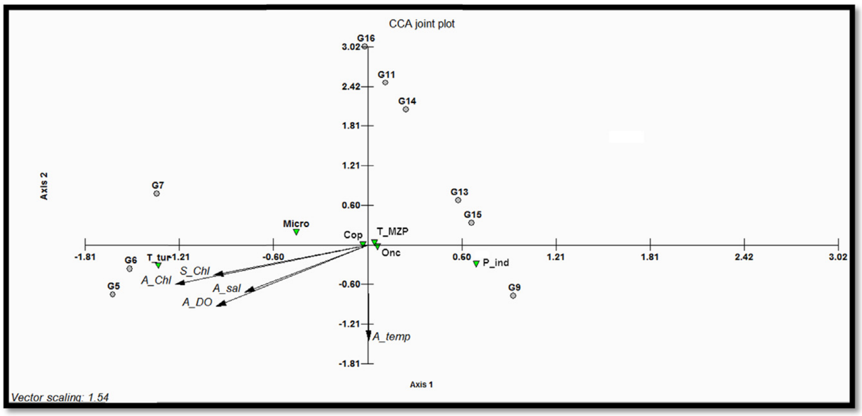

Fig. 7. The CCA ordination plot for copepods in relation to environment and sampling locations. Environmental parameters: S_temp, surface temperature; A_temp, average column temperature; S_sal, surface salinity; A_sal, average column salinity; DO, averaged column dissolved oxygen; S_chl, surface chlorophyll; A_Chl, average column chlorophyll; S_phaeo, surface phaeopigment; A_phaeo, average column phaeopigment. Mesozooplankton: cop, copepods; T_MZP, total mesozooplankton; Micro, *Microsetella* spp.; T_turb, *Temora turbinata*; P_ind, *Pleuromamma indica*; Onc, *Oncaea* spp.

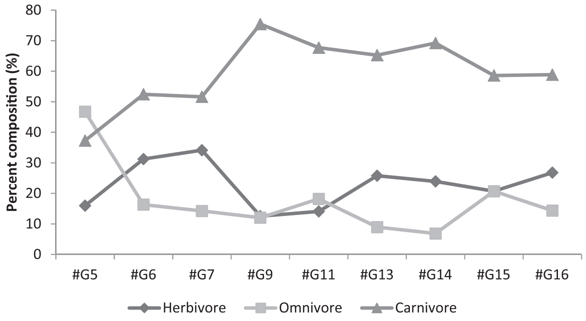

Fig. 8. Spatial variation in percent composition of herbivore, omnivore and carnivore copepods in the eastern Arabian Sea.

resurgence. However, single sampling prevents a robust conclusion on this aspect and long-term studies would be needed to confirm such an effect in Arabian Sea.

During the present study, species of copepods contributed about 72–99% to the total mesozooplankton abundance, similar to previous studies from the Arabian Sea (Wishner et al., 2008; Smith and Madhupratap, 2005; Gauns et al., 2015), Bay of Bengal (Fernandes, 2008; Fernandes and Ramaiah, 2009, 2013) and other parts of the world ocean (Mackas and Galbraith, 2002; Lenz, 2012). Copepods may be abundant due to their capability of detecting the hydrodynamic disturbances created by approaching predators and of their escapes with high velocities (Verity and Smetacek, 1996). These traits are facilitated by the sensory-armed antennae and their streamlined, muscular bodies (Kiorboe et al., 2010). The second most abundant mesozooplankton group from the continental shelf location were the

Table 2
Classification of feeding habits of copepods and their abundance (individuals/100 m^3) across the transect in the Arabian Sea.

Feeding habit	Copepods	G5	G6	G7	G9	G11	G13	G14	G15	G16
Herbivore	*Acrocalanus* spp.	20,484	1763	28,477	294,054	1802	917	1627	520	10,014
	Canthocalanus sp.	0	0	4219	0	0	0	0	57.8	0
	Clausocalanus spp.	6827.9	0	14,766	17,297	0	1737	232	289	6828
	Eucalanus spp.	0	0	3164	34,595	0	145	310	231	455.2
	Lucicutia spp.	0	0	0	0	139	555	77.5	116	4097
	Paracalanus spp.	13,656	235	7383	51,892	277	1593	930	462	0
	Rhincalanus spp.	0	0	0	0	69.3	0	0	0	0
	Subeucalanus sp.	0	470	6328	0	0	0	0	0	0
	Temora spp.	20,484	7991	23,204	0	0	0	0	116	910.4
	Undinula spp.	0	117.5	1055	0	0	0	232	57.8	0
	Calocalanus spp.	0	0	0	34,595	554	193	232	520	3186
Omnivore	*Metridia* spp.	0	0	0	112,432	0	0	0	0	0
	Pleuromamma indica	0	0	0	95,135	0	145	0	347	0
	Undeuchaeta sp.	0	0	0	8648.6	0	0	0	0	0
	Centropages spp.	91,038	470	4219	34,595	2218	1062	77.5	1272	4552
	Pontellina spp.	2276	0	1055	34,595	0	96.5	77.5	173	455.2
	Acartia spp.	27,312	352.5	9492	69,189	0	241	387	0	4097
	Calanopia spp.	0	235	0	0	0	0	0	57.8	0
	Pseudodiaptomus sp.	0	235	1055	0	69.3	48.3	0	0	0
	Euterprina spp.	50,071	2820	7383	0	1109	0	0	231	0
	Clytemnestra spp.	0	0	0	17,297	0	0	38.7	0	910.4
	Macrosetella spp.	0	0	0	8648.6	0	0	232	0	0
	Microsetella spp.	9103.8	1293	12,657	8648.6	277	96.5	77.5	289	2276
	Sapphirina spp.	0	0	1055	17,297	0	48.3	38.7	0	455.2
	Copilia spp.	0	117.5	0	8648.6	0	48.3	116	0	910.4
Carnivore	*Euchaeta* spp.	2276	0	10,547	155,676	1940	1496	1937	347	3642
	Labidocera spp.	0	0	0	8648.6	0	0	0	0	0
	Oithona spp.	29,587	1645	33,751	406,486	2218	4151	1162	1850	17,297
	Lubockia spp.	4551.9	0	0	0	69.3	0	0	0	0
	Oncaea spp.	100,142	14,924	75939	1,513,514	7484	6274	5812	3411	26,856
	Coryaceaus spp.	6827.9	470	8438	51,892	970	603	930	983	3642
	Farranula spp.	0	470	5274	432,432	970	386	310	116	1821
	Haloptilus spp.	0	0	0	17,297	0	48.3	0	0	910.4
	Candacia spp	0	235	0	17,297	0	48.3	387	0	1821

meroplanktonic larval decapods. Dominance of decapods larvae may be influenced by the duration of the larval phase, dispersal (Bhaud, 2000), settlement (Eckman, 1996), copious food supply (Jorgensen, 1981), predation and physiological stresses due to temperature and salinity (Eckman, 1996; Highfield et al., 2010). Coordination of the favorable factors must have led to dominance of larval decapods to the coastal mesozooplankton community (Williams and Collins, 1986; Pillai et al., 2014). Notably, the continental slope region harbored ubiquitous ostracods as the second most abundant mesozooplankton group. Purushothaman (2015) reported detritivorous ostracods (planktonic) in high abundance during summer monsoon in the oceanic waters of the Arabian Sea. These ostracods are known to thrive in the epipelagic realm and primarily employ detritivorous feeding habits (Angel, 1983) and are known as scavengers (Chavtur and Bashmanov, 2007). Nonetheless, they consume autotrophic as well as heterotrophic biomass (Hopkins and Torres, 1988; Vannier et al., 1998). These organisms are affected by environmental factors like salinity and temperature along with primary productivity (Purushothaman, 2015).

Mesozooplankton such as Appendicularia, Chaetognatha, Tunicata, Polychaeta and Gastropoda were the other abundant groups in the community. The present study indicates a longitudinal variation in distribution of these mesozooplankton similar to earlier reports (Fasham and Angel, 1975; Madhupratap et al., 2001). In central and eastern Arabian Sea during the month of May, environmental conditions are reported to be oligotrophic with high abundance of bacteria and picoplankton (Ramaiah et al., 1996), microzooplankton (Gauns et al., 1996) and low phytoplankton (Bhattathiri et al., 1996) with increased number of *Trichodesmium* spp. (Sawant and Madhupratap, 1996). Also, these environmental conditions supported high abundance of mesozooplankton during April-May as reported by Madhupratap et al. (1996). The latter study suggests that due to the ability of large copepods to feed on smaller plankton (microzooplankton or even bacteria) enables them to maintain relatively invariable biomass between the seasons in the eastern Arabian Sea. Collectively, such biological conditions may link the mesozooplankton abundance during the present study with control of the microbial loop in the eastern Arabian Sea.

4.3. Copepod species associations with the geography

Many copepod species are widely distributed across the studied transect and show variations in abundances. The dendrogram of the station–associations illustrates relationships between the geography due to a few remarkable species as identified by SIMPER test (Fig. 6) and confirmed by CCA plot (Fig. 7). Euryhaline copepods *Microsetella* spp. and *Temora turbinata* were responsible for differentiating the continental shelf stations. Among these copepods, *Microsetella* spp. can tolerate a wide temperature range of 9–27 °C (Uye et al., 2002), whereas *T. turbinata* prefer temperature within 25.0–26.3 °C (Resgalla Jr. et al., 2008; Dias and Boneckar, 2009). Additionally, these copepods showed strong relation to DO and phytoplankton biomass. The low DO (57.2 µm) at the shelf break seems to favor the dominance of *Pleuromamma indica* as this species is known for being tolerant to low oxygen waters and a tendency towards vertical migration (Goswami, 1994; Padmavati et al., 1998). Furthermore, *Oncaea* spp. was linked to the continental slope stations. The poecilostomatoid, *Oncaea* spp. is ubiquitous and abundant in marine environments (Madhupratap et al., 1996; Paffenhofer, 1993; Gonzalez and Smetacek, 1994) probably due to its capability to exploit wide ranges of food items. Specifically, *Oncaea* spp. has been observed to feed on marine snow, faeces (Alldredge, 1972; Gonzalez and Smetacek, 1994) and mesozooplankton like chaetognaths and appendicularians (Go et al., 1998). Also, *Oncaea* spp. is considered to be an omnivore (Turner, 1986) and detritivore (Yamaguchi et al., 2002). Therefore, the comparatively low chlorophyll slope region would favor *Oncaea* spp. abundance.

4.4. Copepod diversity

The present study enhances our knowledge of species composition and diversity of copepods from the hitherto scarcely studied region of the Arabian Sea. Nineteen taxonomic groups and 50 copepod species were detected, all of which have been previously reported from the Indian Ocean region (Madhupratap et al., 2001; Smith and Madhupratap, 2005; Gauns et al., 2015). They included coastal and oceanic species mostly of Indo-Pacific origin and few of cosmopolitan nature (Pillai et al., 2014). In terms of dominance, copepod families were represented by Paracalanidae, Oithonidae, Oncaeidae, Clausocalanidae, Centropagidae and Temoridae. Previously, these families dominated the winter monsoon (Padmavati et al., 1998) and were reported to persist throughout the seasons in the Arabian Sea (Madhupratap et al., 2001; Jagadeesan et al., 2013). The copepod species, *Acartia* spp., *Centropages tenuiremis*, *Subeucalanus pileatus, Temora turbinata*, *Oithona plumifera*, *Euterpina acutifrons*, *Microsetella* sp., *Oncaea* spp. and *Corycaeus* spp. were abundant at the continental shelf. Similar distribution of copepod species was observed by Madhupratap et al. (2001). Concurrently, *Pleuromamma indica*, *Metridia* spp., *Euchaeta* spp., *Calocalanus* sp., *Acrocalanus* spp. *Oithona* spp., *Oncaea* spp. and *Farranula* spp. were present abundantly at the shelf break and slope. This is consistent with the copepod species composition reported earlier by Padmavati et al. (1998) at the slope. Apparently, dominance of small-sized (< 2 mm) copepods capable of exploiting the phytoplankton and microzooplankton (Stoecker and Capuzzo, 1990; Roman and Gauzens, 1997) is typical in the tropical waters (Hopcroft et al., 1998). They are capable of switching their feeding habits by preying on microzooplankton in the period of low phytoplankton especially in the inter-monsoon. In addition, less productive inter-monsoons may favor the microbial loop as an important food source to sustain the high abundance of mesozooplankton (Madhupratap et al., 1996).

Three diversity indices indicated moderate copepod diversity (H′: 2.59–3.73) similar to that of previous studies from the Arabian Sea (Padmavati et al., 1998) and Bay of Bengal (Fernandes, 2008). The numbers of species vary depending on the stability of the environment (Margalef, 1958; Deevey, 1971). In this regard, the studied region seems to be a stable ecosystem. Collectively, this systematic study describes copepod diversity from the continental shelf, break and slope region enhancing our understanding of copepod variability just before the onset of productive southwest monsoon period.

4.5. Feeding habits of copepods and their association with geography

Predation by carnivorous plankton has the capability to structure the mesozooplankton community (Jagadeesan et al., 2013) as opposite distribution of copepod abundance and carnivorous plankton has been previously reported by Hansson et al. (1990). The carnivorous copepods especially *Candacia* spp. and *Euchaeta* spp. were generally abundant towards the continental slope where the chlorophyll concentration is reportedly low (Naqvi et al., 2006). On the contrary, herbivorous copepods occurred in high densities in the shelf waters where chlorophyll concentration is reportedly high (D'souza and Gauns, 2016). There was no significant correlation observed between chlorophyll and different orders of copepods. However, when copepods were separated by feeding strategy, omnivorous ($r^2 = 0.65$) and carnivorous ($r^2 = 0.66$) copepods abundances were significantly correlated with water column averaged chlorophyll concentration. Copepods with herbivorous feeding habits such as *Acrocalanus* spp., *T. turbinata* and *Paracalanus* spp. are known in the Arabian Sea waters (Madhupratap and Haridas, 1990; Smith and Madhupratap, 2005). Members of Calanidae family, *Canthocalanus pauper* and *Undinula vulgaris* are amongst the distinct residents that consume autotrophs from the Arabian Sea (Madhupratap and Haridas, 1990; Madhupratap et al., 1996). However, preponderance of herbivorous copepods towards the continental slope confirms their ubiquity. Furthermore, copepods are well-known to switch their feed preferences based on the feeding locale (El-Sabaawi et al., 2009), an advantage to thrive in low production oceanic waters. Omnivores like *Acartia* spp. and *Centropages* spp. showed no particular trend of dispersal and seem to be more adaptable to change in geography.

Generally, the high percent abundance of carnivorous copepods (Fig. 8) in the eastern Arabian Sea persists has been recorded earlier (Madhupratap and Haridas, 1986, 1990; Madhupratap et al., 1990; Padmavati et al., 1998; Smith and Madhupratap, 2005). Moreover, it seems to be a general observation as Longhurst and Pauly (1987) observed that the biomass of predators is almost double compared to herbivore and detrivores in the tropics than polar region. However, it is important to point out certain drawback in the present data and interpretations. Firstly, the mesh size (200 µm) employed for sampling could have limited the collection of small-sized carnivores like poecilostomatoids and cyclopoids (Böttger-Schnack, 1996). Secondly, in view of dwindling food supply, copepods might have engaged in coprophagy instead of carnivory (Madhupratap et al., 2001). Thirdly, depending upon the prey availability, most of the forms may prefer the omnivorous feeding habit. Moreover, the classification of trophic groups in the present study was based on the literature (Longhurst, 1967; Timonin, 1971; Madhupratap and Haridas, 1990) and may be debatable. However, for comparison of the data with previous studies (Padmavati et al., 1998; Madhupratap et al., 2001; Smith and Madhupratap, 2005) the same trophic classification was followed.

5. Conclusion

Mesozooplankton, in general was dominated by copepods just prior to the onset of monsoon in the eastern Arabian Sea. Further, calanoids dominated the copepod population with highest number of the genera and species. Poecilostomatoida and Cyclopoida showed similar distribution across the three study regions. In contrast, the phytophagus genera, *Acrocalanus gibber*, *Paracalanus parvus* and *Temora turbinata* were abundant at the shelf stations. While carnivorous genera, *Euchaeta concinna*, *Oncaea vensuta* and *Oithona plumifera* were abundant at the slope stations. Observations on the mesozooplankton community just prior to the onset of southwest monsoon have revealed a strong coupling between geography and copepod species. Different species distribution may be in response to the relative contributions of the euryhaline species that characterized the continental shelf (*Microsetella* spp. and *Temora turbinata*), slope (*Oncaea* sp. and *Oithona* sp.) and the shelf break (*Pleuromamma indica*). The differential distribution of copepod groups and their species richness and diversity across the transect from shelf to slope just prior to onset of southwest monsoon was noteworthy. Monitoring the mesozooplankton assemblages more frequently will ascertain whether the recorded observation is transitory or is a regular feature in this region. The elevated abundance and diversity of copepods appears to be an indicator of rich secondary productivity in this region.

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