Ecology of Chaetognaths in the Indian EEZ

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by

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Declaration

I here by declare that the thesis entitled **"ECOLOGY OF CHAETOGNATHS IN THE INDIAN EEZ"** submitted by me is an authentic record of research carried out by me, under the supervision of Dr. T.V. Raveendran, Senior Principal Scientist, National Institute of Oceanography, Regional Centre, Cochin -18, in partial fulfillment of the requirement for the Ph. D degree of the Cochin University of Science and Technology in Marine Science and that no part of this thesis has been presented before for any other degree, diploma, or associateship in any university.

Kochi

20-6-2012

(Kusum Komal Karati)

Certificate

I hereby certify that the thesis entitled "ECOLOGY OF CHAETOGNATHS IN THE INDIAN EEZ" submitted by Kusum Komal Karati, Research Scholar (Reg.No. 3787), National Institute of Oceanography, Regional Centre, Cochin-18, is an authentic record of research carried out by him, under my supervision in partial fulfillment of the requirement for the Ph. D degree of Cochin University of Science and Technology in Marine Science and that no part of this thesis has previously formed the basis for the award of any degree, diploma, or associateship in any university.

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List of acronyms and abbreviations

AS	**Arabian Sea**
ASHSW	**Arabian Sea High Salinity Water Mass**
BoB	**Bay of Bengal**
BoBPS	**Bay of Bengal Process Studies**
BT	**Base of the Thermocline**
cm	**Centimetre**
CTD	**Conductivity Temperature Depth**
DH	**Depth of Haul**
DO	**Dissolved Oxygen**
DV	**Displacement Volume**
E	**East**
e.g.	**exempli gratia (Latin word, meaning ‘for example’)**
etc.	**et cetera (Latin word, meaning ‘and other similar things’)**
EEZ	**Exclusive Economic Zone**
EICC	**East India Coastal Current**
et al.	**et alii (Latin word, meaning ‘and others’)**
Fig.	**Figure**
FIM	**Fall Inter Monsoon**
FORV	**Fisheries and Oceanographic Research Vessel**
GFO	**Geosat Follow-On**
GISST	**Global Sea Ice Sea Surface Temperature**
i.e.	**id est (Latin word, meaning ‘that is’)**

ICOADS	**International Comprehensive Ocean Atmospheric Data Set**
IIOE	**International Indian Ocean Expedition**
JGOFS	**Joint Global Ocean Flux Studies**
LL	**Lakshadweep Low**
M	**metre**
MLD	**Mixed Layer Depth**
ml	**millilitre**
mm	**millimetre**
MPN	**Multiple Plankton Net**
N	**North**
ODW	**Oxygen Depleted Water**
OMZ	**Oxygen Minimum Zone**
PCA	**Principal Component Analysis**
RV	**Research Vessel**
S	**South**
SM	**Summer Monsoon**
Sp.	**species**
SW	**South West**
SSS	**Sea surface salinity**
SST	**Sea Surface Temperature**
TC	**Thermocline**
VWF	**Volume of Water Filtered**
Viz	**videlicet (Latin word, meaning ‘namely’ or ‘that is to say’)**
W	**West**
WICC	**West India Coastal Current**
WM	**Winter Monsoon**
μm	**micro meter**

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Chapter 1

Introduction

The oceans and seas cover around 71% of the earth, making the environment the largest habitat in the planet. Pelagic zone, encompassing the entire ocean water column from the surface to the greatest depths is home to a diverse community of microscopic to metazoic organisms. Differences in their locomotive ability categorize the organisms inhabiting the pelagic realm into two main groups, ***plankton*** *a*nd ***nekton*** (Lalli and Parsons, 1997). ***Plankton*** includes all those organisms drifting in water and whose ability of locomotion is insufficient to withstand currents and ***Nekton*** are those organisms having strong locomotive power. The dynamics and functioning of marine ecosystem can be better understood only through extensive ecological studies on plankton community which form the base of the aquatic food chain. The term plankton was first coined by Victor Hensen (1887), the German founder of quantitative plankton and fishery research. It is believed to have originated from the Greek word "***planktos****"* (Lalli and Parsons, 1997) meaning "passively drifting or wandering". Based on their mode of nutrition in the ecosystem planktonic organisms are categorized into ***phytoplankton***; i.e., organisms having autotrophic mode of nutrition and ***zooplankton****;* i.e., organisms having heterotrophy as their main nutritional mode.

Zooplankton encompasses a taxonomically and morphologically diverse community of heterotrophic organisms that drift in the waters of the world's oceans. To delineate the ecological processes active in the ecosystem, qualitative and quantitative studies on zooplankton community are a prerequisite. Zooplankton community plays a decisive role in the pelagic food web as well as on the cycling of elements in the marine ecosystem. They form a vital link in the pelagic food web as the primary grazers of phytoplankton and serve as food for planktivorous organisms at higher trophic levels, particularly the economically important groups such as fish larvae and planktivorous fishes. As they form an important food source for larval, juvenile and adult fish, the dynamics of zooplankton community, their growth, reproduction and survival rate are all important factors determining the recruitment and abundance of fish stocks (Rothschild, 1998; Beaugrand et al., 2003). Importance of zooplankton in marine geochemical cycles has always been a serious topic of research. Zooplankton grazing controls the primary production and helps in shaping the pelagic ecosystem (Banse, 1995). It also, to a large extent, determines the amount and composition of the vertical particle flux to the deep sea (Steinberg et al., 2000, 2002; Ducklow et al., 2001; Sarma et al., 2003). Through grazing in surface waters and subsequent production of sinking fecal pellets and also by the active transportation of dissolved and particulate matter to deeper waters via vertical migration, they help in the transport of organic carbon to deep ocean layers and thus act as key drivers of biological pump in the marine ecosystem. Zooplankton grazing and metabolism in turn, transform particulate organic matter into dissolved forms, promoting primary producer community, microbial demineralization, and particle export to the ocean’s interior (Fasham et al., 1990; Blackford et al., 2004; Gauns et al., 2005; Buitenhuis et al., 2006). Due to their drifting nature, short life span and higher sensitivity to subtle changes, zooplankton communities are ideal indicators of environmental perturbations and water quality changes (Gannon and Stemberger, 1978; Rissik and Suthers, 2008). Through continuous observation on the species diversity, biomass and abundance of zooplankton community, any alteration in the health of an ecosystem can easily be determined. Thus long term monitoring of marine zooplankton community has become an indispensable tool in predicting the impact of climate changes on pelagic ecosystem and has been receiving considerable research interest lately (Beaugrand and Ibanez, 2004).

The idea of utilizing plankton as a source of food for mankind has drawn significant interest among earlier naturalists to present day scientists. More than 120 years ago, Herdman (1891) first proposed copepod as a food item. Later several scientists have reported on the utility of zooplankton as a source of food (Clarke, 1939; Hardy, 1941; Jackson, 1954; Parsons, 1972). During the Second World War, due to food shortage, the suggestion of harvesting marine plankton in industrial scale as human food and also as a supplement to stock and poultry food received much attention (Moore, 2011). Omori (1978) reported that around 11% of the total crustacean catch in the world is contributed by planktonic crustaceans. Thus in future, the possibility of zooplankton fisheries taking an important role in the food resources for mankind cannot be ruled out.

1.1. Ecological groups of zooplankton

Based on size, duration of planktonic life, food preferences and habitat, zooplankton are categorized into several ecological groups. As they vary greatly in size from microscopic to metazoic forms, the classification of zooplankton based on size have utmost importance in the field of quantitative plankton research. During 1892, Schütt, first described three major size divisions among zooplankton, viz. micro, meso and macrozooplankton. Later, several scientists have elaborated and made amendments in the size classifications (Omori and Ikeda, 1984; Redden et al., 2008) and among them, the classification by Seiberth (1978), given below is the widely accepted one.

1. Femtoplankton (0.02 ‐ 0.2 µm)
2. Picoplankton (0.2 ‐ 2.0 µm)
3. Nanoplankton (2 ‐ 20 µm)
4. Microplankton (20 ‐ 200 µm)
5. Mesoplankton (0.2 ‐ 20mm)
6. Macroplankton (2 ‐ 20 cm)
7. Megaplankton (20 ‐ 200 cm)

Zooplankton, on the basis of duration of planktonic life are categorized into ***Holoplankton*** (organisms which completes their entire lifecycle as plankton) and ***meroplankton*** (those which are planktonic during the early part of their lives such as the larval stages of benthic and nektonic organisms). ***Tychoplankton*** are the organisms which live a temporary planktonic life, such as the benthic crustaceans, which ascend to the water column at night for feeding. e.g., cumaceans, mysids, isopods, etc. Certain ectoparasitic copepods are also included under this category, which during their breeding cycle may leave the host and spend their life as plankton.

According to depth of the habitat which they inhabit (horizontal or vertical), they are categorized into several ecological groups. According to the horizontal distribution pattern they are divided as ***Neritic*** (organisms inhabiting shallow water column overlying continental shelves) and ***Oceanic*** (organisms inhabiting deep water column greater than 200 m).

Vertical habitats among zooplankton vary greatly and based on the depth range of their habitat they are grouped as ***Neustonic*** (Organisms inhabiting the upper few centimeters of water column), ***Pleustonic*** (Organisms living on the upper layer and part of the body is exposed), ***Epiplanktonic*** (Organisms inhabiting upto 200 m depth), ***Mesoplanktonic*** (Organisms inhabiting depth zone between 200 and 1000 m) and ***Bathyplanktonic*** (Organisms inhabiting depths greater than 1000 m in the water column).

Zooplanktonic organisms based on their food preferences are classified as ***Herbivores*** (organisms which primarily feed on phytoplankton), ***Carnivores*** *(those* feeding on other heterotrophic organisms), ***Omnivores*** (feeding on a mixed diet of phyto and smaller zooplankton) and the ***Detritivores*** (organisms living on dead organic material).

1.2. Chaetognath, a carnivorous zooplankton

Chaetognaths, a phylum of predatory invertebrates are conspicuous members among zooplankton in the pelagic realm. The term chaetognath originated from two Greek words*; "**Chaeto**"* meaning bristle and *"**gnathos**"* meaning jaw. They are commonly called "***arrow worms****"* because of their darting movement. Chaetognaths are the primary carnivores in the pelagic realm and are mostly holoplanktonic organisms, except for the genera *Spadella*, *Bathyspadella* and *Krohnitella*. They occur in all marine habitats including open oceans, tidal pools, polar waters, marine caves, coastal lagoons, estuaries and the deep sea (Bone et al., 1991). Chaetognaths represent about 5-15% of the zooplankton biomass and 10-30% of the copepod density in the world oceans (Ryther, 1969; Reeve, 1970a; Bone et al., 1991). Their trophodynamics in the pelagic realm is known to play an important role in global ocean ecology (Froneman and Pakhomov, 1998). As an active planktonic predator in the marine system (Reeve, 1964; Ghirardelli, 1968; Froneman et al., 1998), this carnivorous zooplankton have a crucial role in shaping the pelagic food web by preying mainly on copepods (Feigenbaum, 1991; Álvarez -Cadena, 1993; Pakhomov et al., 1999). They in turn form the important prey organisms for many pelagic fishes and squids. Thus they have a vital role in the marine ecosystem as an important mediator between primary consumers and organisms at higher trophic levels.

Chaetognaths are often regarded as valuable indicators of water masses along different parts of the global ocean. Meek (1928), Russell (1935, 1939) and Fraser (1937, 1939) have recognized different chaetognath species as indicator organisms in Northumbrian region, English channel, Scottish water and North Sea. Later Bieri (1959) gave a detailed description on the indicator species of chaetognaths of all major water masses in the Pacific Ocean. Alvariño (1964a,c, 1965b) has also attempted to correlate different chaetognath species with particular water masses in the Pacific and Indian Oceans. Pierrot-Bults (1982) has also reported different chaetognath species associated with different water masses in northwest Atlantic. Later Pierrot-Bults and Nair (1991) have attempted to relate the preferences of chaetognath species towards specific water masses in global ocean. Chaetognaths have also been recorded as ideal indicators of different physical processes active in the marine system.

Eukrohnia hamata has been reported as indicator of upwelling event in coastal upwelling water of Chile (Ulloa et al., 2000, 2004).

1.3. General biology of chaetognath

Chaetognaths are bilaterally symmetrical coelomate animals with a thin, slender, transparent or translucent body. They are generally called glass *worms* because of their elongated and transparent body form. Size of chaetognath usually range between 2 and 105 mm and thus according to Sieburth et al. (1978), are grouped under the category mesozooplankton. The largest chaetognath, *Sagitta gazelle* has been recorded in the Southern Ocean waters from the shores of Antarctica to about 40°S. Generally the epiplanktonic species and species inhabiting the low latitude regions are relatively smaller in size compared to bathyplanktonic and species of higher latitude regions. Currently around 130 chaetognath species have been identified throughout the global oceans of which 100 are pelagic and 30 are benthic.

1.3.1. Distribution

They enjoy wide distribution pattern and are found from tropics to polar oceans and also from neritic to oceanic regions. Though they are known to inhabit pelagic waters from surface to greatest depths, they reportedly have high density in the surface waters of the marine system. But, no single species has a universal distribution, though some are cosmopolitan (Alvariño, 1964 a,b). Based on depth distribution, Fowler (1906) and Alvariño (1964a) have classified chaetognaths into epipalnktonic (upper 150 – 200 m), mesoplanktonic (200 – 1000 m) and bathyplanktonic (below 1000 m level).

Bieri (1959) made an attempt to classify the distribution of the planktonic chaetognaths in the Pacific Ocean based on their relationship to water masses. This result was based on 2,900 samples from more than 900 stations and some important groups observed were Pacific equatorial, Subarctic and Pacific central water species. Later Alvariño (1964a) classified the chaetognath distribution in the Pacific into 10 groups depending on their relation to different water masses. Based on their distribution during the monsoon expedition in Indian Ocean, Alvariño (1964c) grouped them into five groups such as cosmopolitan, cold water representative, tropical- equatorial and restricted to the Indo-Pacific water, meso planktonic and deep water species. Later Nair (1972) described the distribution of chaetognaths in the Indian Ocean based on the International Indian Ocean Expedition (IIOE) samples and described a modified classification of that of Alvariño (1964a). Recently Pierrot-Bults and Nair (1991) classified the chaetognath species according to their distribution in all three major oceans.

1.3.2. Morphology

Morphology of chaetognath was studied and described in detail by Hyman (1959), Alvariño (1965a) and Bone (1991). A transverse septum divides the body into three morphologically different regions viz., head, trunk and tail (Fig. 1). Chaetognaths have a relatively small but a well developed head. Head generally bears grasping spines or hooks, two rows of teeth (anterior and posterior), vestibular organ and a ventral mouth. A pair of ***eye spots*** composed of a pigment cell encircled by photoreceptive cells is situated on the dorsal side of the head region; the size and pigment of which may vary with species. Four to twelve chitinous ***bristles*** on either side of the head give them the name ***"Hair jaw" or "chaetognatha".*** The bases of the bristles are often enlarged and are connected with the muscles whereas the tip is curved like a hook to help them capture and hold the prey while feeding. Two rows of ***teeth*** situated on both sides of the head aid them in piercing the exoskeleton of the prey captured. An extensive ***hood,*** usually a fold of body wall located in the neck region covers the entire head portion and protects the bristles when not feeding. It also helps to reduce the water resistance while swimming. ***Corona ciliata***, a circle of cilia, which is of sensory function, positioned on the dorsal side of the head helps in sensing the currents and the vibrations associated with the movement of prey. A ***ventral mouth*** and a vestibular organ, which is a plate like ridge composed of cylindrical epithelial cells, are the feeding organs in chaetognath. ***Vestibular organ*** and associated papilla like processes armed with pores helps to hold the prey by suction while feeding. *Vibrio alginolyticus,* bacterial colonies associated with the pores of the papillae secretes a tetrodotoxin which helps them in immobilizing the prey captured.

Chaetognaths have a long and narrow ***trunk*** which is separated from the head and tail portions by a transverse septum. ***Lateral fins*** which are usually the lateral extensions of the epidermis supported by fin rays are positioned on either side of the trunk for balancing and floatation. In some species thickened vacuolated cells called ***collarette,*** are also seen extending from the neck to trunk region. The ventral mouth in the head often leads to a bulbous ***pharynx*** which continues as a straight intestine positioned within the trunk. A pair of ***intestinal diverticula*** located in the anterior portion of the intestine and several glandular and absorptive cells scattered throughout the intestinal epithelium facilitates digestion and absorption of the food particles. Excretion is carried out through an ***anus*** situated at the centro-ventral surface of the trunk in front of the trunk-tail septum. A pair of ovaries which are the female reproductive organs, filled with ***oocytes*** are also positioned in front of the trunk-tail septum. From the lateral side of each ovary an ***oviduct*** or ***seminal receptacle*** extends out to form the ***spermatheca*** *or* ***gonopore*** through which mature sperms enter the ovaries during copulation.

Posterior part of the trunk forms the tail region which terminates into a triangular shaped ***caudal fin***. A pair of ***testes***, which form the male reproductive organ, are located on either side of the anterior part of the tail region. When sexually mature, they release a cluster of ***spermatogonia*** which later gets transformed to form the ***spermatocytes*** and spermatozoa while circulating through the ceolomic fluid. Mature sperms later enter the ***seminal vesicles*** located in the caudal region through a ciliated funnel, ***vas deferentia****.* The size, shape and position of the seminal vesicles vary with species and are often used as key criteria used for the identification of species.

1.3.3. Food and feeding

From earlier periods, significant studies have been carried out on the food and feeding of chaetognaths. Chaetognaths are regarded as voracious carnivores feeding on small crustaceans, larval fishes and other chaetognaths. The earliest report on chaetognath diet by Krohn (mentioned in Busk, 1856) described fragments of minute fish, crustaceans and other chaetognaths in their digestive tract. Later Scott (1892, 1893) reported presence of larval and post larval fishes, copepods and small amphipods in their diet. Shipley and

MacBride (1901) first reported about phytoplankton (diatoms) and infusorians as their diet items. Elaborate studies on food and feeding of chaetognaths was carried out by Alvariño (1985) and pointed out that their diet includes representatives from every taxa of plankton, such as diatoms, dinoflagellates, ciliates, tintinnids, medusae, copepods, cladocerans, amphipods, euphausiids, pteropods, heteropods, ostracods, chaetognaths, appendicularians, fish eggs and fish larvae. Though their diet includes a wide range of planktonic organisms, they particularly prefer copepods as their food (Feigenbaum and Maris, 1984).The diet of chaetognath varies with age, size and also the prey abundance (Sullivan, 1980). Cannibalism is also observed among some species of chaetognaths and is more common among adults. Cannibalism is often followed to meet the energetic demands during unfavourable conditions (Pearre, 1982).

Feeding in chaetognaths usually commence a few days after hatching (Terazaki, 2000). Juvenile chaeotgnath often feed on copepod nauplii, tintinnid and meroplankters whereas the adults prefer copepodite and adult stages of copepods (Feigenbaum, 1991). Benthic chaetognaths are often described as “ambush” predators. They affix themselves to a substrate using adhesive secretions, raise the head, and protrude the mouth, flaring the spines around the mouth. Potential prey swimming nearby are detected (probably by mechanoreceptors) and then captured by a rapid movement of the head while the rest of the body remains attached to the substratum. The spines grasp and manipulate the prey, which is then swallowed whole (Conover, 1979; Brusca and Brusca, 2003). Planktonic chaetognaths by their darting movement grab prey using their grasping spines. They usually detect their prey by sensing their body movement. The beat produced by the moving organism helps chaetognath to trace them. The distinct turbulence generated by the movement of copepod, barnacle larvae and appendicularians makes them most vulnerable to chaetognath attack. Fish larvae and other chaetognaths are detected either by their tail beat or their lateral motion itself (Feigenbaum and Reeve, 1977). The planktonic chaetognath starts their attack with a sudden flexing and flick of their tail (Terazaki, 2000) and often covers a short distance. Feigenbaum and Reeve (1977) has reported that species like *Spadella schizoptera* and *Sagitta hispida* covers a maximum attacking distance of 3 mm from the body and the prey is not pursued if it is missed or is tough to capture. Generally, the prey is captured with the hooks and the teeth are used to hold or grasp prey (John, 1933b; Parry, 1944; Hyman, 1959; Furnestin, 1977). The hood folds backward and the mouth projects forward while the hooks take the prey inside the mouth. Nagasawa (1985) has pointed out that though the prey is rarely pierced by the hooks they become immobilized before getting ingested. The tetrodo-toxin secreted by the bacterial colonies in the vestibular organ, paralyze them and thus prevent damage to the gut lining of chaetognath (Burfield, 1927; Bieri et al., 1983). The mucus secretions from the vestibular organ and the esophagus facilitate easy movement of prey in the digestive tract. After ingestion, the prey gets wrapped by a peritrophic membrane secreted by the esophagus (Reeve et al., 1975; Sullivan, 1977) and is passed to the posterior gut by peristaltic movement of the gut wall (Parry, 1944). Once in the posterior gut, the prey may be moved back and forth throughout the gut or may remain near the anus until defecation (Canino and Grant, 1985; Fiegenbaum, 1991; Terazaki, 2000). The mean digestion time among chaetognaths varies depending on the prey category (Øresland, 1987). They generally does not take more than one prey at a time (Newbury, 1978; Feigenbaum, 1979) though ingestion of multiple prey is also recorded in some chaetognaths depending on the abundance of the prey (Sullivan, 1980). If several preys are ingested in rapid succession, they are lined up one in front of the other within the gut to extend forward, depending on their size and number (Cosper and Reeve, 1975).

1.3.4. Breeding

Chaetognaths are hermaphrodites with paired ovaries in the trunk and paired testes in the tail. They are protandric hermaphrodites i.e., the testes matures before ovary. Cross-fertilization is the common fertilization process (Alvariño, 1965a, 1967; Reeve and Cosper, 1975) but in some species self-fertilization have also been reported (Reeve, 1970 a,b). Though the development of sperm and ovum (egg) starts together, the protandricity helps to avoid the self fertilization to some extent. When mature, the spermatozoa from the testes pass through the vas deferens and reach the seminal vesicles which in turn get transferred to the seminal receptacle of another individual during copulation. Muscular activity of the gonads and the chemotactic action also help in accelerating the entry of sperm and the filling of the seminal receptacle (Alvariño, 1990). Fertilization in chaetognath is internal and is of very short duration which merely takes 20-30 minutes to complete. After fertilization eggs are released in clusters covered by a mucilaginous matrix. In several genera (*e.g., Eukrohnia, Bathyspadella, Krohnitta,* and *Heterokrohnia*), fertilized eggs are usually enclosed in a sac formed at the opening of oviducts. In *Pterosagitta,* eggs are laid in a capsule; in *Sagitta,* eggs are discharged into the surrounding water one at a time in several cycles; and in *Spadella,* eggs have an adhesive coat and a stalk and attach to any surface (Vasilijev; 1924; Ghiraredelli, 1968; Sanzo, 1937). Fecundity i.e. the number of eggs produced per individual varies between species and also within the same species inhabiting different geographical areas. The bathyplanktonic chaetognaths and species living under stress (e.g. cold-water species) often produce more number of ova (Alvariño, 1983). Egg often hatches out into larvae which closely resemble the adults in their morphological characteristics. Larval development in chaetognaths is rapid and within hours of hatching the tail fin and the digestive system completes the growth and within 48 hours of hatching, the juvenile starts feeding (Alvariño, 1983).

The factors that significantly affect the reproductive capacity of chaetognaths are temperature and availability of sufficient food (Alvariño, 1983). Any changes in the quality and quantity of food and also high temperature considerably inhibit breeding in chaetognaths. In some species, parasitism is also reported to affect the gonadal development (Alvariño, 1983).

The reproductive cycle among chaetognatha also varies greatly between species. Species like *Sagitta friderici* has only one reproductive cycle, at the end of which the animal dies (Cavalieri, 1963) whereas species like *Sagitta enflata* has multiple cycles of maturity during their life span. Generally, in tropical and sub-tropical chaetognath communities, uninterrupted reproduction takes place though the survival rate of the fall intermonsoon generation is higher than the winter monsoon generation (Alvariño, 1983.). Changes in the biotic and abiotic components of the environment during different seasons may strongly influence the breeding cycle of the species occurring in those regions.

Species with wide distribution, when inhabiting different geographical locations differ in their breeding cycles. Species like *Sagitta bipunctata* and *Pterosagitta draco* reproduce throughout the year in tropics, but when inhabiting the temperate regions, breed only in spring and summer (Alvariño, 1983). Chaetognaths of the polar areas, mostly from Artic and Antarctic regions undergo a 'diapause' in their breeding cycle which is often a strategic delay in the development of eggs and larvae to overcome the adverse environmental conditions or lack of food (Russel, 1936; Alvariño, 1983).

1.4. Historical resume

Chaetognath was first described by a Dutch naturalist, Martin Slabber in 1778, based on the samples collected from the Dutch coastal region. He named them as *Zee-worm* (sea worm) or *Sagitta* or *pyl* (arrow). After many years Scoresby in 1820, in Artic region mentioned these organisms as food of whales. First detailed description of a chaetognath species (*Sagitta bipunctata*) was given by Quoy and Gaimard (1827) from the samples collected from Straits of Gibralter. In 1843, d'Orbigny described three new species and classified them under mollusca. Later, Forbes (1843) studied chaetognath around British region and added one more new species to the British fauna of chaetognaths. In 1844, Darwin described the structure and propagation of the genus *Sagitta*. During this period, another zoologist Krohn (1844, 1853) also succeeded in adding valuable information regarding the anatomy and physiology of this genus. Huxley (1852) was the first to state firmly the close resemblances of chaetognath with annelids. Leuckart (1854) through his extensive works made more progress on the systematic position of chaetognath and proposed a separate group for chaetognath and placed it between nematodes and oligochaetes. Later, Busk (1856) made clarification on the morphology of this group and in 1880, Hertwig in his monograph "Die Chaetognathen" gave a detailed account of the anatomy, systematics and histology of chaetognatha. Detailed research was carried out on the anatomy, systematics and embryology of the chaetognaths by Grassi (1883) while working on flora and fauna of Naples. He compared this group with other metazoans and further pointed out the need for a separate grouping for chaetognaths. Later, Doncaster (1902, 1903a) studied the embryology of the group and opposed the molluscan affinity of chaetognatha. His detailed descriptions on several chaetognath species from Maldive and Laccadive archipelagoes added new information regarding this group (Doncaster, 1903b). The paleontological analysis by Walcott (1911) indicated their higher affinity towards annelidans whereas MacBride and Heape (1914) proposed chaetognaths as relatively unmodified offshoots of a primitive protocoelomate stock from which all coelomate animals were derived. Based on the anatomical comparisons of the chaetognaths with other main invertebrates, Burfield (1927) suggested that this group cannot be grouped with other invertebrate phylum. Hyman (1959) pointed out that chaetognaths should be regarded as being diverged at an early stage from the primitive ancestor of the bilateria at the time when the dipleurula ancestor became differentiated and therefore assigned the rank of phylum for chaetognaths under the smaller coelomate groups.

Although chaetognaths constitute a separate phylum, its phylogenetic affinities have long been uncertain and have been under much debate. Several zoologists (Ducret, 1978; Ghiradelli, 1981) have described the chaetognaths as distant relatives of the three major deuterostome phyla (Hemichordata, Echinodermata and Chordata). Recently, Brusca and Brusca (2003) and Margulis and Schwartz (1998) have placed the chaetognaths within the deuterostomes. But Telford and Holland (1993), based on molecular analysis proposed that the most likely position of the chaetognaths is as descendants from an early metazoan branch possibly originating prior to the radiation of the major coelomate group. In another view, Tudge (2000) confirmed their close relation with the protostomes. Valentine (2004) placed the chaetognaths within the Paracoelomata but termed them as "*incertae sedis"* which is defined as a taxonomic group where its broader relationships are unknown or undefined. Recently Giribet et al. (2007) and Dunn et al. (2008) placed them at the base the Protostomata as the sister group to all other protostomes. Very recently, Edgecombe et al. (2011) pointed out that a proper understanding on the systematics of the chaetognatha could provide much insight into critical morphological and developmental characters that were common to some of the earlier bilaterians and thus placed them at the base of Protostomata. Recently, Nielsen (2012) also agreed with Edgecombe et al. (2011) on their systematic position and confirmed chaetognath as a basal protostomian group.

1.5. Classification

Leuckart (1854) was the first to classify chaetognaths. He created the order chaetognathii containing two genera *Sagitta slabber* and *Spadella langerhans*. Later Langerhans (1880) added another genus *Krohnia* which was later supported by Strodtmann (1892). Their classification included genus:

Sagitta with two pairs of lateral fins, and two rows of teeth;

Spadella with one pair of lateral fins on the tail segment, and two rows of teeth;

Krohnia with one pair of lateral fins extending on the trunk and tail, and one row of teeth.

Later in 1909b, Ritter-Záhony replaced the name *Krohnia* with *Eukrohnia*. Hertwig (1880) combined *Spadella* and *Eukrohnia* into one genus *Spadella* characterized by the presence of single pair of lateral fins. In course of time, various taxonomists and zoologists proposed changes to the original classification based on different morphological characteristics. Grassi (1883) proposed a new classification mainly based on the characters of the trunk muscles and described the species under two genera; *Spadella* and *Sagitta*. This classification raised confusion among biologists and was later rejected. Based on the fin characters, Abric (1905) classified chaetognath into nine genera under two large divisions, but this classification was not much accepted. During this period, Fowler (1906) based on total length, tail length, number of jaws and the number of anterior and posterior teeth classified the sixteen species of chaetognaths collected during Sibogae expedition into three genera.

Ritter –Záhony's (1911) studied these taxa in detail and classified 27 species of chaetognaths into six genera: *Sagitta, Pterosagitta, Spadella, Eukrohnia, Heterokrohnia* and *Krohnitta*. He has also taken into account all synonym species and thus his observation is considered as one of the most reliable work among early classification. Oye (1918) added one more genus *Zebo* to the systematics of chaetognath, which was later discarded by Tokioka (1952). A new chaetognath *Bathyspadella* was proposed by Tokioka (1939).

Several earlier naturalists initiated grouping of chaetognath species based on their close resemblances with each other. Michael (1913) grouped the closely related species into “couplets” whereas several zoologists (Thiel, 1938; Thomson, 1947; Tokioka, 1952; Furnestin, 1957; Colman, 1959; Alvariño, 1961).classified them into species group like ‘maxima group’ and ‘neglecta group’. Later, David (1963) had proposed eight genera among the pelagic chaetognath species with 70 – 80 species. However Alvariño (1965a) in her monograph on the chaetognaths supported the reliability of only about 52 species for the seven genera. Classification higher than the genus level was not suggested for chaetognaths during earlier periods of systematics until Tokioka (1965) proposed his new classification. According to him, the phylum chaetognatha is subdivided into two classes, Archisagittoidea for the monotype fossil genus *Amiskyia* (Walcott, 1911) and Sagittoidea for the living forms, comprising two orders and five families. In this new classification, several species have been promoted to higher categories, recognized under 15 genera with 65 species, three subspecies, one variety and three forms. This classification has been later modified and is being followed by some naturalists (Casanova, 1985; Bieri, 1991 a,b) whereas majority of the biologists are following the classical taxonomy (Nair, 1978, 2003; Pierrot-Bults, 1982; Pierrot-Bults and Nair, 1991; Nagai, 2006).

1.6. Review of literature on Indian Ocean chaetognaths

In the Indian Ocean, the pioneering work on chaetognath was done by Doncaster (1903a), based on samples collected during Stanley Gardiner’s expedition during 1899 and 1900 in the Maldive Laccadive archipelagoes. Of the 15 species reported during the study, six was regarded as unknown species. A detailed account on their systematics and distribution pattern was also reported. He accounted that a variation in morphological characteristics (e.g. variation in number of teeth) can occur if the same species is distributed in widely separated areas. The next remarkable work on chaetognaths was by Burfield and Harvey (1926), based on the Sealark expedition from the Indian Ocean (3°31′ - 6°1′ S., and 69°16′ - 72°27′ E) during 1905. Total of eighteen species belonging to four genera were reported from that region. Sampling was done covering 800 fathom water column and the maximum density was observed in the epipelagic layer, i.e. in the upper 100 fathom layer.

John (1933a) studied chaetognath from Madras coast and described five species under the genus *Sagitta* and later gave description on their seasonal variation pattern too (John, 1937). Later John in 1943; gave a detailed account of the reproductive organs of this genus. Subramaniam (1937) critically reviewed John’s observation on the seasonal variation of the genus *Sagitta* and concluded that they occur throughout the year in Indian coasts. Subramaniam (1940) reported the occurrence of *S. bedoti* and also suggested the species *S. gardineri*, (described by John, 1933a, 1937) as a synonym of *S. enflata.* Chaetognaths around Bombay coast was studied in detail by Lele and Gay (1936) and reported three species, of which one (*S. bombayensis*) was new to science. Later George (1949) worked on chaetognaths from different parts of Indian coastal waters and named *S. bombayensis* suggested by Lele and Gay (1936), as a synonym of *S. robusta* Doncaster. He also for the first time recorded *S.pulchra* from Indian coastal waters. Later Rao and Kelly (1962b) described *S. bombayensis* as a different species and Silas and Srinivasan (1968) supported their findings with a redescription of this species.

Varadarajan and Chacko (1943) studied the chaetognaths around the Krusadai Island in the Gulf of Mannar and reported the occurence of six species belonging to three genera, *Sagitta*, *Spadella* and *Krohnia*, based on 273 hauls of plankton during 1939 – 1941. They also described the seasonal variation in the distribution and reported that the maximum density was usually observed during September – December. Later Chacko (1950) made a detailed study on the chaetognaths from the same area and supported the earlier findings. Chaetognath diversity around the coast of Trivandrum was studied in detail by Menon (1945). Of the four species recorded by Menon, identification of *S. tenuis* is doubtful as this species is reported mostly in the Atlantic Ocean (Alvariño, 1965a). George (1952) has studied the chaetognaths in the Malabar Coast. His description included a key for the identification of 12 species of chaetognaths belonging to three genera. He also studied the ecology of chaetognath by correlating the seasonal fluctuation of chaetognath abundance with rainfall, salinity and surface water temperature and opined that the individual species have their own seasonal cycle of abundance.

Ganapati and Rao (1954) reported the chaetognaths of the Visakhapatnam coast and studied their relation with salinity and temperature. Later a series of works by Rao (1958a,b, 1966a,b) Rao and Ganapati (1958) and Rao and Kelly (1962a,b) provided a clear account on the chaetognaths along the east coast of India, mostly along Waltair and off Visakhapatnam coast. These investigations also revealed the influence of hydrographical conditions and physical factors on chaetognath community and also on their abundance distribution.

In 1961, Sudarsan based on the sampling around Mandapam region (9°16' N, 79°08' E) during 1955-58 reported the occurrence of nine species of chaetognath. Of the two areas around Mandapam, Gulf of Mannar was quantitatively rich in chaetognath population. He observed a close relationship between the chaetognath and copepod breeding cycles and also suggested the probability of *S. neglecta* being brought down from the north into Palk bay by coastal currents.

In the western part of the Indian Ocean studies on chaetognath was initiated by a group of eminent biologists. Steinhaus (1896) recorded 3 species of chaetognath from the Red Sea. Later, Ritter Záhony (1909a) described four other species of chaetognath from that region. Schilp (1941) recorded 3 chaetognath species from the samples collected during the “Snellius” expedition. Ghirardelli (1947) recorded eight species of chaetognaths from the Gulf of Aden, off Somalia and various locations in the Red Sea. Later, Furnestin (1958) gave an account of five species occurring in this area. His works was an important addition to the knowledge on chaetognath of this region. A series of work by Furnestin and Radiguet (1964), Furnestin and Balanca (1968), Furnestin and Codaccioni (1968) and Furnestin (1976) helped in adding valuable information regarding chaetognath from the western part of the Indian Ocean.

Tokioka (1952) in his review of the chaetognaths from the Indo-Pacific region reported the occurrence of 36 species. He has dealt in detail the characteristics of Indo-Pacific fauna and concluded that this region sustains the greatest number of the chaetognath species in the world (83%) and stated that endemic forms (38% of the known species) of chaetognath dominate this region. Later in 1955, he studied the chaetognaths of the north-eastern part of the Indian Ocean. Tokioka (1956) in the central Indian Ocean along northern part of the Sealark stations (5°37′N - 4°35′ S, 67°43′ - 81°07′ E) observed around thirteen species of which S*. pacifica* (= *S serratodentata pacifica*) had relatively high dominance followed by *S. enflata*, *S. bedoti* and *S. regularis*. Compared to the Sealark samples, *S. bedoti* was more common in these collections and *S. minima* was new addition to the list of these species. Further, Tokioka (1962) listed around 30 species. This work was a comprehensive review on the chaetognaths study of the Indian Ocean. He also suggested that *S. bedoti* could be used as a reliable indicator to trace the movement of inshore water masses.

Tsurata (1963) studied chaetognaths around the south eastern part of the Arabian Sea between 4°52′ - 13°24′ N, 66°39′ - 72°50′ E and recorded 15 species of which *S. enflata* and *S. pacifica* were the most common forms and *S. minima* had moderate abundance.

Alvariño (1965a) in her outstanding contribution on chaetognaths had critically reviewed all the previous studies on chaetognaths and codified the nomenclature of some of the species recorded from the Indian Ocean. She has given a detailed account of the geographical and bathymetric distribution of chaetognaths, based on the previous work done from all the oceans. Her review also included the ecological studies carried out on chaetognath.

Silas and Srinivasan (1970) by reviewing the earlier works on chaetognaths in the Indian Ocean published a list of about 33 commonly occurring species of the region. Based on the sampling on RV Varuna and Anton Bruun during its 5th International Indian Ocean Expedition (IIOE) cruise in the Indian Ocean from January to May 1964, they recorded 23 species and provided a key to the observed genera and species. They had also made general remarks on the status and systematic position of some species recorded in the Indian Ocean.

Silas and Srinivasan (1969) reported 14 species from the Laccadive sea and off the West coast of India (between 7°30′ - 18°0′ N, 70°31′ - 75°58′ E). *S. enflata* was the most abundant species in their collection followed by *S. pacifica*, *S. decipiens*, *Pterosagitta. draco* and *S. regularis*. Abundance of *S. pacifica*, *S. regularis* and *S. robusta* were higher during the day hauls, the reason for which was not clear. The species list included one new species *Eukrohnia minuta*. According to the authors, the existence of a small species of *Eukrohnia* showing affinities to *E. hamata* was more interesting as it suggested the replacement of the latter species in the equatorial belt and northwards by the newly described species.

Nair (1969) has reported the seasonal changes in the abundance of chaetognaths from different regions of the Indian Ocean based on the IIOE data. The period mid April to mid October (SW monsoon) showed a comparatively higher density of chaetognaths in all regions except the eastern part of the Arabian Sea. During both seasons the areas in the western part of the Arabian Sea exhibited relatively higher abundance.

1.7. Scope and purpose of study

Qualitative and quantitative studies on plankton community is highly essential in evaluating the health and productivity of the marine ecosystem as they directly respond to physical process, global warming, climate changes and perturbations occurring in marine system. As a major carnivorous zooplankton group, chaetognath which is often found as the second abundant group after copepod, has a crucial role to play in the marine food web. Thus the knowledge on the ecology and the response of various environmental variables on the community structure of chaetognath is of utmost importance in understanding its dynamic role in the pelagic system. The Arabian Sea (AS) and Bay of Bengal (BoB) are two major regions in the Indian Exclusive Economic Zone (EEZ) and because of their unique characteristics acts as an important zone to study this major carnivorous zooplankton.

Although information on chaetognaths in the Indian Ocean is available from the Gardiner's expedition (1899 - 1900) onwards, those were mostly localized information and lacked systematic observation. Later during International Indian Ocean Expedition (1960 – 1965) a broad coverage of the Indian Ocean was done but it was mostly limited to upper 200 m depth. Though this study gave a detailed description of the taxonomic distribution of the chaetognath species, the ecological interactions with different temporal basin scale and meso scale physical process and environmental variables was not addressed. Later, during the Indian Joint Global Ocean Flux study (1994 - 2000) and the Bay of Bengal Process Studies (2000-2006) not much emphasis was given on the chaetognath ecology. Thus the present study under the multidisciplinary project "Marine Research on Living Resources" funded by the then Department of Ocean Development (Govt. of India) provided an ample opportunity and impetus to systematically study the ecology of chaetognaths occurring in the Indian EEZ. A definite information on any plankton species can be made only on the basis of continuous monitoring in any region. Thus with respect to earlier studies, in the present study an attempt has been made to understand the changes that are happening to this major planktonic group/community as a result of the recent climate changes.

The main objectives of the study are:

1. To study the mesozooplankton biomass and abundance along different season and their response towards different physical processes.
2. To investigate the importance of chaetognath in mesozooplankton community along different depth layers
3. To study the detail spatial and temporal distribution of chaetognath along different depth layers in upper 1000 m water column.
4. To investigate the role of different physico-chemical variables and different physical processes in the distribution of chaetognath population.
5. To identify the indicator species of particular events like upwelling etc.
6. To study the differential response in behaviour of chaetognath species along different growth stages.
7. To understand the changes in chaetognath community in response to recent climatic changes.

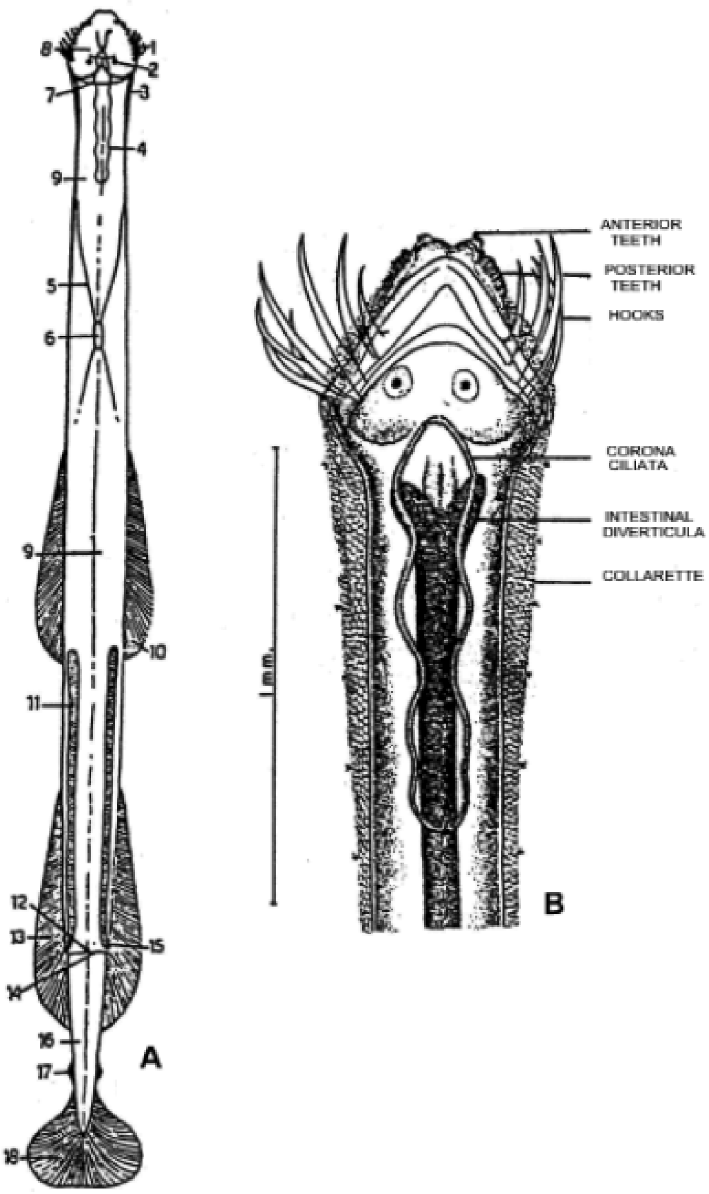

Figure 1. A typical chaetognath (adapted from Hyman, 1959 and Nair, 2003). A – *Sagitta* (ventral view); B – Details of head. (1. Grasping spines; 2. Eyes; 3. Collarette; 4. Corona ciliata; 5. Circumentric connectives; 6. Ventral ganglion; 7. Head-trunk partition; 8. Head; 9. Trunk; 10. Anterior lateral fins; 11. Ovary; 12. Anus; 13. Posterior lateral fins; 14. Trunk-tail partition; 15. Female gonopores; 16. Tail; 17. Seminal receptacles; 18. Tail fin).

Chapter 2

Study area

Exclusive economic zone (EEZ) is the oceanic province over which a state has complete right for the exploration and utilization of both living and non-living marine resources. Indian EEZ, covering an area of 2.172 million km^2 is a region of high ecological diversity and economic significance. The optimum utilization and conservation of the potential marine resources available within the EEZ are possible only if the oceanographic and ecological processes are well understood. The present study covers a major part of Indian EEZ, the Arabian Sea (AS) and the Bay of Bengal (BoB) in the northern Indian Ocean (Fig. 2). These two major ocean basins are geographically positioned in the tropical basin, mostly on the Australian plate and are landlocked at the northern boundary by Asian landmasses. This uniqueness in the geographical setting of the northern Indian Ocean when compared to both the Atlantic and the Pacific Oceans, leads to the development of distinctive climatological and hydrographical characteristics. The difference in specific heat capacity between continents and oceans, especially between the large Asian continent and the Indian Ocean induces the monsoons, strong seasonal fluctuations in wind direction, and precipitation over oceans and continents. Over the Indian Ocean, during summer (June – September), strong winds blow from the southwest whereas during winter (November – February) weaker winds blow from the northeast. The monsoons are strongest over the western part of the Indian Ocean and the Arabian Sea. The high seasonal variability arising due to the reversing monsoonal system strongly influences the hydrography and the biological productivity of the northern Indian Ocean.

Indian Ocean is known for its high biological productivity and is considered as the most productive among the world oceans. Earlier, Ryther and Menzel (1965) reported that the western Indian Ocean is twice as productive as the open ocean which was later confirmed through a series of extensive productivity studies (Baars and Oosterhuis, 1997). Northern Indian Ocean is well known for the presence of one of the major oxygen minimum zones in the global ocean (Levin, 2002; Levin et al., 2009; Naqvi et al., 2006) which is more prominent along its western part. The formation and sustenance of this thick oxygen minimum zone (OMZ) in the northern Indian ocean is the resultant effect of high local respiration rates in response to high biological production in surface waters, the longer periods taken for organic decomposition due to slow advection of water (Sverdrup et al.,1942), and influx of oxygen depleted water from the south (Swallow, 1984).The densely populated littoral countries around this landlocked basin in turn, make the sensitive oxygen depleted environment much more vulnerable to anthropogenic perturbations (Naqvi et al., 2006). The ecological sequelae of this OMZ is very important as only a few species can tolerate this extreme oxygen deficiency thereby constraining the vertical habitat of most marine organism (Prince and Goodyear, 2006; Bertrand et al., 2010). High biological productivity and the existence of thick OMZ in the intermediate waters of the northern Indian Ocean makes it a unique environment for extensive ecological research. AS and BoB, though occupy the same tropical basin, vary greatly in their hydrographic and biological features, mainly arising due to the differences in the atmospheric and physical forcing (Gauns et al., 2005). A better understanding of the ecological and long term changes occurring in this unique environment with time is possible only through continuous monitoring of its biological characteristics.

Arabian Sea

AS occupies a major part of northwestern Indian Ocean and is bounded by the Asian and African landmasses to the west and north and Indian subcontinent to the east. It is connected directly to the Persian Gulf and the Red Sea through a narrow sill of Bab-el-Mandeb. It is considered as a region of negative water balance as evaporation exceeds both precipitation and river runoff in most of the regions. High sea surface salinity is a characteristic feature of AS, resulting mainly by the excessive evaporation rates and also by the influx of high saline waters from Red Sea and the Persian Gulf. During winter monsoon, the wind direction is predominantly from the north or the north-east. The weak winds (~5 m/sec) during this period are not much efficient in inducing any appreciable offshore Ekman transport (Madhupratap et al., 1996a). But as they are coming over the continent, their cold and dry nature results in the increase of surface density through evaporation and cooling. Low solar radiation during this season further aids in cooling the surface waters which in turn lowers the sea surface temperature leading to winter cooling (Prasanna Kumar and Prasad, 1996). This in turn, results in convective mixing mostly in the northern Arabian Sea (Prasanna Kumar and Prasad, 1996; Prasanna Kumar et al., 2000). During this period, the West India Coastal Current (WICC) flows towards the north (Shetye, 1998) and the North equatorial current flows towards west (Prasad et al., 2001).

During summer monsoon, the atmospheric and surface oceanic flow reverses completely. In the eastern part, the WICC flows equatorward (Shetye, 1998) and in the western part, Somali current flows northward with the greatest strength in July (Schott, 1983). A part of this Somali current extends across the AS towards the Gujarat coast of India, as Findlater Jet (Findlater, 1969). The gradients in winds across the jet force produces open ocean upwelling in the north and west of this feature and downwelling in the south and east. During this period, strong upwelling zones are also observed along the west coast of India, bringing nutrient rich deeper waters to the surface layers, resulting in high biological productivity.

During the transitional intermonsoon periods (spring and fall), the surface winds are weaker and solar radiation is quite high (260 W m^{-2}, Hastenrath and Lamb, 1979). Higher sea surface temperature along with weak wind pattern often leads to strong near surface stratification.

Though the direction of wind and current differs along seasons, the northern AS remains quite productive throughout the year (Madhupratap, 1996 a,b) and is often the result of a widely accepted phenomenon called “Arabian Sea paradox”. Recently, Jyothibabu et al., (2010) has opposed this paradox and has shown the difference in secondary production between the northern and southern part of eastern AS. During winter, the convective mixing triggers higher primary production which subsequently leads to high meszooplankton abundance. Swarms of pelagic tunicates are frequently observed during winter season. During summer monsoon, the upwelling along the Somalia (Bruce 1974; Brown et al., 1980; Tsai et al., 1992), Arabian coasts (Sastry and D’Souza, 1972; Smith and Bottero, 1977) and along the west coast of India

(Banse, 1959, 1968; McCreary and Chao, 1985; Johannessen et al., 1987; Shetye et al., 1990; Shankar et al., 2005), results in uplifting of nutrient rich water which in turn facilitates high biological production in AS. During intermonsoon periods, high sea surface salinity and high solar radiation results in strong stratification in surface waters which in turn transforms AS into an oligotrophic basin limiting the growth of larger phytoplankton. During this period biological production is mainly supported by regenerated inorganic nitrogenous forms such as ammonia and urea. In AS, the sustenance of mesozooplankton community during this oligotrophic period is mainly through a microbial loop active during this period. High dissolved organic carbon occurring following the senescence of summer and winter blooms is utilized by the abundant bacterial population for their growth. They in turn help in the proliferation of heterotrophic nanoflagellate and microzooplankton community which are in turn grazed upon by the mesozooplankton community (Gauns et al., 2005). Carnivorous zooplankton density is also quite high in this region, (Madhupratap et al., 1990, 1996b) and is often double compared to that of temperate regions (Longhurst and Pauly, 1987). Thus it further demands elaborate studies on the ecological role of chaetognath which is one of the major carnivorous mesozooplankton taxa in this unique ecosystem.

Based on the water mass property (Jackett and McDougall, 1997) AS, is characterized by the presence of seven different water masses (neutral density layer): BoB Surface water, AS High Salinity Water Mass (ASHSW), Persian Gulf Water, Red Sea Water, North Indian Deep Water, Circumpolar Deep Water, and Somali Basin Bottom Water. Of these seven water masses the first four are observed to occur in the upper 1000 m water column whereas the

North Indian Deep Water is observed only during the upwelling event. As chaetognaths are considered as ideal indicators of different water masses, a detail study on their ecology and distribution pattern in association with different water masses will further aid in generating new information regarding the ecological processes active in AS.

Bay of Bengal

BoB is located in the northeastern part of the Indian Ocean, between 5° to 23° N latitude and 80° to 100° E longitude. It is a semi-enclosed basin covering 4.087×10^{6} km^{2}, sharing 0.6% of the world ocean (La Fond, 1966). The eastern boundary of it is guarded by Myanmar and Andaman Nicobar islands whereas the western parts are covered by Indian peninsula and Srilanka. It is connected to the Pacific Ocean through the Strait of Malacca and the Australian seaways.

BoB is characterized by the very high fluvial inputs through some of the world's largest rivers (Milliman and Meade, 1983). The major rivers systems that drain into BoB includes Brahmaputra, Cauvery, Ganges, Damodar, Godavari, Irrawady, Krishna, Mahanadi, Mahaweli, Pennar and Salween (Varkey et al., 1996) .The rivers along the Indian subcontinent itself contribute to about 13.86×10^{6} terrigenous material annually to the BoB (Subramanian 1993). The excessive river runoff (1.6×10^{12} m^{3} y^{-1}) (Subramanian, 1993) and rainfall results in a positive water balance in most of the regions of BoB (Ramanathan and Pisharody, 1970). High river influx often results in the formation of a low saline cap in the surface waters which along with high sea surface temperature during summer results in strong summer stratification. The riverine influx is one of the major contributors of nutrients for the biological production in the oceanic surface layer (Ittekkot et al., 1991), although a major part of it is thought to be lost to the deep waters because of the narrow shelf (Qasim, 1977; Sengupta et al., 1977; Radhakrishna et al., 1978)

The BoB basin is also strongly influenced by the monsoonal winds which have semiannual seasonality (Ramage, 1971) in occurrence. During winter monsoon, the weak winds coming from the northeast, brings cool and dry continental air to the BoB in contrast to summer monsoon with strong southwest wind bringing humid maritime air. The surface circulation of the basin also follows semiannual reversal and is not strictly in accordance with the wind reversal. During winter monsoon, the East India coastal current (EICC) flowing northward along the western boundary of BoB, peaks during March-April (spring intermonsoon), when the winds are weak and lead to the formation of anticyclonic curls (Shetye et al., 1993). Similar to AS, BoB is also characterized by the presence of OMZ in mid depth waters.

BoB is traditionally considered as a less productive system compared to its counterpart Arabian Sea (Prasanna Kumar et al., 2010a). Although the average surface biological production in BoB has been found to be higher than AS (Krey and Babenerd, 1976), the column production has been proved much lower (Qasim, 1977). Overall, BoB sustains moderate productivity throughout the year (Prasanna Kumar et al., 2010a). The physical processes that have profound influence on the biological productivity of BoB are strong wind, cyclones and eddy. Cyclones which generally occur during summer monsoon and fall intermonsoon, enhance the productivity of BoB to a great extent (Madhu et al., 2002). Along the western BoB, upwelling has also been observed to occur during summer monsoon but is of low intensity compared to AS (Shetye et al., 1991) and thus has meager effect on productivity. The cold core eddies occurring during different seasons also play a prominent role in the enhancement of biological productivity (Prasanna Kumar et al., 2004, 2007; Muraleedharan et al., 2007) in BoB.

Summary

Though both AS and BoB are located in the same tropical basin, their different hydrographical characteristics along with unique climatic and oceanographic processes make them an ideal area for studying the ecology of the mesozooplankton community in the Indian EEZ. In both ocean basins, though chaetognaths have been reported as a major carnivorous group among zooplankton, their significant role in the ecological processes of the pelagic ecosystem is not clearly understood. Thus this study covering a major portion of the EEZ of India, comprising the two major regions of the North Indian Ocean, provides an excellent opportunity to study the ecology of chaetognaths, which has a vital role in marine ecosystem and food web dynamics.

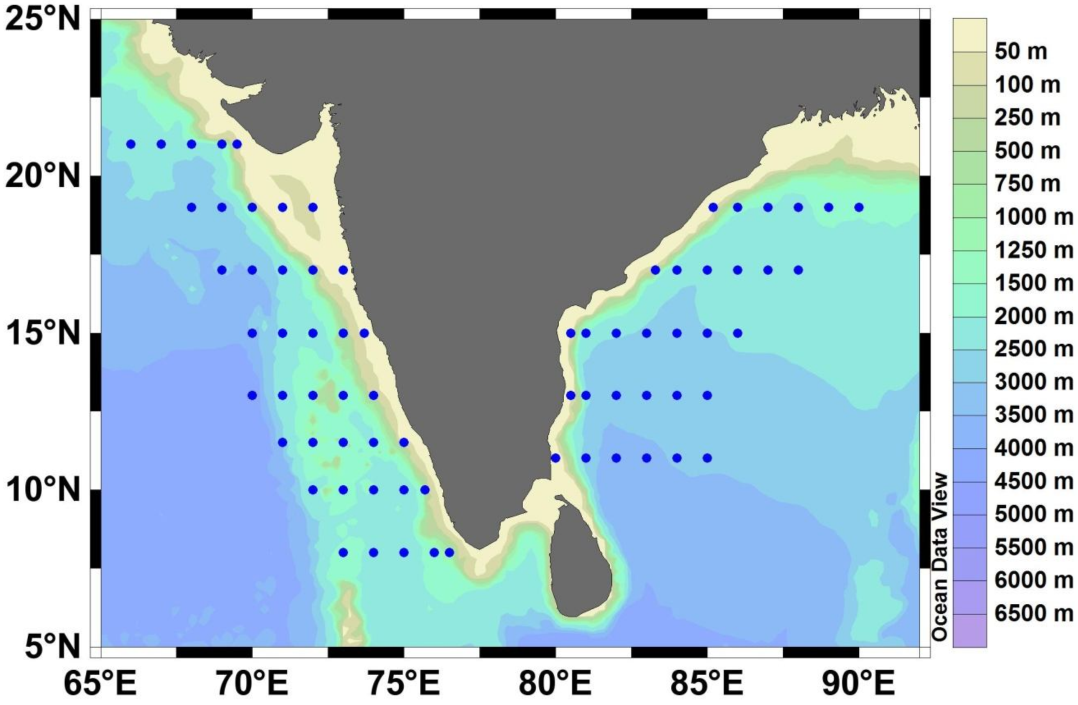

Figure 2. Sampling locations in the Indian Exclusive Economic Zone.

Chapter 3

Materials and methods

3.1. Sampling

Oceanographic research cruises for the present study were conducted on FORV Sagar Sampada (Plate 1) in the AS and BOB, covering a major part of Indian EEZ. Sampling was carried out covering three seasons, viz. Summer monsoon (SM: June to September), Fall inter monsoon (FIM: October) and Winter monsoon (November to February). The classification of season was based on the Indian Joint Global Ocean Flux studies (JGOFS) programme for AS and Bay of Bengal process studies (BoBPS) programme for the BoB (Madhuparatap et al., 2003). Stations were fixed along different zonal transects. Each transect was spaced at 2° latitude interval, and along each transect, the stations were fixed at an interval of 1° longitude, extending from the coast to offshore (Fig. 2). Along each transect, the stations with less than 200 m depth were designated as ‘coastal,’ and those with more than 200 m depth were designated as ‘oceanic stations’. One coastal station and one oceanic station along each transect were selected for the diurnal observations and the sampling was carried out at 6 hourly interval along a diel scale. At all other stations, the time of sampling was noted to have a better understanding on the temporal variations. In AS, the sampling stations were distributed along eight latitudinal transects viz. 8° N, 10° N, 11.5° N, 13° N, 15° N, 17° N, 19° N and 21° N. During SM, sampling was carried out covering most of the transects mentioned above (8° - 19° N). During FIM, the central and the southern parts of

AS were covered (8° - 13° N) while during WM, the central and northern parts were sampled (15° - 21° N). In BoB, five latitudinal transects were sampled during all the seasons (11° N, 13° N, 15° N, 17° N and19° N) (Fig. 2) but during SM, sampling was not possible along 19° N transect, due to rough sea conditions.

3.2. Physico-chemical variables

At all stations, a CTD (SBE Seabird 911 plus) was used to obtain the temperature (accuracy ± 0.001° C) and salinity (conductivity ± 0.0001 S/m) profiles of the water column (Plate 2). This instrument was operated close to the bottom at the coastal stations and up to 1000 m at the oceanic stations. The sea surface temperature (SST) was monitored using a bucket thermometer (accuracy ± 0.1° C). Salinity measured by CTD was further calibrated against water samples collected from discrete depths using Autosal (Guildline 8400A) onboard. The surface meteorological parameters (surface temperature, wind speed and wind direction) along the ship's track were monitored continuously using a ship based automated weather station. In AS, the mixed layer depth (MLD) was determined as the depth up to which a decrease of 0.5° C temperature occurred from SST. In BoB, it was determined as the depth where the density difference from the surface was 0.2 kg m^{-3} (Shetye et al., 1996). In both basins, the thermocline (TC) was defined as the depth where the temperature attained 15°C.

Water samples were collected in Niskin bottles (5 L) using a Rosette sampler connected to CTD from standard depths up to near bottom at coastal stations and up to 1000 m at oceanic stations (surface, 10, 20, 30, 50, 75, 100, 150, 200, 300, 500, 750 and 1000 m) with remotely operated closing mechanism. For dissolved oxygen (DO) estimation, water samples were carefully transferred into DO bottles (125 ml) without trapping air bubble. Samples were analysed using Winkler's method (Grasshoff, 1983) with visual end point determination. Samples were immediately fixed by adding 0.5 ml Winkler A (Manganous chloride) and 0.5 ml of Winkler B (Alkaline potassium iodide) solutions. It was mixed well before the precipitation occurs. Then after acidification with 50% hydrochloric acid, samples were titrated against standard sodium thiosulphate using starch as indicator. The DO concentration was calculated as,

$$\text{DO (ml / Litre)} = 5.6 \times N \times (S - b_m) \times V / (V - 1) \times 1000 / A$$

Where, N = Normality of the thiosulphate,

S = Titre value for sample,

b_m = Mean titre value for blank,

V = Volume of the sampling bottle,

A = Volume of sample titrated (50 ml)

3.3. Biological variables

3.3.1. General zooplankton

Mesozooplankton sampling was carried out using multiple plankton net (MPN: Hydrobios, Germany; Weikert and John, 1981) (Plate 3). The MPN works based on the principle of opening and closing of a series of individual plankton nets in succession. The sampler consists of mostly two units. The first one is the deck command unit for closing the individual net. The second unit consists of a square shaped stainless steel frame (mouth area 0.25 m^2) with 5 canvas parts and to each of them one net bag is attached (mesh size 200 µm).

The opening and closing of the nets at prefixed depth zone is controlled by electronic sensors. An integrated depth motor allows the continuous monitoring of the actual operating depth, which is always displayed in the deck command unit.

Samples were collected from five discrete depth zones up to 1000 m, including the mixed layer depth (MLD), the thermocline (TC), the base of the thermocline (BT) to 300 m, 300 – 500 m and 500 – 1000 m, based on the temperature and density characteristics of the water column. For every collection, the net was first deployed down to reach the maximum limit of the deepest stratum. The sampling was initiated from the deepest stratum and subsequently covering the shallower strata as the net was towed vertically towards the surface. The speed of the vertical tow of the net was maintained as 1 m. sec^{-1}.

Biomass estimation of the mesozooplankton was done following the biovolume method. The term biomass indicates the amount of living matter present in the mesozooplankton sample. It is of critical importance in evaluating the secondary production in the system. For this estimation, at first the zooplankton sample collected was sieved using a 200 µm mesh net. The excess water was removed by absorbent paper and the displacement volume (DV) was measured (Harris et al., 2000). The biomass per unit area was obtained from the DV by using the following calculation,

Biomass = DV / VWF

VWF = DH × A

Where, DV = Displacement volume

VWF = Volume of water filtered

DH = Depth of haul

A = Mouth area of the net

The biomass is expressed in ml / 1000 m^3.

After the estimation of the biomass, the zooplankton samples were immediately preserved in 4% buffered formalin (Steedman, 1976; Harris et al., 2000) and then stored in wide mouthed plastic containers for further detailed analysis on the abundance and species wise composition.

The mesozooplankton taxa were sorted from the whole sample or from an aliquot (50%) using a Folsom splitter (Sell and Evans, 1982) (Plate 4) and counted under a stereomicroscope. The zooplankton was primarily sorted to the major taxonomic groups according to the standard identification manuals (Newell and Newell, 1973; Todd and Laverack, 1991) (Plate 5). The abundance is expressed as ind / 1000 m^3 by using the formula,

Abundance (ind / 1000 m^3) = No. of individuals of the particular taxa / volume of water filtered.

3.3.2. Chaetognath

Chaetognaths were sorted out from the mesozooplankton samples and were further identified to species level (Plate 6). For detailed species level identification, non-meristic characters were given more importance as the meristic characters are often unreliable since they vary greatly with age, season and geographic locations and also exhibit considerable overlapping. The species level identification of chaetognaths was carried out following the published works of Ritter Záhony (1911), John (1933a,b), Tokioka (1939), Thomson (1947), Fraser (1952), George (1952), Alvariño (1962, 1965a, 1967), Silas and Srinivasan (1969, 1970), Nair (2003).The classification of chaetognaths into different species is mainly based on the characters detailed below as per Nair (1972),

i. Degree of transparency of body: Transparent, translucent or opaque
ii. Nature of the body: Flaccid or turgid
iii. Muscle characteristics: thin, thick or wide
iv. Total body length
v. Ratio of tail segment to the total length
vi. Number of caudal fins, its position and shape
vii. Presence or absence of fin rays, partially or fully rayed
viii. Presence or absence of intestinal diverticula
ix. Presence or absence of collarette, its position and extent
x. Size of the head compared to the body
xi. Shape and position of the eye
xii. Shape of eye pigment
xiii. Shape of seminal vesicle and its position relative to the posterior caudal fin and tail fin
xiv. Shape and extent of ovaries, arrangement of ova in the ovaries.

The species-wise abundance is expressed as (ind. / 1000 m^3). Based on ovarian development, the chaetognaths were grouped into 3 maturity stages, viz. Stage I or immature (specimens with no visible ovaries); Stage II or maturing (those with developing ova); and Stage III or matured (individuals with one or more mature ova) (McLaren, 1969; Zo, 1973). All spent individuals were considered under stage III. To study the differential response in behaviour of chaetognath species along different growth stages, this stage-wise analysis were done during two seasons (FIM and WM) in both AS and BoB.

3.4. Long term monitoring of chaetognaths

In order to assess the long term temporal changes of chaetognath community in response to hydroclimatic forcing in the Indian Ocean, the present study was compared with the earlier available records from International Indian Ocean Expedition (1960 – 65). Four *Anton Bruun* cruise's (Cruise I, II, IVA and VII) data were analyzed for this purpose. In case of AS, stations along 6° to 24° N and 64° to 77° E were selected while in BoB stations distributed in the region of 7° to 20° N and 80° to 97° E were chosen.

Samples during IIOE were collected from surface down to 200 m depth. To compare with these data sets, the total chaetognath abundance in the upper two layers of the present study was only used. The average depth of upper two layers was 202 and 168 m, respectively in AS and BoB during the present study. The small difference in the sampling depths between the earlier and present studies was not considered to affect the comparison. However, the differences in the mesh size of the nets used during IIOE collections and the present study was thought to be another serious problem for comparison. But, again this issue was resolved because the size range of all the chaetognaths in both past and present samples were greater than 330 µm and it is assumed that it would not have affected the chaetognath abundance. To assess the long term changes in chaetognath distribution in both AS and BoB, the abundance values of all the three seasons were considered. To see whether any variation occurred in chaetognath abundance between the northern and southern parts of both AS and BoB, the abundance of these two parts were treated separately. For this purpose, the data collected on cruises which covered both northern and southern part of AS and BoB only were considered.

3.5. Statistical analysis

3.5.1. Diversity indices

a. Shannon – Weaver (1963) species diversity index (*H′*)

$$H' = -\sum_{i=1}^{i=s}[p_i log_2(p_i)]$$

Where, $p_i = \left(\frac{n_i}{N}\right)$,

n_i is the number of individuals of i^{th} species

N is the total number of individuals of all the species

S is the total number of species present during the study.

Shannon diversity (H′) is one of the most widely used index for comparing the diversity between various habitats (Clarke and Warwick, 2001)**.** The species diversity of chaetognath along different locations and different seasons was calculated to assess the spatial as well as temporal changes in diversity.

b. Pielou's (1966) evenness index (*J′*)

$$J' = \frac{H'}{Log\ (S)}$$

Where *H′* is the Shannon – Weaver (1963) species diversity index

S is the total number of species present during the study.

3.5.2. Cluster analysis

Species wise abundance of chaetognath along different depth strata was subjected to hierarchical cluster using the Bray- Curtis similarity index with standardised log10 (x + 1) data using PRIMER version 5.2.8 (Clarke and Warwick, 1994). This was done for the better understanding of the habitat preferences among the chaetognath species.

3.5.3. Principal component analysis

Principal component analysis (PCA) was carried out using the statistical programme PAST version 2.02 (Hammer et al., 2001), to understand the interrelationships between the biotic and abiotic variables. The mean values of the abiotic parameters for each depth stratum at all stations were considered for the analysis.

3.5.4. Mann-Whitney test

The Mann-Whitney U test was performed between the average surface values of the physicochemical variables of AS and BoB along different seasons to understand whether any significant difference between AS and BoB exists or not. The test was also done between the $\log_e$ transformed biomass and abundance values of AS and BoB to check whether any significant difference exists between these two major parts of the north Indian Ocean. The $\log_e$ transformed abundance values of chaetognaths in AS and BoB were also used for this purpose. The statistical software Graph Pad Prism (version 5.01) was used for this purpose.

3.5.5. Wilcoxon matched pair test

A Wilcoxon matched pair test was carried out between the day and night abundances of chaetognaths at different depths at the diurnal stations, to determine whether the diel vertical migrations of these groups affected their abundance. This was done as a nonparametric test, not assuming Gaussian distributions, with two-tailed P-values and a 95% confidence interval using the statistical software Graph Pad Prism (version 5.01).

Plate 1: *FORV* Sagar Sampada

Plate 2: CTD rosette with Niskin bottles

Plate 3: Multiple Plankton Net

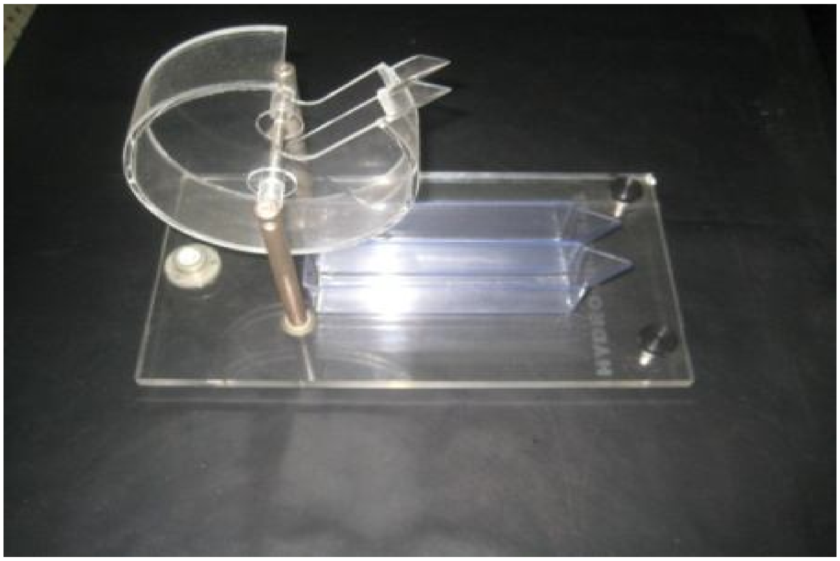

Plate 4: Folsom splitter

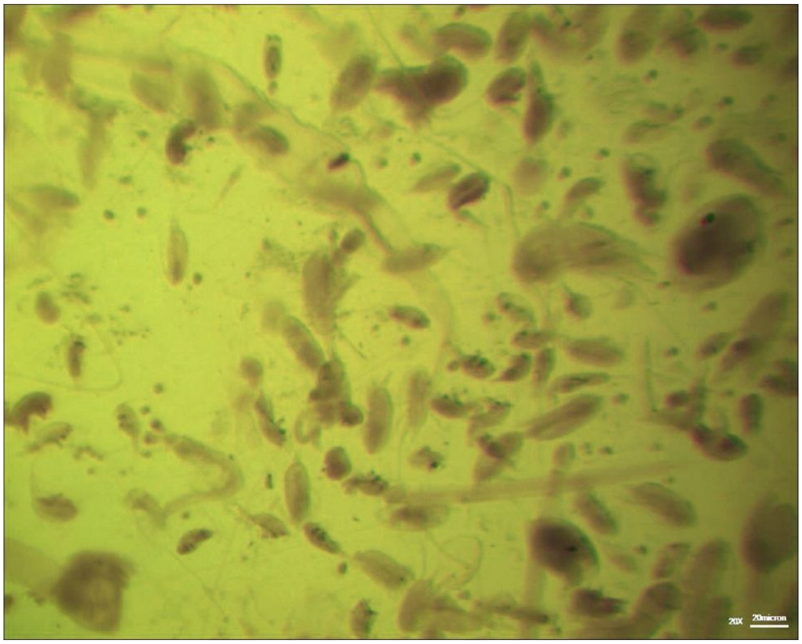

Plate 5: Mesozooplankton assemblage

Plate 6: A typical chaetognath (*Pterosagitta draco*)

Chapter 4

Results – Physico-chemical features

4.1. Physical features

4.1.1. Arabian Sea

4.1.1.1. Summer monsoon

During this season the Northern part (15° - 19° N) of the AS exhibited relatively high Sea surface temperature (SST ≥ 31°C) than the Southern part (8° - 13° N; ~ 30°C). The SST ranged between 29.8° and 31.6°C with an average of 30.6 ± 0.4°C. Upper 300 m layer was thermally stratified with higher gradients towards the surface layer. An uplifting of the isotherm was evident in surface, upper subsurface and lower subsurface layers in five locations signifying clear signatures of upwelling (Fig. 3). Along 10°N 75.5°E, uplifting of the isothermal lines (19° to 27° C) occurred around 100 m as an indication of surface zone upwelling. Upwelling signatures in the upper subsurface zone, where the uplifting of thermocline bottom layer occurred around 50 and 75 m were observed at two stations, along 13° N 72° E and 19° N 70° E. The signature of lower subsurface upwelling with clear upsloping of the isothermal lines of ≤ 15° C was prominent along 8°N 75°E and 17° 71°E.

Sea surface salinity (SSS) during summer monsoon varied between 34.2 and 37. It showed an increasing trend towards north with lesser gradients (Fig. 4) resulting in a higher SSS in the northern part (36.4 ± 0.5) when compared to the southern part (35.3 ± 0.4). The average SSS found during this period was 35.7 ± 0.7. The upsloping of the isohaline in the vertical profiles of salinity gave clear indication of the upward movement of the water mass from subsurface to surface layer, thus corroborating the occurrence of upwelling identified through temperature profiles.

The MLD depth varied greatly and ranged between 20 and 53 m. Transect wise, MLD was minimum along 8° N (28.4 ± 6.2 m) and maximum along 15° N (35.8 ± 5.7 m). The depth range of the bottom of thermocline layer also varied and was between 149 and 273 m with an average of 194 ± 34 m. It showed a gradual increasing tendency towards north (163 ± 16, 170 ± 16, 186 ± 16,197 ± 22, 203 ± 12, 225 ± 44 and 246 ± 24 m along 8°, 10°, 11.5°, 13°, 15°, 17° and 19° N, respectively).

4.1.1.2. Fall inter monsoon

During this period, the SST varied between 27.7- 29.2° C with an average value of 28.5 ± 0.3° C. Along different latitudes no prominent trend was noticed in the SST distribution. The coastal stations experienced relatively low temperature compared to oceanic stations (Fig. 6). In the vertical profile of temperature, an intense stratification was observed in the upper 100 m. Along 10° N 73° E, the SST was relatively lower and an upsloping of isothermal lines were observed in this region. Low sea surface height along with anticlockwise geostrophic current was observed in the CCAR global near real-time altimeter geostrophic velocity vector image produced from Jason, TOPEX / Poseidon (T/P), Geosat Follow-On (GFO), ERS-2 and Envisat altimeter data (Fig. 7). This clearly indicated the occurrence of a cold core eddy region which is particularly termed as Lakshadweep Low (LL) and a unique feature of this region.

SSS ranged between 33.7 and 36.6 with an average value of 35.4 ± 0.7. In the vertical profile of salinity marked variation was observed mostly in the upper 100 m along 8° - 11.5° N and in upper 200 m along 13°N. A subsurface salinity maxima was observed along all transects at about 50 m depth (Figs. 8 and 9). The changes were very marginal in deeper layers.

The MLD varied widely from 11 to 62 m with an average depth of 37 ± 15 m. Latitude wise, the MLD exhibited a deepening tendency towards south. The shallow MLD in coastal stations (29 ± 9 m) gradually deepened towards the oceanic stations (52 ± 10 m). Depth range of bottom layer of TC also varied from 131 to 206 m. It also showed a deepening tendency towards south.

4.1.1.3. Winter monsoon

SST showed a gradual decrease from south to north (Fig. 10). Along 15°N, it was 29°C and at 17°N, it ranged between 28.2 and 28.8°C. Relatively low SST (~27.5°C) was recorded along 19°N, and the lowest value was observed along 21°N (25.7°C). The upper 200m layer was intensely stratified, with a strong vertical thermal gradient of 11–14°C along 15° and 17° N. Along 19° and 21°N, this value was between 8 and 9 °C (Fig 10). MLD ranged from 21 to 63 m, with an average of 45 ± 12 m. The minimum was observed along 17° N and the maximum along 21°N. A marked difference in MLD was evident between the northern (49±12 m) and southern (40±12 m) regions. The bottom of the thermocline layer varied greatly between stations, ranging from 194 to 314 m. The TC layer progressively deepened from south to north (217 ± 29, 220 ± 48, 261 ± 55 and 297 ± 12m along 15°, 17°, 19° and 21°N transects, respectively;) Spatial variation in SSS was marginal (34.6–36.6), and the gradients decreased towards the north (Fig. 11).

4.1.2. Bay of Bengal

4.1.2.1. Summer monsoon

During SM, SST ranged between 26 and 29.5°C with an average value of 28.3 ± 0.9°C. Along different transects, the average SST values showed less variation with relatively high values along southern transects (28.5 ± 1, 28.8 ± 0.4, 28.1 ± 0.9 and 27.7 ± 1°C along 11°, 13°, 15° and 17°N transects, respectively). Along all transects, the oceanic stations had relatively higher SST than the coastal stations (Fig. 13). The vertical profile showed a continuous drop in temperature with increasing depth and the gradient was maximum in the upper 200 m depth (Fig. 13). The signatures of coastal upwelling with the uplifting of isothermal lines was observed along all the transects from 11° to 15°N (Fig. 13). Along 13° and 15° N, the oceanic stations experienced higher SST than the coastal stations. Along 17° N, SST was relatively lower along 17°N 84°E and the doming of temperature profile was also observed in this region. The temperature profile based on the average value of all the sampling locations showed a difference of ~22°C in the upper 1000 m water column (Fig. 15).

The SSS during this period ranged between 32.5 – 34.4 with an average of 33.8 ± 0.5. The vertical profile of salinity showed a marked difference within the upper 75 m along all transects (Fig. 14). An uplifting of the isohaline (34.5) was observed along the coastal stations of 11° - 15°N. This phenomenon further supported the signatures of upwelling in the coastal stations as found from the uplifting of isothermal lines (Fig. 14). Along 17° N, SSS was relatively higher at 17°N 84°E. The low SST and higher SSS along with doming of temperature profile indicated the occurrence of a cold core eddy in this region.

Muraleedharan et al. (2007) reported the occurrence of coastal upwelling, cold core cyclonic eddy region at 17°N 84°E and the presence of warm gyre along the oceanic stations at 13° and 15° N during this period.

. During this season MLD was relatively deep in most of the region. It ranged between 20 and 81 m with an average of 51 ± 19 m. The MLD was deeper along 13° and 15°N (60 ± 22 and 59 ± 22 m, respectively) than their northern and southern counterparts (43 ± 7 m and 37 ± 10 m at 17° and 11°N respectively). The coastal stations were characterized with relatively cool waters and shallow MLD whereas in the oceanic region, the MLD deepened with relatively high temperature. The depth of bottom of the thermocline layer varied between 126 and 214 m. It was relatively deeper along 13° and 15°N (175 ± 14 and 190 ± 25 m respectively) compared to 11° and 17°N (153 ± 15 and 154 ± 29 m respectively).

4.1.2.2. Fall inter monsoon

Fall intermonsoon is described as the transitional period between summer and winter monsoon. Though the average wind speed during this season was 5 ± 2.5 m sec^{-1}, it varied greatly along different transects. Along 19°N, the speed was maximum (7.9 ± 2.7 m sec^{-1}) and along 13°N it was minimum (2.9 ± 1.5 m sec^{-1}). Warm surface (SST >28.3) waters prevailed in the entire region during this season. The SST ranged from 28.4 to 29.8° C with an average of 29.1 ± 0.4°C, which was higher than that recorded during SM and WM. SST showed an increasing tendency from north to south (Fig. 16). The vertical profile of temperature showed a wide variation along depths with relatively higher gradients in the upper 250 m (Figs. 16 & 18).

The SSS distribution showed a similar tendency as that of SST. It gradually decreased towards north (Fig. 17). The difference between the SSS of the northern most (19°N) and southern most (11°N) transect was around 3, clearly indicating the differential freshwater input into the northern and southern part of BoB. The SSS ranged from 29.3 to 34.4 with an average of 32.6 ± 1.5. This was less than the values observed during SM and WM. The vertical profile of salinity exhibited variations between the northern and southern transects. Due to the presence of low saline water in the upper layers of the northern part, the salinity gradient was much higher along the northern transects. Along 19°N, salinity difference was ~4 within the upper 75 m whereas along 11°N it was ~1.2. Salinity distribution in deeper layers, did not show much variation along different transects (Fig. 17).

The MLD ranged from 7 to 46 m with an average depth of 20 ± 11 m. There was wide variation in the MLD of northern and southern parts. Along 11° and 13°N it was 30 ± 13 and 27 ± 13 m , respectively while along 15°, 17° and 19°N same was 12 ± 4, 16 ± 11 and 18 ± 7 m, respectively. The bottom of thermocline varied between 133 and 178 m with an average of 166 ± 17 m. Transect wise, the minimum was observed at 11°N (137 ± 17 m) and the maximum at 15°N (170 ± 17 m).

4.1.2.3. Winter monsoon

During this season, relatively low SST prevailed in the entire region (Ave. 26.8 ± 0.4) compared to SM (28.3 ± 0.9°C) and FIM (29.1 ± 0.4°C). Along different latitudes, the average temperature did not show much variation (26.7 ± 0.3°, 26.4 ± 0.4°, 26.8 ± 0.3°, 27 ± 0.4°, and 27 ± 0.6° along 11°, 13°, 15°, 17° and 19°N, respectively). Along 13°N 83°E and 15°N 83°E, a marked doming of the isothermal line towards surface was observed, thus resulting in the reduction of the surface temperature in these regions (Fig. 19). A temperature inversion was observed with a slight increase of temperature in the subsurface layer compared to SST. This phenomenon was observed only during this season and was more prominent in the northern transects. The temperature profile based on the average value of all the sampling locations showed a marked difference of ~22.5°C in the upper 1000 m water column (Fig. 21).

The SSS ranged from 31.6 – 34.1 with an average of 33.1 ± 0.5. Similar to FIM, the SSS gradually decreased towards north, but the variation between the northernmost (19°N) and southernmost transect (11°N) was only ~1, less than that observed during FIM (~3) (Fig. 20). The vertical profile of salinity showed a marked gradient in the upper 100 m in the northern part and in the upper 75 m in the southern part. Similar to temperature profile, a doming of isohaline lines towards the surface was clearly seen along 13°N 83°E and 15°N 83°E indicating the occurrence of a cold core cyclonic eddy.

The MLD varied widely between different sampling locations and ranged between 11 – 69 m. The average MLD during this season was 41 ± 17 m. The MLD showed an increasing trend towards north. In general, the MLD in the coastal region was lower than that observed in the oceanic region. The bottom of TC layer also varied widely from 75 – 225 m with an average of 171 ± 32 m.

4.2. Chemical feature

4.2.1. Arabian Sea

4.2.1.1. Summer monsoon

Dissolved oxygen (DO) in surface layer did not show much variation and ranged between 4.7 and 5.7 ml l^{-1} with an average of 5.1 ± 0.2 ml l^{-1}. Along different transects, surface DO varied between 4.8 ± 0.1 (19°N) and 5.2 ± 0.3 ml l^{-1} (11°N). The vertical profile of DO exhibited a sharp gradient in the upper 100 m of southern AS and upper 200 m of northern AS (Fig. 22). Along all transects a pronounced OMZ layer (< 0.5 ml l^{-1}) was observed in varying thickness (Fig. 4). At 8° N, OMZ was less prominent and was represented by two small patches at around 200 m and 300 m, whereas at 10° N, it got thicker and extended between 300 m and 400 m. An increase in thickness of OMZ layer was evident along 11.5° and 13° N and was observed between 150 - 350 m and 250 – 800 m, respectively (Fig. 22). Towards the north along 15° N, the OMZ layer got further thickened and extended from 140 to 800 m. An acute hypoxic layer (< 0.2 ml l^{-1}) (Kamykowski and Zentara, 1990; Helly and Levin, 2004), termed as oxygen depleted water (ODW) (Naqvi et al., 2009) was also present between 150 – 200 m depth (Fig. 22). The 17° N transect experienced a thicker OMZ (150 – 1000 m) and thicker ODW layer (180 – 250 m and 450 – 750 m). The upper OMZ boundary deepened slightly along 19 °N (180 – 1000 m) and the ODW layer was quite thick mainly in the coastal stations (Fig. 22). Thus an increasing tendency in the thickness of OMZ was observed from south to north of the AS.

4.2.1.2. Fall inter monsoon

During this season, the DO in the surface layer varied between 4.5 to 5.2 ml l^{-1} with an average of 4.79 ± 0.17 ml l^{-1}. The average surface DO along 8° and 10° N was 4.6 ± 0.1 and 4.7 ± 0.1 ml l^{-1}, which was lower than the value observed along 11.5 ° and 13° N (5 ± 0.1 and 4.9 ml l^{-1}, respectively). The vertical profile of DO showed a marked gradient in the upper 100 m along all transects. (Fig. 23) Similar to SM, a strong OMZ was observed below the subsurface layers. The thickness of OMZ showed a progressive increasing tendency towards north. Along 8°N it was observed only in the coastal stations and was a few meters thick, but along 10° N it prevailed between 100 – 275 m depth. Along 11.5°N the OMZ was thicker (between 90 – 500 m depth) and the maximum thickness was seen along 13° N (between 100 – 800 m depth). Unlike SM, ODW layer was absent during this period (Fig. 23).

4.2.1.3. Winter monsoon

The surface DO did not exhibit considerable variation during this period (4.2–4.8 ml.l^{-1}). Along different transects, the average surface DO values from south towards north were as follows: 4.4 ± 0.1, 4.4 ± 0.2, 4.5 ± 0.1, 4.3 ± 0.1 ml l^{-1} at 15°, 17°, 19° and 21°N respectively. Though the variation in surface DO was negligible, a marked gradient was observed in the vertical profile along all transects, with a pronounced OMZ layer (<0.5 ml l^{-1}) below subsurface waters (Fig. 24). Along 15°N (southern transect), the OMZ occurred between 120–1000 m. It was acute (ODW< 0.2 ml l^{-1}) between 280–400 m at coastal stations and from 150–400m at the oceanic stations (Fig. 24). Along 17°N, the OMZ prevailed from 150 to 1000 m, and the ODW was observed between 200–775 m. In the northern part along 19°N, the ODW was found to extend between

200–820 m, while along 21°N, it was found between 180–800 m (Fig. 24). Thus, an increasing trend in the thickness of the ODW layer was observed from south to north of AS during this season.

4.2.2. Bay of Bengal

4.2.2.1. Summer monsoon

A marked variation in surface DO was observed which ranged between 3.5 to 4.79 ml l^{-1} with an average of 4.42 ± 0.25 ml l^{-1}. Along all transects, the surface DO was relatively low in the coastal stations compared to the oceanic stations (Fig. 25). The minimum value was observed along 17°N 84°E. The vertical profile of DO showed a marked gradient in the upper 100 m water column (Figs. 15 & 25). A thick layer of OMZ was present along all transects below the subsurface layer and its thickness gradually increased from south to north. Along 11° and 13°N, it prevailed between 100 – 500 and 100 – 650 m, respectively, whereas at 15° and 17° N it was observed between 100 – 675 and 75 – 675 m, respectively. An acute OMZ (ODW< 0.2ml l^{-1}) was present mostly along the coastal stations at all transects except at 11°N and the thickness was relatively more along 13° and 15°N. The DO values showed an increasing tendency below 400 m (Fig. 25).

4.2.2.2. Fall inter monsoon

Surface DO did not show much variation and ranged between 4.02 to 4.88 ml l^{-1} with an average of 4.44 ± 0.16 ml l^{-1}. From south to north (except at 19°N), a tendency for increased surface DO distribution was seen (4.39 ± 0.04, 4.4 ± 0.07, 4.5 ± 0.17, 4.53 ± 0.21 and 4.37 ± 0.15 ml l^{-1} at 11°, 13°, 15°, 17° and 19°N, respectively) . Similar to SM, a marked gradient in the vertical profile was prominent at upper 100 m (Fig. 26). A thick layer of OMZ was evident below subsurface layer and it gradually increased from south to north. Along 11°N, it ranged between 140 to 580 m whereas at 19°N it was between 75 and 775 m (Fig. 26). The ODW layer was also prominent during this season and the thickness varied along the northern and southern parts of BoB. From 11° to 15° N, ODW thickness was only a few meters while along 17°N it was ~300 m (150 – 450 m). Along 19°N it was seen from 80 to 320 m in the coastal stations (Fig. 26).

4.2.2.3. Winter monsoon

During this season, the surface DO varied from 4.4 to 5.3 ml l^{-1}. The average DO content was 4.7 ± 0.2 ml l^{-1} which was higher than those observed during both SM (4.42 ± 0.25 ml l^{-1}) and FIM (4.44 ± 0.16 ml l^{-1}). Along different transects, the DO was relatively higher in the southern parts (4.72 ± 0.09, 4.99 ± 0.21 and 4.76 ± 0.32 ml l^{-1} at 11°, 13° and 15°N, respectively) than in the northern part (4.66 ± 0.17 and 4.67 ± 0.04 ml l^{-1} at 17° and 19°N, respectively) (Fig. 27). The vertical profile exhibited a marked gradient in the upper 75 m in the southern part and upper 120 m in the northern part. Similar to both SM and FIM, a thick layer of OMZ prevailed below subsurface layer and it gradually increased towards north (Fig. 27). The ODW layer was absent along 11° and 13°N while along 15°N it was observed as a thin layer in the coastal and oceanic stations. In the northern part along 17° and 19°N, the thickness of this layer was greater than 100 m. Below 500 m depth, the DO value showed a gradual increasing pattern as compared to the low values observed in the mid-depth layers (Figs. 21 & 27). Similar to temperature and salinity profiles, the isopleths of DO domed towards surface along13°N 83°E and 15°N 83°E, resulting in cool, high saline, less oxygenated region and thus signifying the occurrence of a cold core eddy.

4.3. Statistical analysis

The Mann-Whitney U test was done between the average surface values of the physicochemical variables of AS and BoB during different seasons. In case of SST, there was no significant variation ($P > 0.05$) between the values in AS and BoB, but the SSS values showed a significant variation ($P < 0.05$). Similar to SST, there was no significant variation between the surface DO values in AS and BoB ($P > 0.05$). Both the MLD and bottom of TC layer depths did not show any significant difference between AS and BoB ($P > 0.05$).

4.4. Summary

Spatial distribution of SST showed a general decreasing tendency towards north (i.e. increasing distance from the equator) during most of the seasons in both AS and BoB.. A strong stratification with intense vertical thermal gradient was observed in the upper layers of both AS and BoB though the intensity of the stratification differed both temporally and spatially. Both in AS and BoB the distribution of SSS exhibited an opposite trend to that of SST. In AS, the SSS generally increased towards north, whereas in BoB it showed a decreasing tendency towards north. Irrespective of seasons, the SSS was lower in BoB and this resulted in a significant variation between AS and BoB. In the vertical profile, an intense salinity stratification with marked gradient in upper layers was observed in BoB and these gradients were relative high when compared to that of AS. Regardless of seasons, the existence of a thick OMZ below subsurface layers was a remarkable feature in both AS and BoB and the thickness gradually increased towards north. In AS, the signature of upwelling was well marked in some regions and it was strong during the SM. During FIM, a cold core eddy which is generally designated as Lakshadweep low was observed in south eastern AS. In BoB, signature of coastal upwelling was observed during SM and during the winter monsoon, features of cold core eddy was prominent. In both AS and BoB, the MLD and the depth of bottom of TC varied both temporally and spatially, depending on the physical processes active in upper layers.

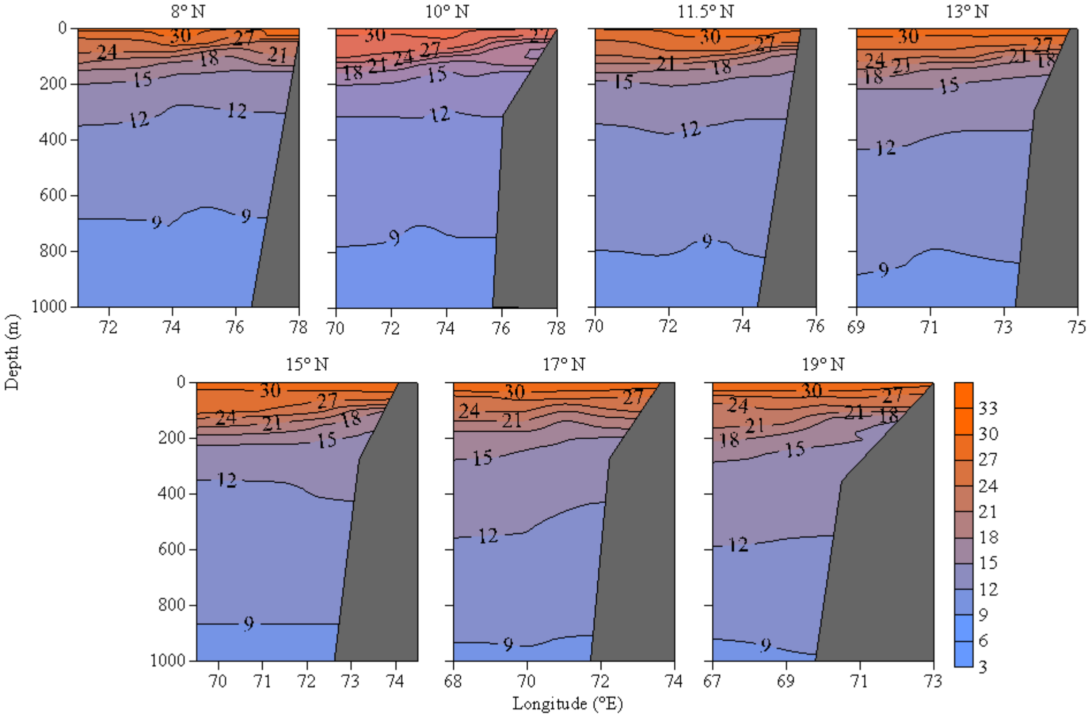

Figure 3. Vertical distribution of temperature (°C), along different latitudinal transect in the upper 1000 m of the Arabian Sea during summer monsoon.

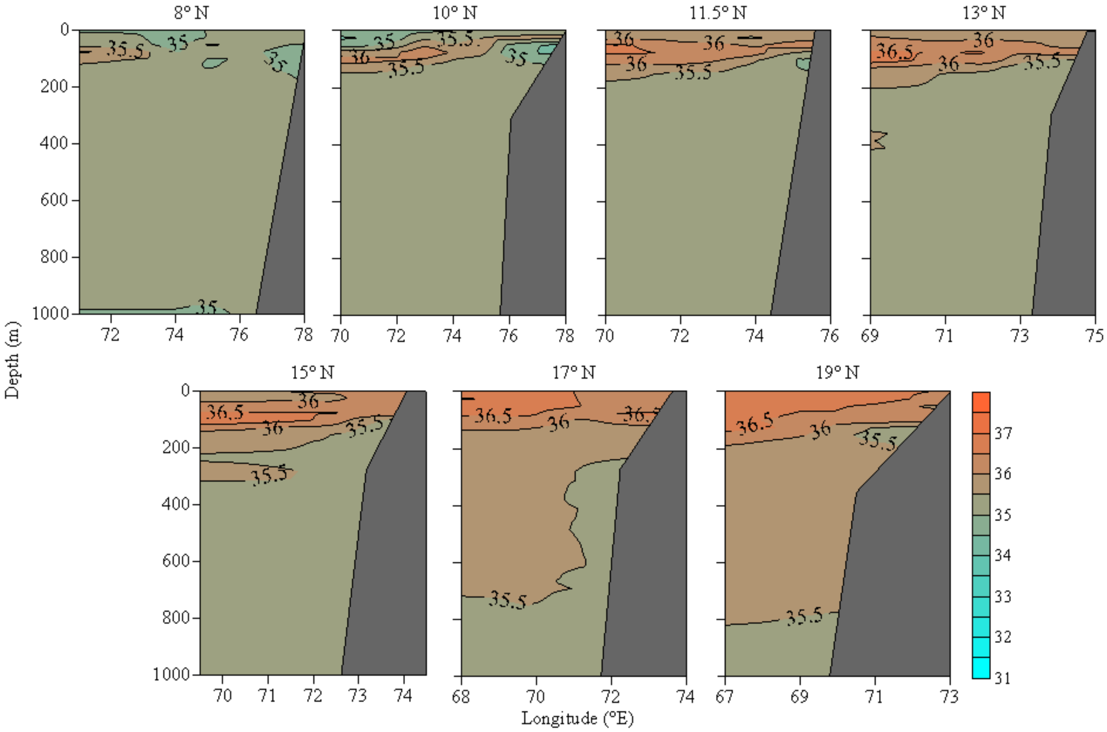

Figure 4. Vertical distribution of salinity, along different latitudinal transect in the upper 1000 m of the Arabian Sea during summer monsoon.

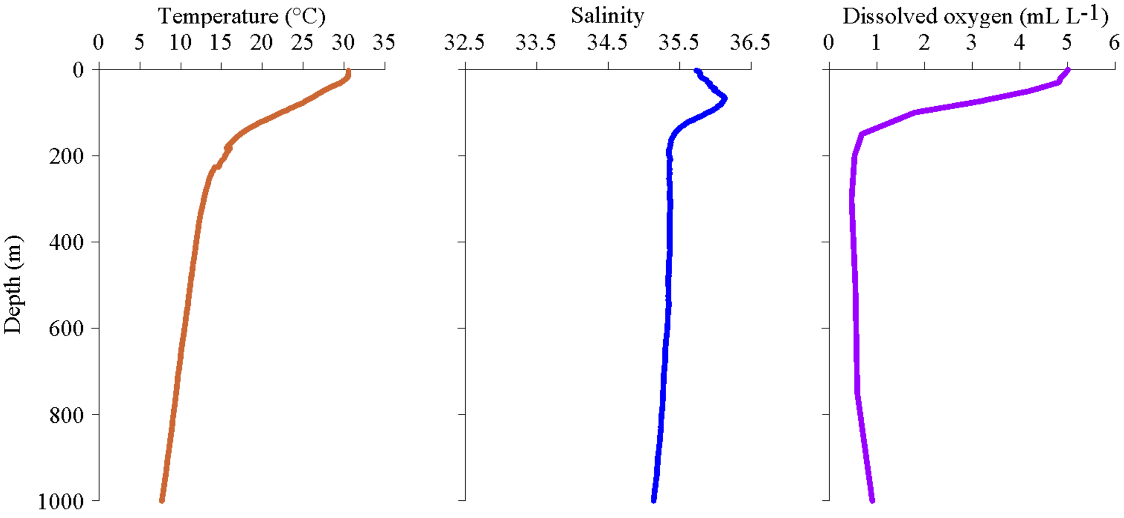

Figure 5. Vertical profiles of the physicochemical variables, in the upper 1000 m of the Arabian Sea during summer monsoon.

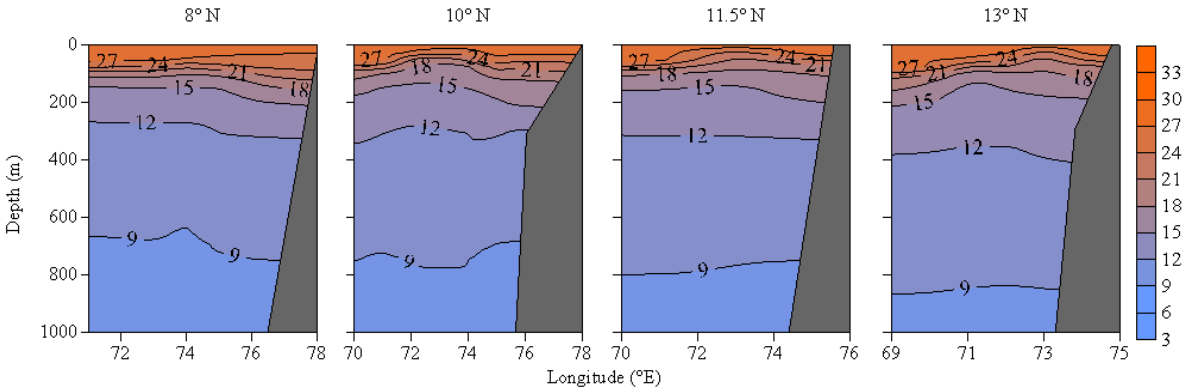

Figure 6. Vertical distribution of temperature (°C), along different latitudinal transect in the upper 1000 m of the Arabian Sea during fall inter monsoon.

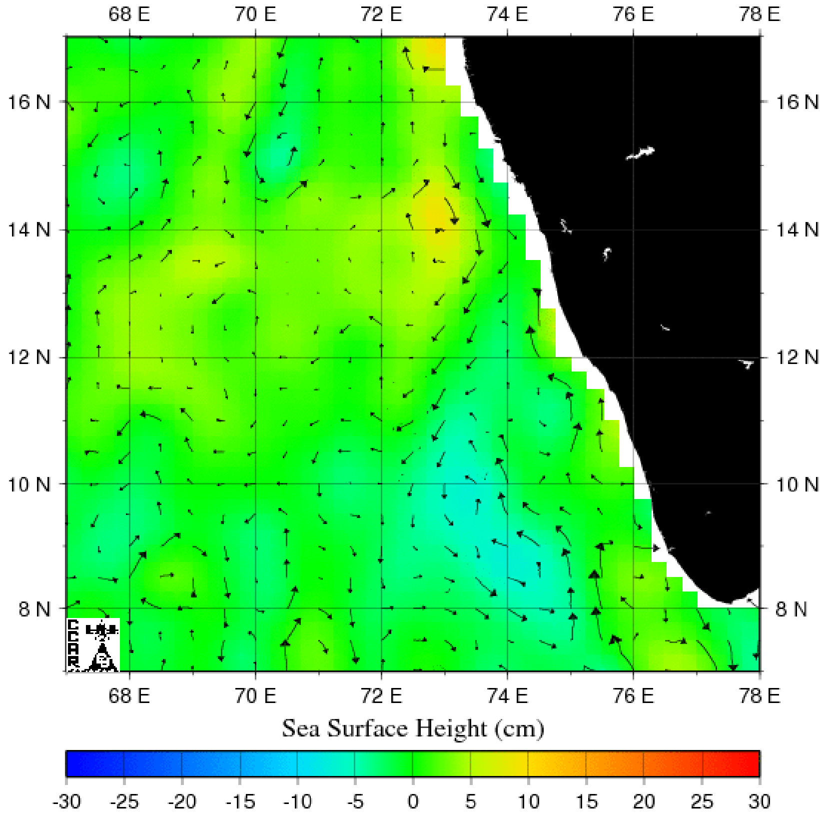

Figure 7. Merged altimetric sea surface height anomaly from Jason, TOPEX / Poseidon (T/P), GFO, ERS-2 and Envisat overlaid with geostrophic currents from SSHA in Arabian Sea during fall inter monsoon.

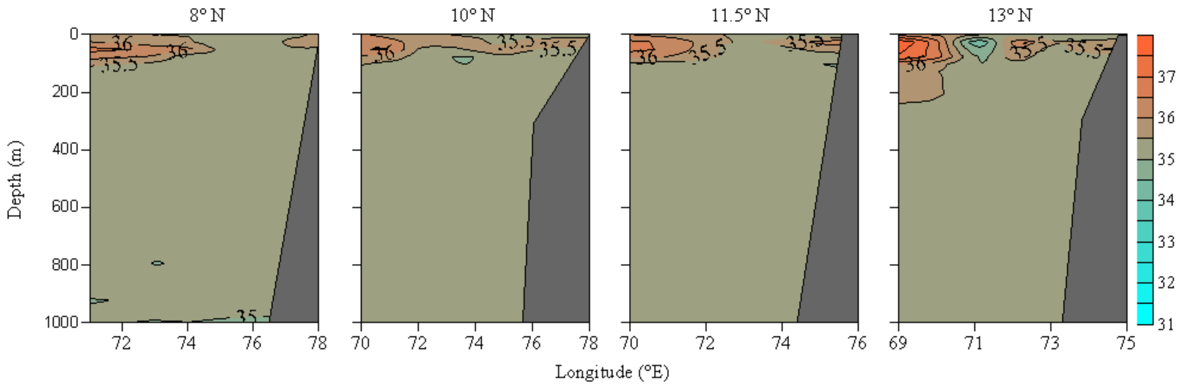

Figure 8. Vertical distribution of salinity, along different latitudinal transect in the upper 1000 m of the Arabian Sea during fall inter monsoon.

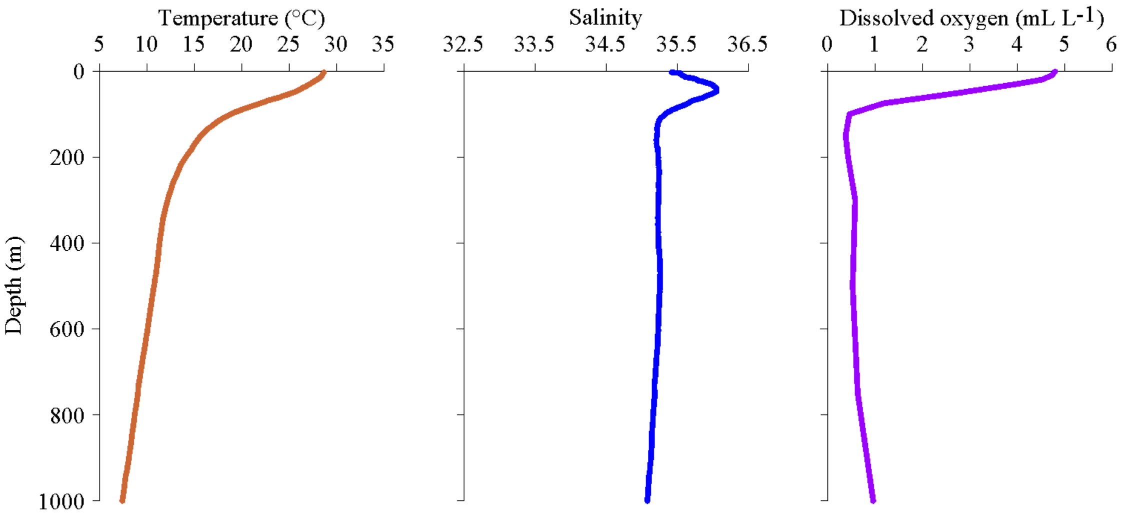

Figure 9. Vertical profiles of the physicochemical variables, in the upper 1000 m of the Arabian Sea during fall inter monsoon.

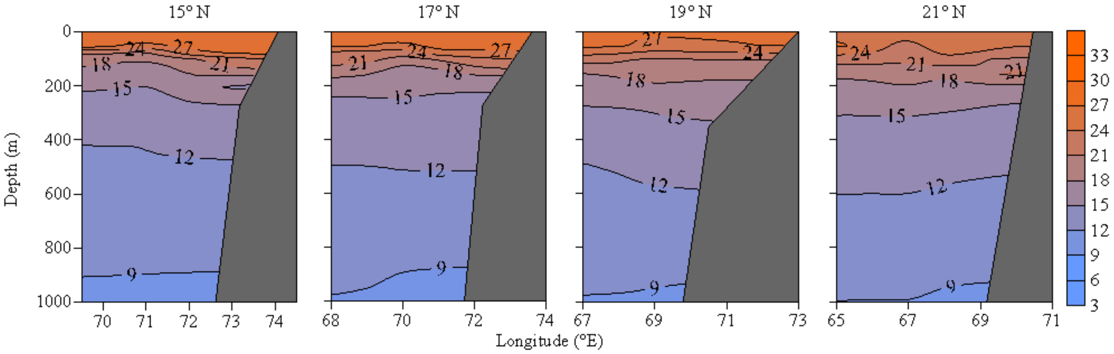

Figure 10. Vertical distribution of temperature (°C), along different latitudinal transect in the upper 1000 m of the Arabian Sea during winter monsoon.

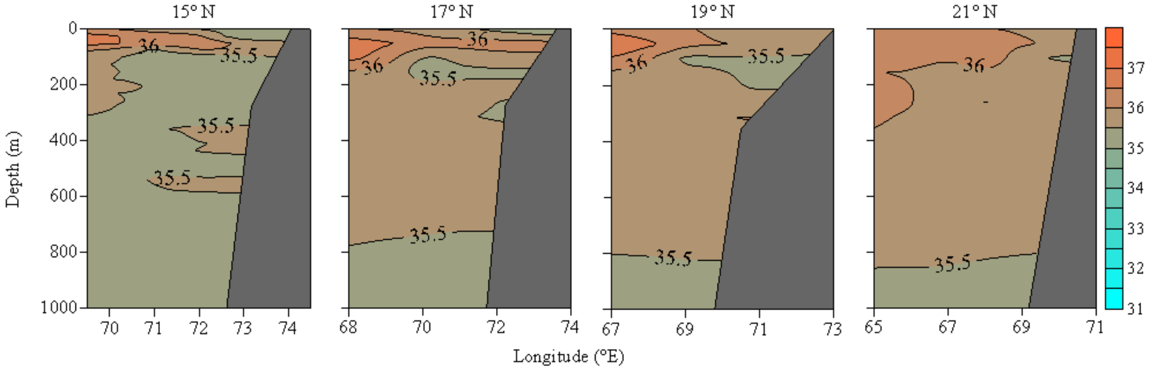

Figure 11. Vertical distribution of salinity, along different latitudinal transect in the upper 1000 m of the Arabian Sea during winter monsoon.

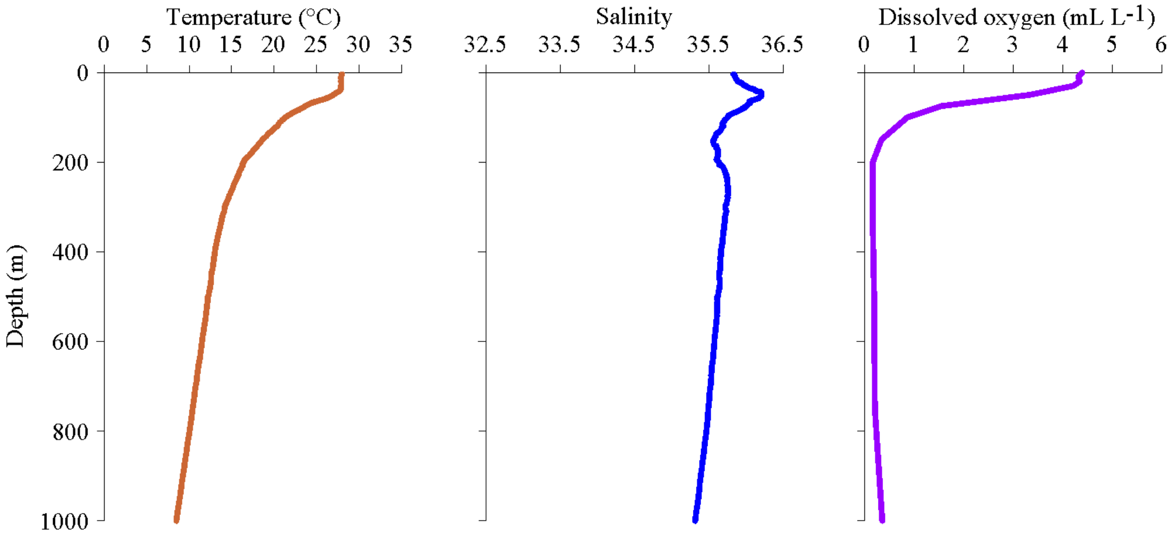

Figure 12. Vertical profiles of the physicochemical variables, in the upper 1000 m of the Arabian Sea during winter monsoon.

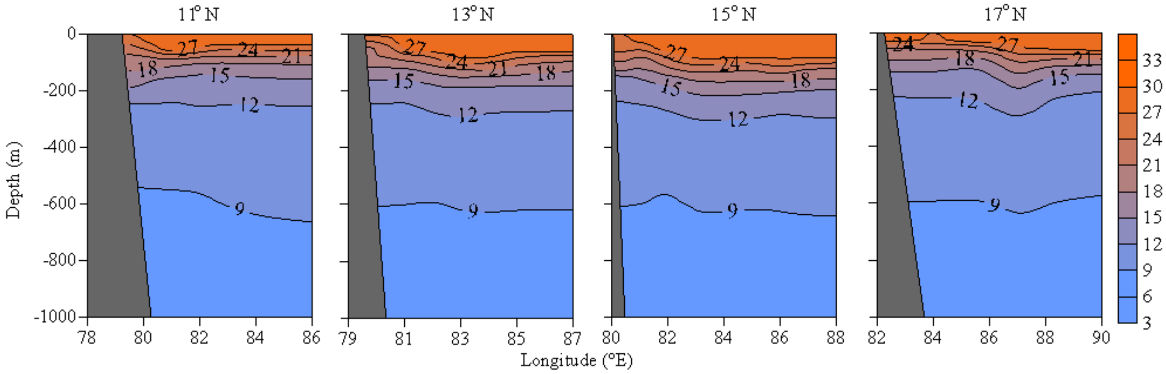

Figure 13. Vertical distribution of temperature (°C), along different latitudinal transect in the upper 1000 m of the Bay of Bengal during summer monsoon.

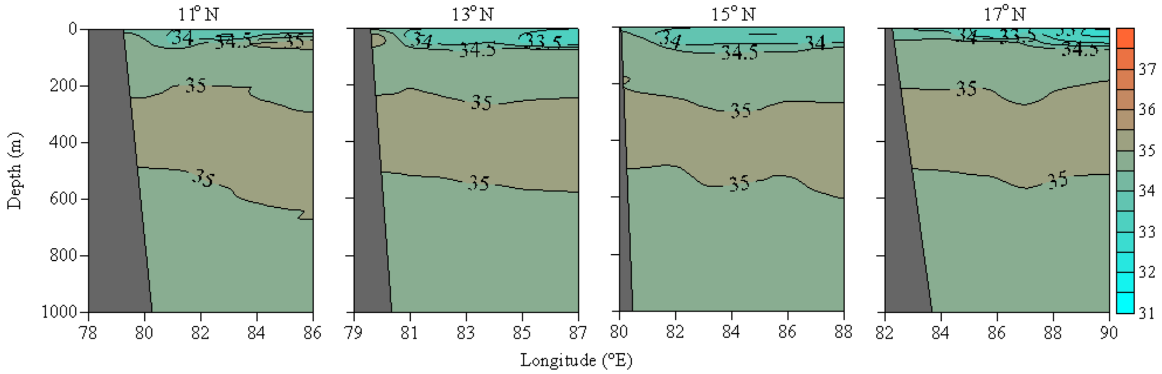

Figure 14. Vertical distribution of salinity, along different latitudinal transect in the upper 1000 m of the Bay of Bengal during summer monsoon.

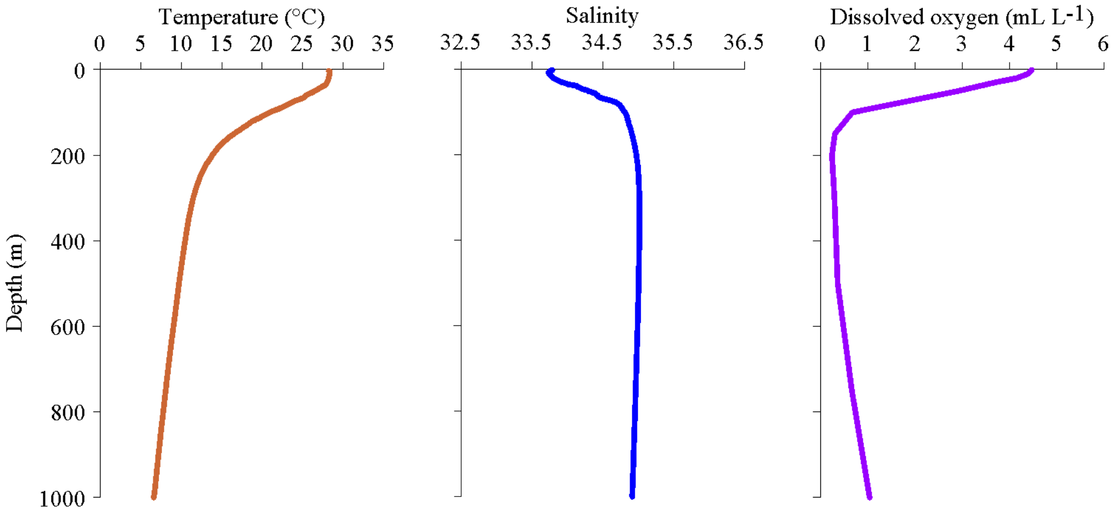

Figure 15. Vertical profiles of the physicochemical variables, in the upper 1000 m of the Bay of Bengal during summer monsoon.

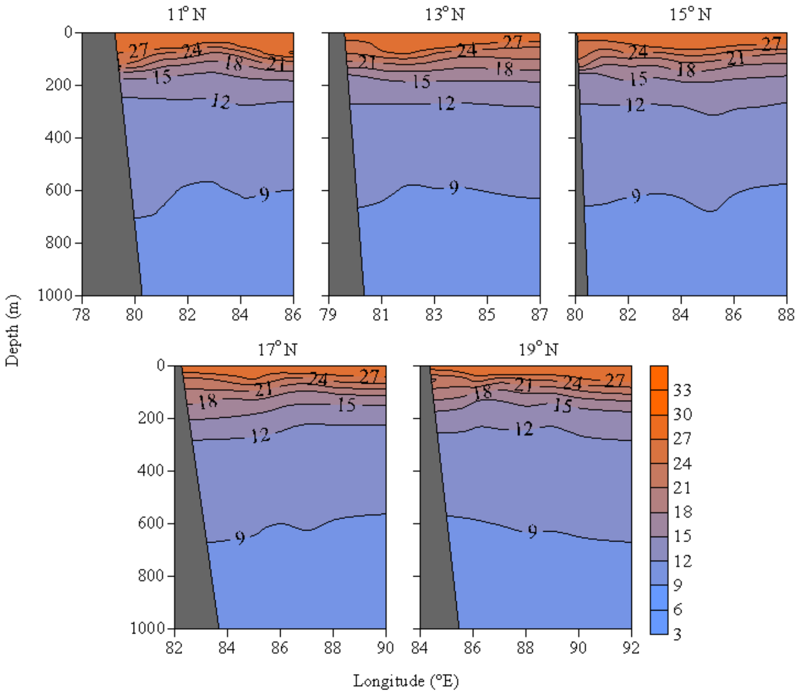

Figure 16. Vertical distribution of temperature (°C), along different latitudinal transect in the upper 1000 m of the Bay of Bengal during fall inter monsoon.

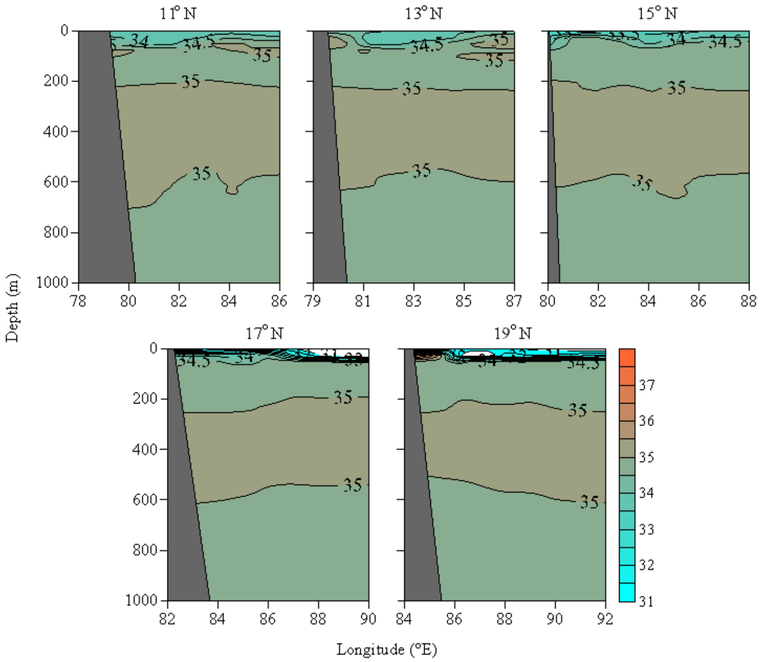

Figure 17. Vertical distribution of salinity, along different latitudinal transect in the upper 1000 m of the Bay of Bengal during fall inter monsoon.

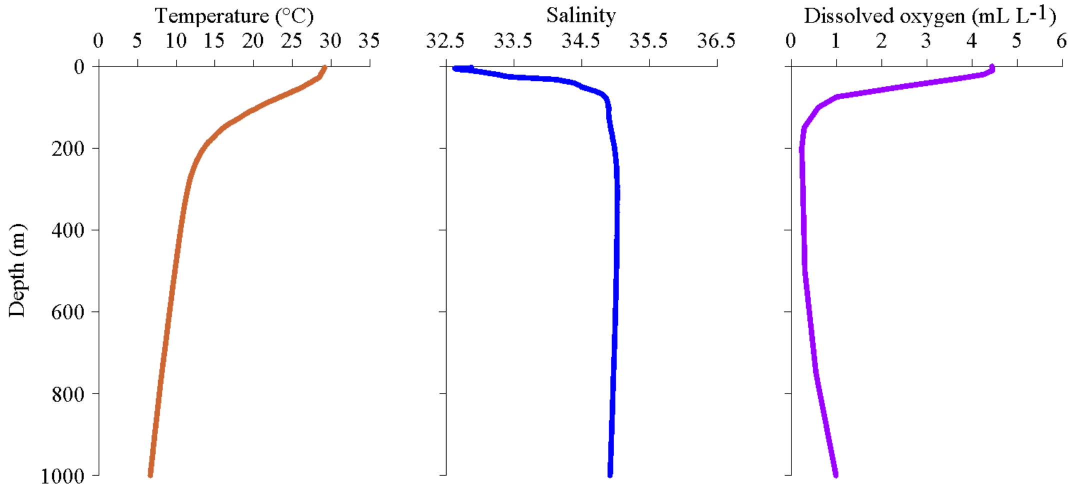

Figure 18. Vertical profiles of the physicochemical variables, in the upper 1000 m of the Bay of Bengal during fall inter monsoon.

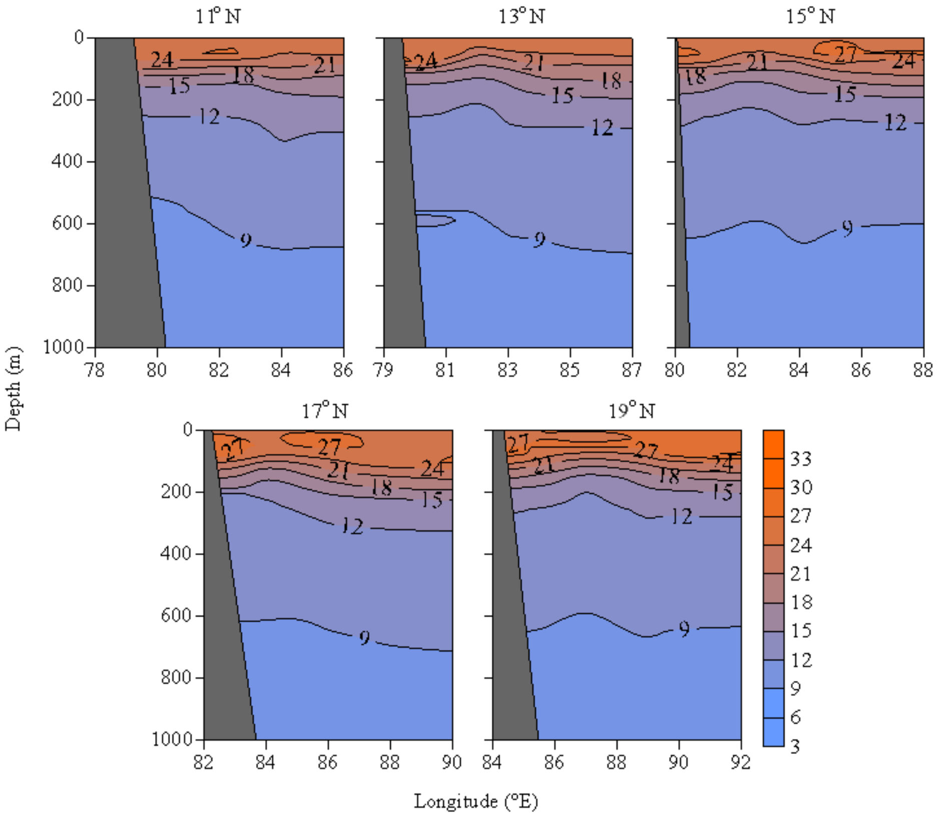

Figure 19. Vertical distribution of temperature (°C), along different latitudinal transect in the upper 1000 m of the Bay of Bengal during winter monsoon.

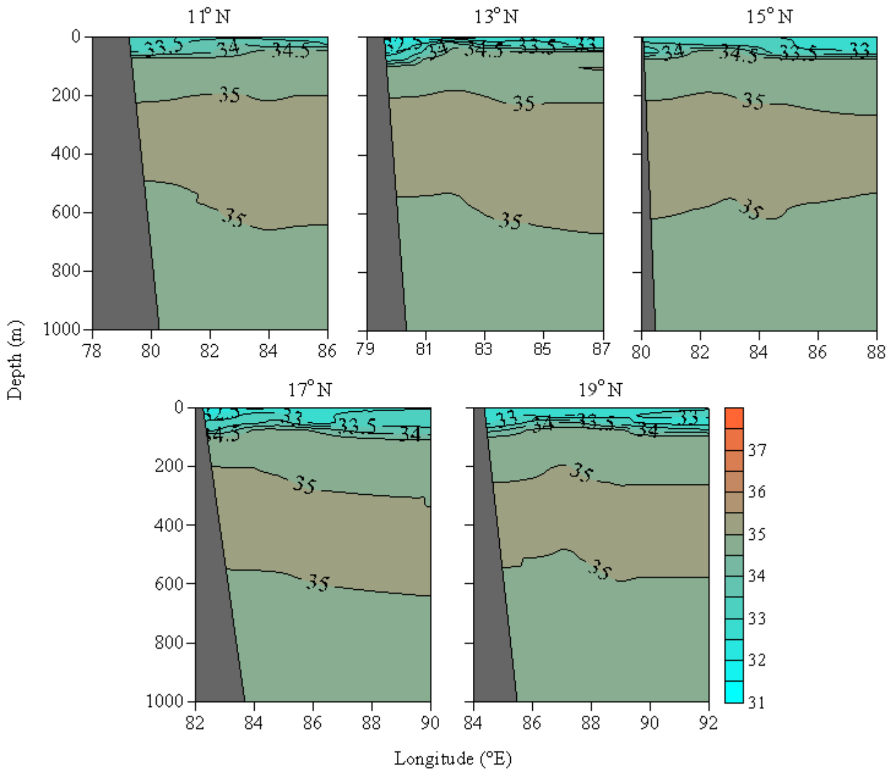

Figure 20. Vertical distribution of salinity, along different latitudinal transect in the upper 1000 m of the Bay of Bengal during winter monsoon.

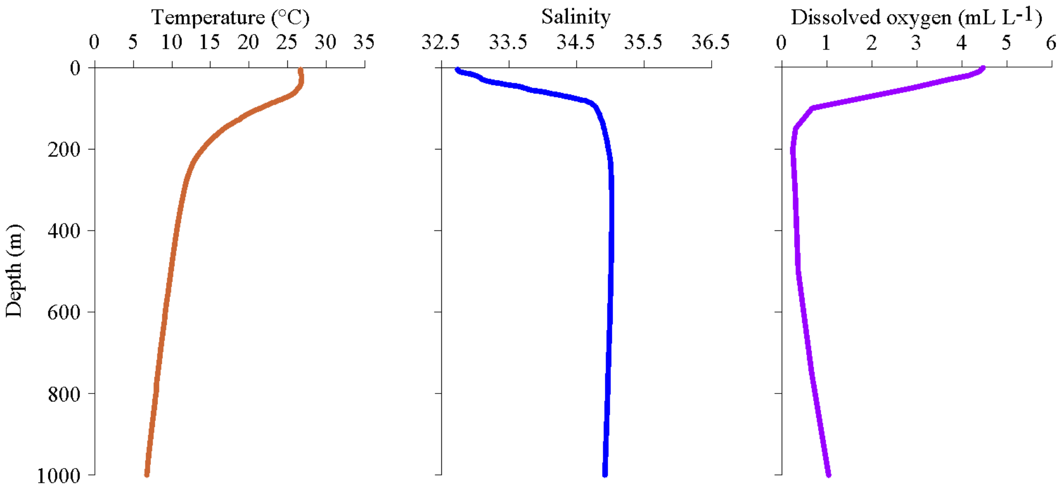

Figure 21. Vertical profiles of the physicochemical variables, in the upper 1000 m of the Bay of Bengal during winter monsoon.

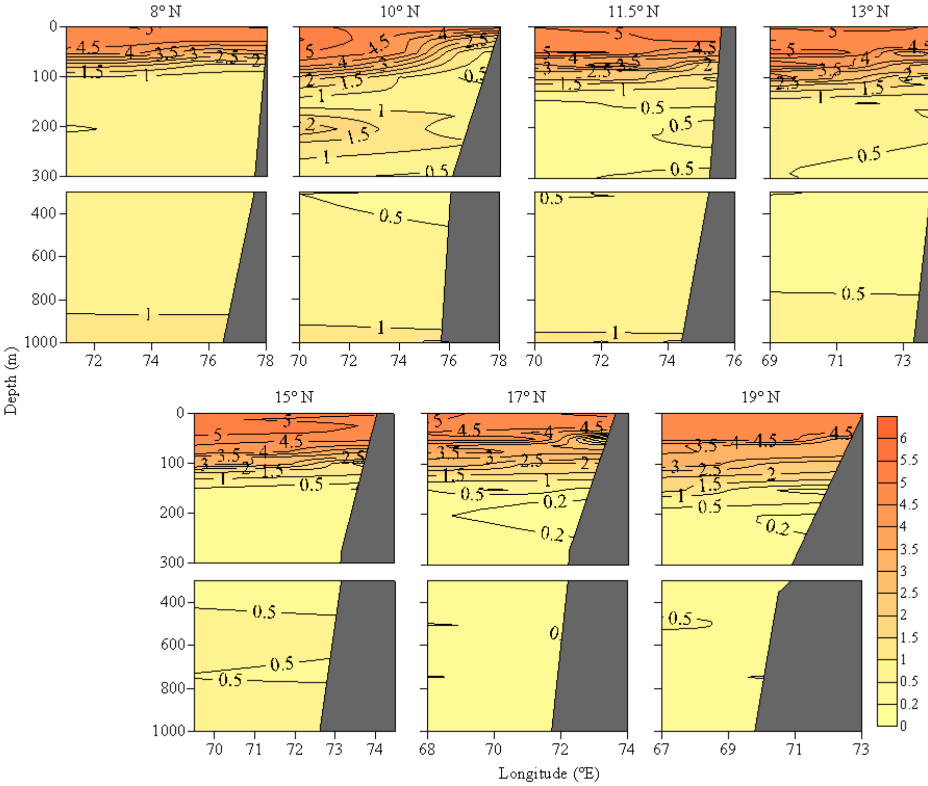

Figure 22. Vertical distribution of dissolved oxygen (ml l^{-1}), along different latitudinal transect in the upper 1000 m of the Arabian Sea during summer monsoon.

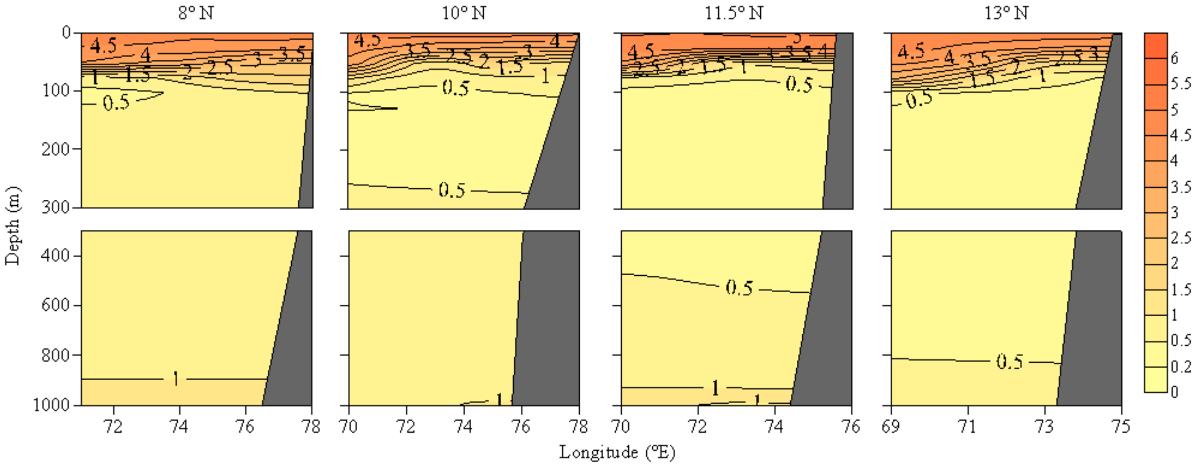

Figure 23. Vertical distribution of dissolved oxygen (ml l^{-1}), along different latitudinal transect in the upper 1000 m of the Arabian Sea during fall inter monsoon.

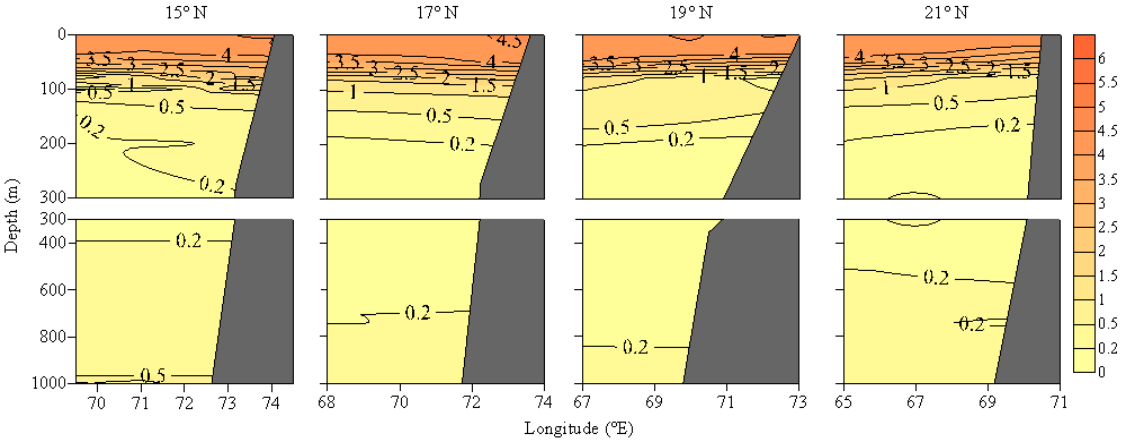

Figure 24. Vertical distribution of dissolved oxygen (ml l^{-1}), along different latitudinal transect in the upper 1000 m of the Arabian Sea during winter monsoon.

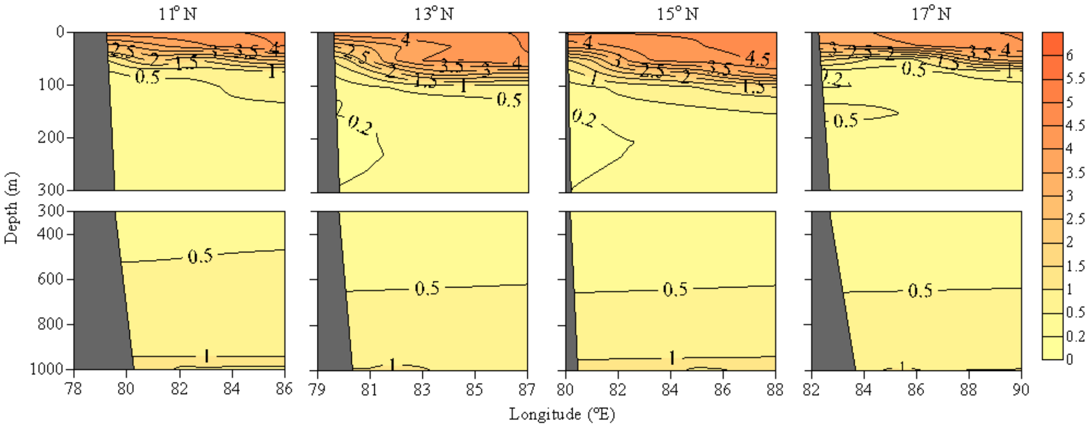

Figure 25. Vertical distribution of dissolved oxygen (ml l^{-1}), along different latitudinal transect in the upper 1000 m of the Bay of Bengal during summer monsoon.

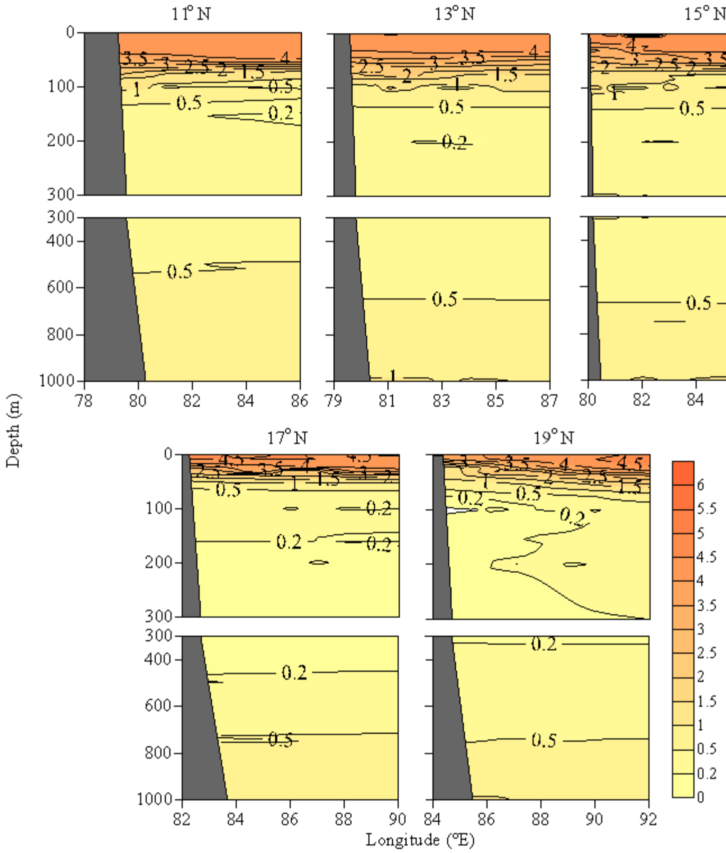

Figure 26. Vertical distribution of dissolved oxygen (ml l^{-1}), along different latitudinal transect in the upper 1000 m of the Bay of Bengal during fall inter monsoon.

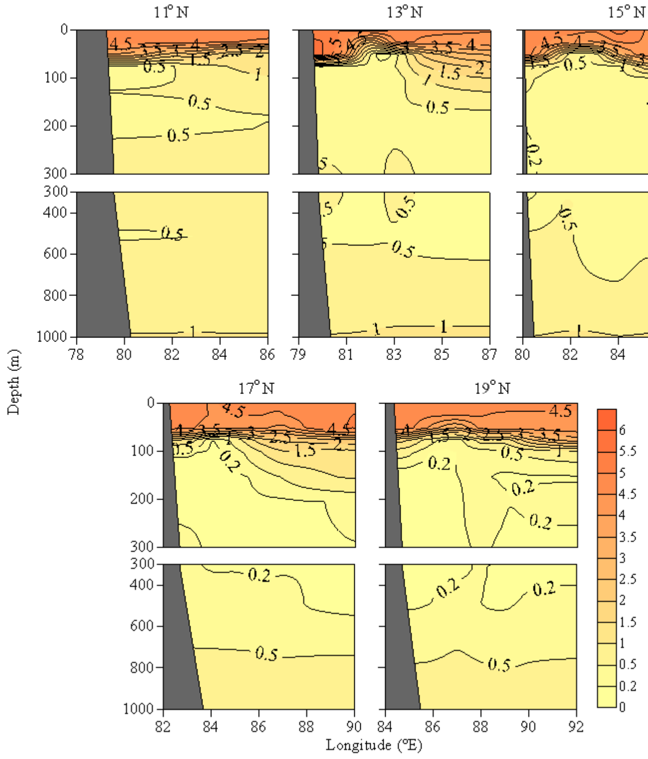

Figure 27. Vertical distribution of dissolved oxygen (ml l^{-1}), along different latitudinal transect in the upper 1000 m of the Bay of Bengal during winter monsoon.

Chapter 5

Results – Biological environment

5.1. Summer monsoon

5.1.1. Zooplankton biomass and abundance

In AS, a marked spatial variation was observed in the distribution of zooplankton biomass and abundance (Figs. 28 - 37). Biomass progressively decreased with depth, as can be seen from the average values in different layers (286 ± 190, 71 ± 47, 45 ± 47, 29 ± 20 and 8 ± 6 ml / 1000 m^3 at MLD, TC, BT – 300 m, 300 – 500 m and 500 – 1000 m, respectively). The abundance also showed a similar pattern in the vertical distribution. In the upper two layers, biomass and abundance was relatively higher in the coastal stations than the oceanic stations (Figs. 28 - 29 and 33 - 34). A surface upwelling zone with relatively higher biomass and abundance was observed along 10°N 75.5°E (Figs. 28 & 33). In this zone the biomass was 2.6 times and abundance was 7 times higher than average biomass and abundance value. In the upper subsurface upwelling zone, i.e, in TC layer, these values were close to the average values of biomass and abundance (Figs. 29 and 34). In the lower surface upwelling zones i.e. in BT – 300 m layer, the biomass and abundance values were 5.8 and 4.7 times higher than the average values. Below 300 m biomass and abundance values were relatively higher in the southern part compared to northern part (Fig. 30 and 35).

In BoB also, zooplankton biomass and abundance showed a wide variation between stations along different depth zones (Figs. 38 – 47). In MLD, it ranged between 98 to 2061 ml / 1000 m^3 with an average value of 404 ± 408 ml / 1000 m^3. In MLD of BoB, a relatively higher biomass and abundance, was observed in the upwelling stations (Figs. 38 & 43). The coastal upwelling stations along 13° and 15° N had comparatively higher biomass and abundance than the oceanic stations in the warm gyre region (1120 and 140 ml / 1000 m^3, 3327496 and 333402 ind / 1000 m^3, biomass and abundance at upwelling and warm gyre region, respectively). The cold core eddy region exhibited relatively higher biomass (670 ml / 1000 m^3) and abundance (1459828 ind / 1000 m^3) than the warm gyre region, but lower than the upwelling region. Biomass showed a decreasing tendency with depth. In TC and BT – 300 m layers, the average biomass was 143 ± 236 and 23 ± 20 ml / 1000 m^3, respectively. In case of abundance, a sharp decline was observed in BT -300 m layer (17627 ± 18389 ind / 1000 m^3) whereas in the 300 – 500 m, the average abundance was relatively higher (26155 ± 22997 ind / 1000 m^3).

5.1.2. Major groups of zooplankton

In both AS and BoB, a diverse range of zooplankton taxa were observed during the study period. The abundance of different taxa varied both spatially (between sampling stations) and vertically (between different layers). In AS, the number of zooplankton taxa decreased towards the deeper layers (24, 25, 22, 20, 19 at MLD, TC, BT – 300 m, 300 – 500 m and 500 – 1000 m, respectively). Copepod formed the dominant group throughout the region and their percentage composition varied from 73.5% (MLD) to 92.7% (300- 500 m). In MLD other than copepod, ostracod, chaetognath, fish egg and pteropod also occurred as good numbers, whereas in TC layer groups like ostracod, chaetognath and copelata shared a fairly good percentage composition (Fig. 48). In BT – 300 m layer, several zooplankton taxa i.e. foraminifera, siphonophore, polychaete, euphausiid, decapod larvae, ostracod and chaetognath shared a large percentage of the total zooplankton population. In deeper layer also, chaetognath and ostracod dominated every other zooplankton group (Fig. 48).

In BoB also copepod dominated the zooplankton groups in every depth zones. Their percentage composition varied in different layers and ranged from 75% (MLD) to 90% (300 – 500 m). In MLD, a total of 24 zooplankton taxa were present during this season. Other than copepod, chaetognath, copelata, ostracod and fish larvae formed the other major groups (Fig. 48). Abundance of fish larvae and fish egg was relatively higher in the upwelling region than regions of cold core eddy and warm gyre. In TC, a total of 23 taxa were observed among which chaetognath, ostracod, euphausiid, fish egg and copelata dominated next only to copepods. In deeper layers, comparatively less number of zooplankton taxa was observed (21, 20 and 23 at BT – 300 m, 300 – 500 m and 500 – 1000 m respectively). Ostracod was a major contributor in BT – 300 m and 300 – 500 m layers whereas copelata formed the second abundant group after copepods in 500 – 1000 m layer.

5.1.3. Contribution of chaetognath

In both AS and BoB, though the percentage composition of chaetognath varied between different depth zones, this carnivorous group always remained as an important component of the total zooplankton population. In AS, their percentage contribution was maximum at MLD (3.1%) and with increasing depth, their abundance decreased till 500 m (Fig. 51). Below 500 m, their percentage contribution showed some increase (Fig. 51). In BoB, they shared 1.7% (300 – 500 m) to 4.1% (TC) of the total zooplankton population (Fig. 52). They formed the second and third dominant group in TC layer and 300 – 500 m depth respectively.

5.1.4. Trophic relationship

The Pearson correlation coefficient (r) was calculated between the copepod and chaetognath abundance to detect their trophic relationship, followed by the linear regression analysis with a 99% confidence band to estimate the magnitude of the relationship. The Pearson correlation coefficient (r) calculated based on the abundance of chaetognaths and copepods at different stations and depth zones, revealed a significant positive correlation between the two groups in both AS ($P < 0.01$, $r = 0.85$) and BoB ($P < 0.01$, $r = 0.75$) (Fig. 53 and 54).

5.2. Fall inter monsoon

5.2.1. Zooplankton biomass and abundance

In AS, the biomass and abundance at MLD were relatively higher than other seasons (Figs. 28 & 33). The average biomass and abundance in this depth layer was 661 ± 735 ml / 1000 m^3 and 1708123 ± 2753609 ind / 1000 m^3 respectively. The maximum biomass and abundance was observed in the Lakshadweep low (LL) region at 10°N 73°E (3500 ml / 1000 m^3 and 9515000 ind / 1000 m^3). Except this region, the abundance was relatively higher in the coastal stations compared to oceanic stations. With depth, biomass gradually decreased (118 ± 57, 66 ± 41, 32 ± 15 and 10 ± 6 ml / 1000 m^3 at TC, BT – 300 m, 300 – 500 m and 500 – 1000 m respectively). Similar to biomass, abundance also progressively decreased with increasing depth. The average abundance in MLD (1708123 ± 2753609 ind / 1000 m^3) was 220 times higher compared to that at 500 – 1000 m depth (7749 ± 8225 ind / 1000 m^3).

In BoB, the upper two layers of the coastal stations experienced relatively higher biomass and abundance compared to that of oceanic stations (Figs. 38 – 39 & 43 - 44). In MLD, the maximum biomass was observed in a coastal station along 17° N (2643 ml / 1000 m^3). In both MLD and TC layer, biomass and abundance were relatively higher in the northern part extending upto 15° N (Figs. 38 – 39 & 43 - 44). In 300 – 500 m layer, maximum biomass was observed at an oceanic station along 13°N (225 ml / 1000 m^3). Compared to the upper two layers of MLD and TC (863780 ± 1029489 and 250824 ± 211545 ind / 1000 m^3, respectively), a sharp drop in abundance was observed at BT – 300 m layer (32377 ± 46635 ind / 1000 m^3) (Fig. 45). In 300 – 500 m layer, the abundance showed a slight increase (45713 ± 78818 ind / 1000 m^3) (Fig. 46). Below 500 m depth, abundance was relatively higher in the northern part compared to the southern part (Fig. 47).

5.2.2. Major groups of zooplankton

A total of 25 taxa of zooplankton were distributed in the water column in AS during this season. Diversity of zooplankton varied among different layers as well as between sampling stations. Copepod formed the dominant group sharing 61.5% (TC) to 92.3% (500 – 1000 m) of the total zooplankton population (Fig. 49). Ostracod was the second dominant group contributing 3.2% (300 – 500 m) to 49% (TC) of the population. Higher abundance of ostracod was observed only during this season. Chaetognath and copelata were the other abundant groups distributed in MLD. During this season, a higher abundance of cladocera (1.1%) was observed in TC layer (Fig. 49). Several other groups like polychaete, amphipod, euphausiid and fish egg contributed to a fair percentage in 300 – 500 m layer.

In BoB, a total of 26 zooplankton taxa were observed throughout the water column. Copepod was the dominant group with varying density along different stations and at different depth layers. Their percentage contribution ranged from 62.5% (300 – 500 m) to 90.2% (500 – 1000 m) (Fig. 49). Chaetognath, copelata, euphausiid and decapod larvae were the major groups in upper two layers. Compared to AS, the abundance of ostracod in upper two layers was very less in BoB. Below 300 m depth, chaetognath, ostracod and foraminifera were the dominant non copepod groups (Fig. 49). One of the remarkable features observed during this period was the presence of large pyrosoma colonies mostly in the deeper layers (Below 300 m). Due to their very large biovolume (up to several litres) compared to the total biovolume of all other zooplankton (few ml), their biomass and abundance values were not considered for calculating the percentage distribution of zooplankton groups.

5.2.3. Contribution of chaetognath

In AS, chaetognath formed the third abundant group after copepod and ostracod. Their abundance varied both horizontally (among sampling stations) and vertically (among layers). In the upper two layers, they contributed to 2.4 and 2.8% of the total population whereas in deeper layers, their percentage contribution was relatively less (Fig. 51). In BoB also chaetognaths formed an abundant zooplankton taxon throughout the water column and in each layer, their abundance varied spatially. Their percentage contribution varied from 0.5% (300 – 500 m) to 3% (500 – 1000 m) (Fig. 52).

5.2.4. Trophic relationship

The Pearson correlation coefficient (r) calculated based on the abundance of the carnivorous group chaetognaths and their major prey copepods at different stations and depth zones during this season also showed a significant positive correlation in both AS ($P < 0.01$, $r = 0.76$) and BoB ($P < 0.01$, $r = 0.72$) (Figs. 55 & 56). This clearly signifies the importance of copepods in the sustenance of chaetognaths in the pelagic realm.

5.3. Winter monsoon

5.3.1. Zooplankton biomass

In AS, the biomass ranged between 35 to 1524 ml / 1000 m^3 and the maximum biomass was observed along 17°N 73°E in MLD (Fig. 28). Except for this station, the biomass in MLD progressively decreased towards south. The abundance also followed more or less the same trend and was relatively higher in the northern part (Fig. 33). However, in contrast with other seasons, the abundance was relatively higher in the oceanic stations than the coastal stations (Fig. 33). In BT – 300 m layer also both biomass and abundance tend to show a gradual decrease towards south. Below 300 m, both biomass and abundance showed an opposite trend. In both 300 – 500 m and 500 – 1000 m layers, biomass and abundance were relatively higher in the southern part (Figs. 31 – 32 & 36 - 37).

In BoB, the biomass was relatively higher in the southern part at MLD, which was in contrast with the observed higher biomass in the northern part during SM and FIM. In this layer, the biomass ranged between 133 and 1454 ml / 1000 m^3 with an average of 600 ± 360 ml / 1000 m^3. With increase in depth, biomass gradually decreased (189 ± 143, 68 ± 40, 44 ± 32 and 15 ± 8 ml / 1000 m3 at TC, BT – 300 m, 300 – 500 m and 500 – 1000 m, respectively). In MLD, the biomass in the cold gyre region did not show much significant difference but abundance was 2.7 times higher than the average abundance recorded in this layer. In this layer, zooplankton abundance varied widely and ranged from 70665 to 4288720 ind / 1000 m^3 (Fig. 43). Similar to MLD, the biomass in TC layer was relatively higher in the southern BoB and the coastal stations experienced relatively higher biomass than the oceanic stations (Fig.39). In this layer, the abundance progressively increased towards south and the maximum abundance was observed at an oceanic station along 11°N (498603 ind / 1000 m^3). Compared to the upper two layers (642081 ± 925660 and 136273 ± 99576 ind / 1000 m^3 at MLD and TC, respectively) there was a sudden drop in abundance values in BT – 300 m layer (36377 ± 15093 ind / 1000 m^3). In 300 – 500 m layer, though the biomass was relatively higher in the southern part the abundance was relatively high in the northern part (Fig. 41 and 46). During this season, the abundance recorded in 300 – 500 m layer (16016 ± 10782 ind / 1000 m^3) was relatively less than that during SM (26155 ± 22997 ind / 1000 m^3) and FIM (45713 ± 78818 ind / 1000 m^3).

5.3.2. Major groups of zooplankton

A total of 25 taxa of zooplankton were observed during this season in AS. Among different depth zones their number varied between 18 (300 – 500 m) to 25 (TC). Similar to SM and FIM, copepod was the dominant group and their percentage contribution varied between 87.2% (300 – 500 m) to 96.4 %

(500 – 1000 m) (Fig. 50). Among the non copepod group, chaetognath dominated in upper three layers (MLD, TC and BT – 300 m). Foraminifera, polychaete, euphausiid, fish egg, chaetognath and ostracod were the other abundant taxa in 300 – 500 m layer. Polychaete and foraminifera contributed a fair percentage of abundance in the deeper layer also (> 500 m) (Fig. 50).

A total of 27 taxa of zooplankton were observed during this period in BoB. The abundance of different zooplankton taxa varied along different stations and also along different depths. Similar to other seasons copepod remained as dominant group and their percentage contribution ranged from 89.4% (MLD) to 95.8 (500 – 1000 m). Among non copepod groups, chaetognath, copelata and amphipod dominated in MLD. Halozoa, which was generally not present during other seasons, was observed in the MLD of some of the stations. In TC layer, several groups i.e. medusa, siphonophore, ostracod, euphausiid, chaetognath and copelata had relatively higher abundance (Fig. 50). In deeper depth zones, ostracod, chaetognath and euphausiid shared a good percentage in the occurrence.

5.3.3. Contribution of chaetognath

Chaetognath formed the major non copepod taxa in both AS and BoB during this period. In AS, it contributed to 3.5% of the total zooplankton population in MLD and with increase in depth its percentage contribution gradually decreased (Fig. 51). In BoB also, this group dominated among the non copepod zooplankton groups in the upper two layers (MLD and TC) and also below 500 m. Compared to deeper layers, its percentage contribution was relatively higher in the upper layers and varied from 1.1% (300 – 500 m) to 4% (MLD and TC) (Fig. 52).

5.3.4. Trophic relationship

Similar to SM and FIM, the Pearson correlation coefficient (r) calculated based on the abundance of chaetognaths and their major prey copepods at different stations and depth zones showed a significant positive correlation in both AS ($P < 0.01$, $r = 0.79$) and BoB ($P < 0.01$, $r = 0.72$) (Figs. 57 & 58). This significant positive correlation clearly indicates the role of copepod in the sustenance of the chaetognath community. Irrespective of season, the significant positive correlation observed between these two major and important zooplankton taxa clearly suggests their significant trophic role in the pelagic food chain.

5.4. Statistical analysis

The Mann-Whitney U test was done between the $\log_e$ transformed biomass values of AS and BoB to check whether any significant differences exists between these two major parts of the northern Indian Ocean. This test was also carried out on the abundance data. Both tests did not show any significant difference on the biomass ($P > 0.05$) or abundance ($P > 0.05$) between AS and BoB.

5.5. Summary

A significant spatio temporal variation was apparent in the distribution of biomass and abundance of zooplankton in both AS and BoB. Vertically, with increase of depth, the biomass and abundance generally decreased in both basins. During SM, relatively higher biomass and abundance was observed in the upwelling regions of the AS. In BoB, relatively higher biomass was observed in the upper layers of the coastal upwelling and cold core eddy region whereas relatively low biomass and abundance was observed in the warm gyre region. Though, some seasonal differences in biomass and abundance between AS and BoB were seen, these were statistically insignificant ($P > 0.05$). In both systems, copepod was the dominant zooplankton group though their percentage contribution varied between sampling stations. Among the non copepod taxa, chaetognath always remained as a major group in both AS and BoB. In several sampling locations they were the second abundant group. Their abundance and percentage contribution to the total zooplankton population varied both spatially and temporally. The role of copepod in sustenance of chaetognath was evident in both the basins indicating the important trophic relation existing between these two major planktonic taxa in the pelagic system.

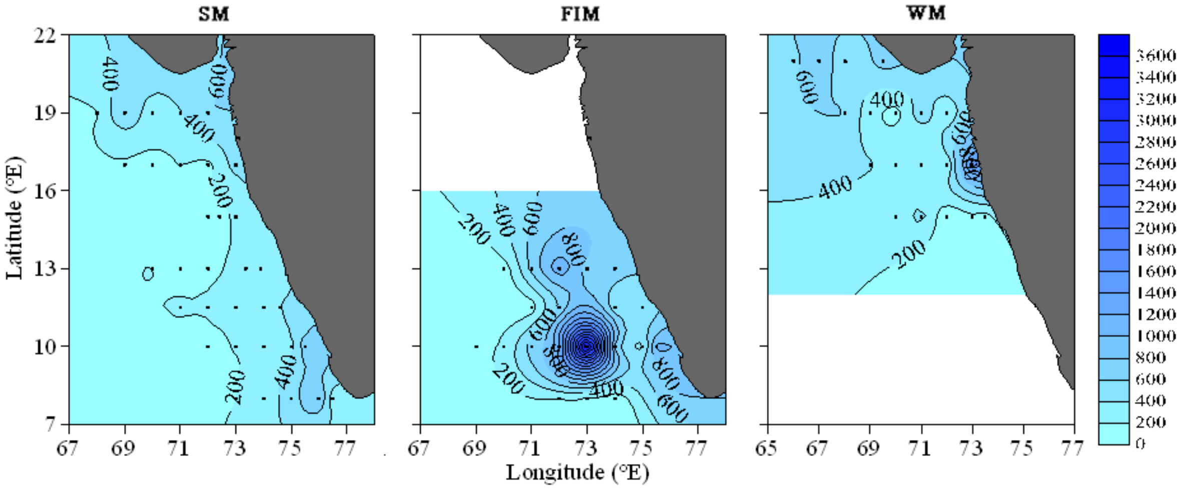

Figure 28. Distribution of mesozooplankton biomass (ml / 1000 m^3) along mixed layer depth in the Arabian Sea.

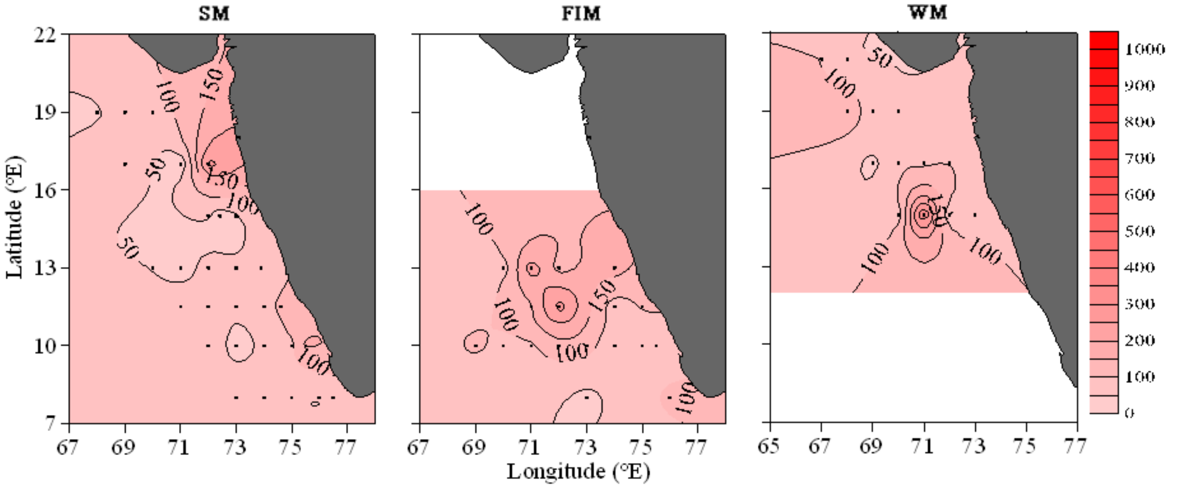

Figure 29. Distribution of mesozooplankton biomass (ml / 1000 m^3) along thermocline in the Arabian Sea.

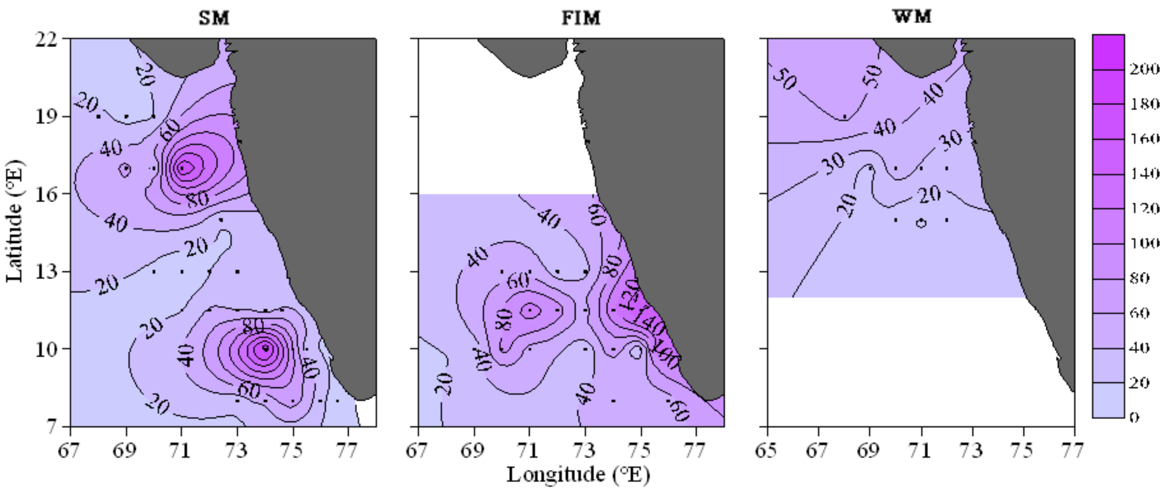

Figure 30. Distribution of mesozooplankton biomass (ml / 1000 m^3) along BT – 300 m depth in the Arabian Sea.

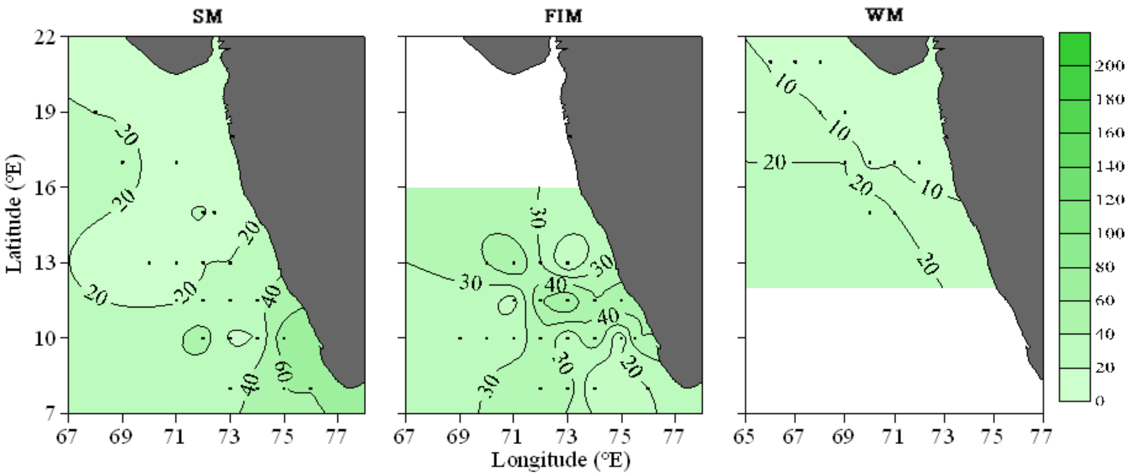

Figure 31. Distribution of mesozooplankton biomass (ml / 1000 m^3) along 300 – 500 m depth in the Arabian Sea.

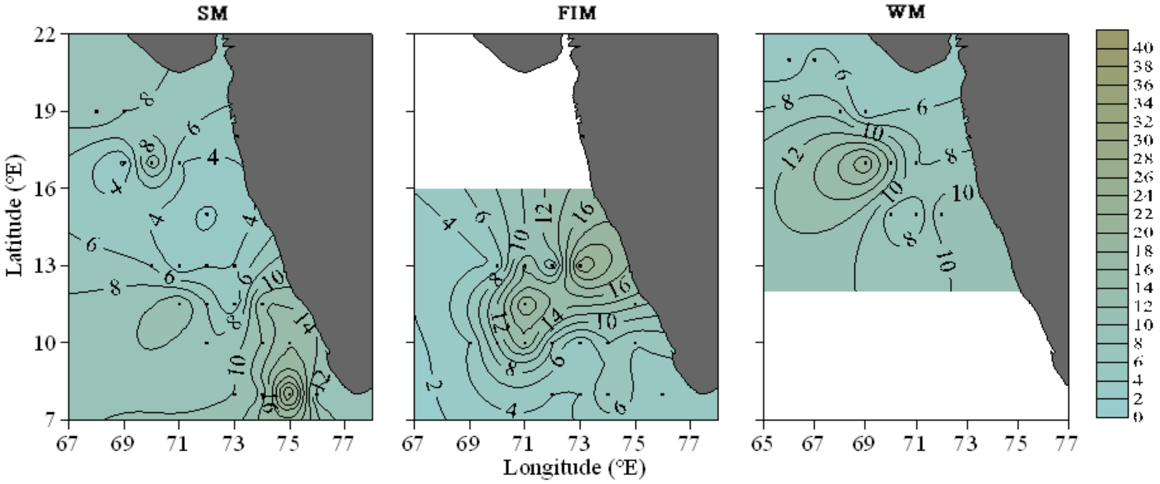

Figure 32. Distribution of mesozooplankton biomass (ml / 1000 m^3) along 500 – 1000 m depth in the Arabian Sea.

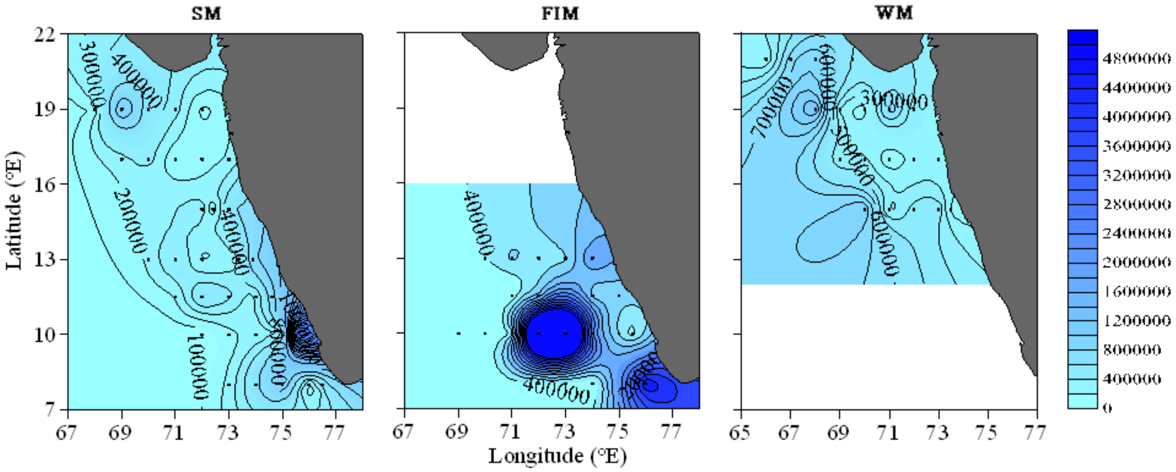

Figure 33. Distribution of mesozooplankton abundance (ind / 1000 m^3) along mixed layer depth in the Arabian Sea.

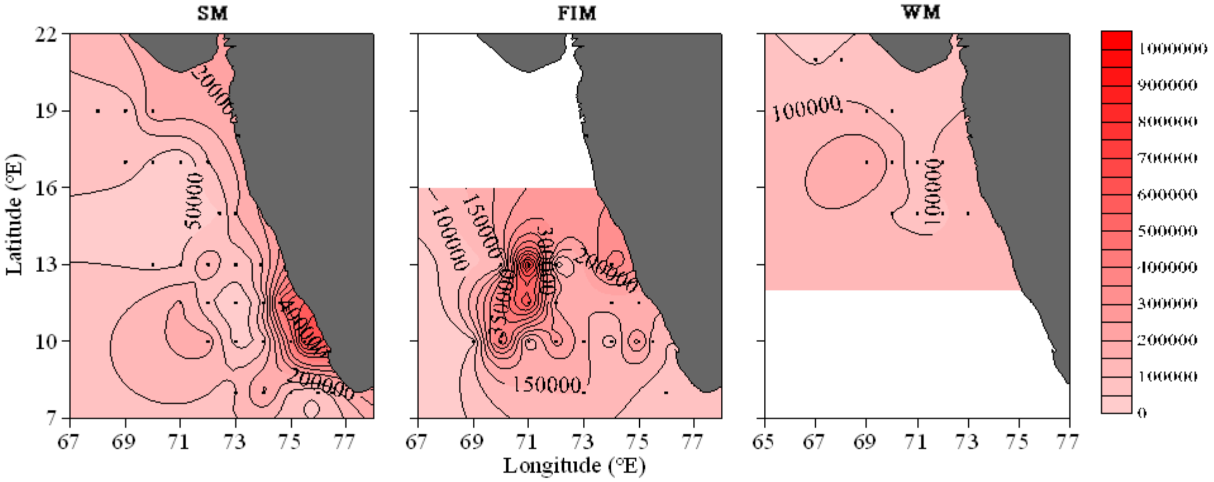

Figure 34. Distribution of mesozooplankton abundance (ind / 1000 m^3) along thermocline in the Arabian Sea.

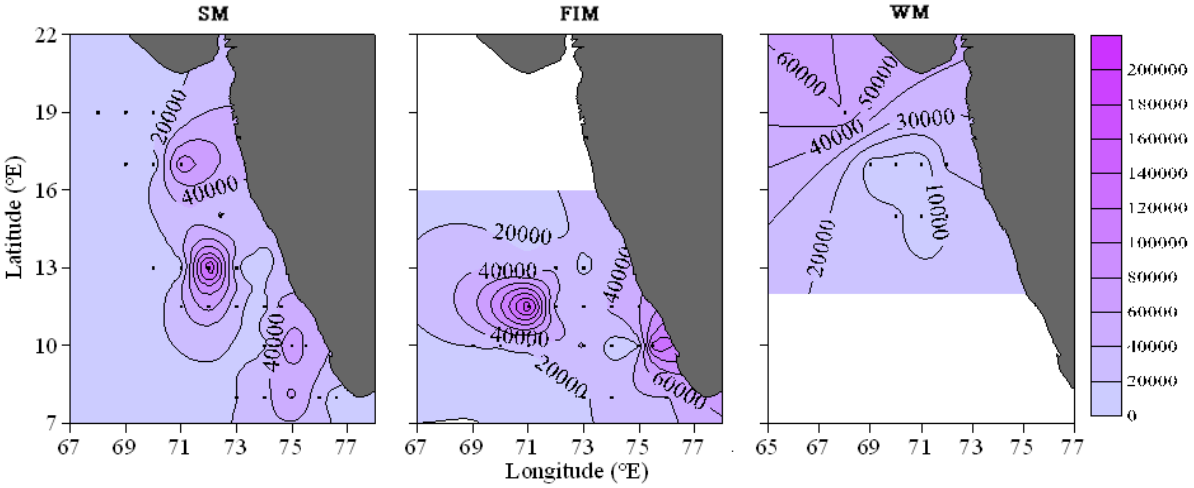

Figure 35. Distribution of mesozooplankton abundance (ind / 1000 m^3) along BT – 300 m depth in the Arabian Sea.

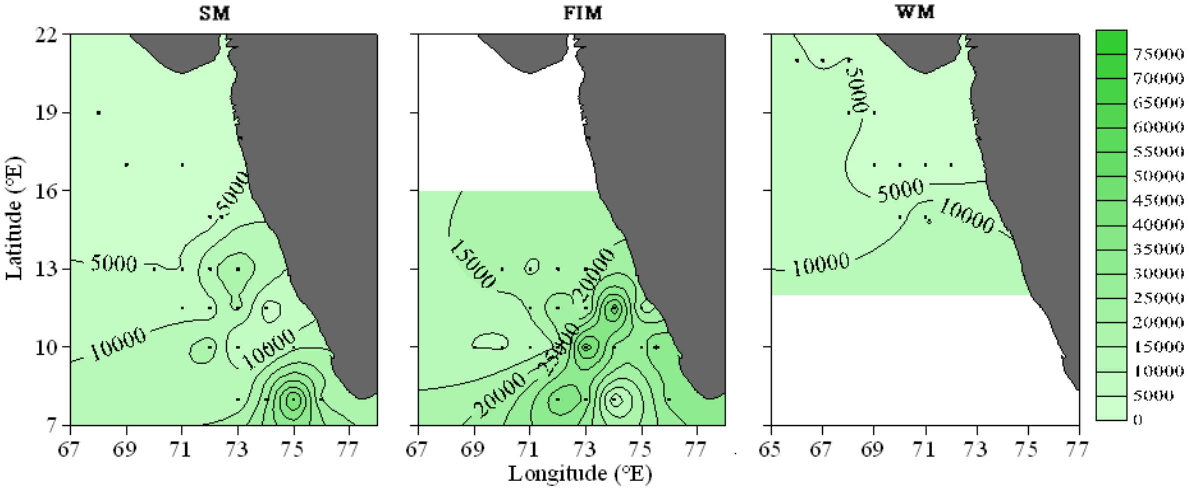

Figure 36. Distribution of mesozooplankton abundance (ind / 1000 m^3) along 300 – 500 m depth in the Arabian Sea.

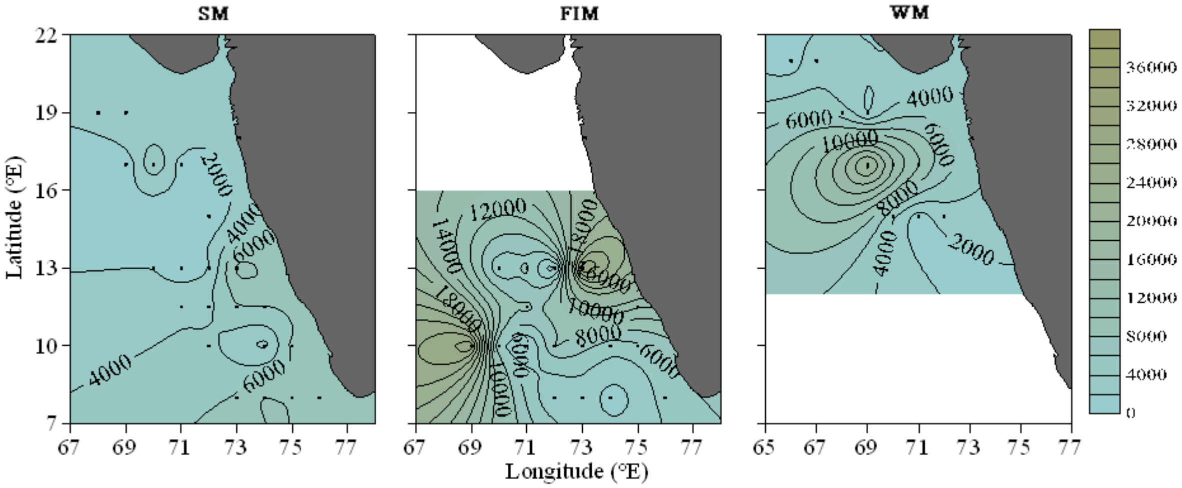

Figure 37. Distribution of mesozooplankton abundance (ind / 1000 m^3) along 500 – 1000 m depth in the Arabian Sea.

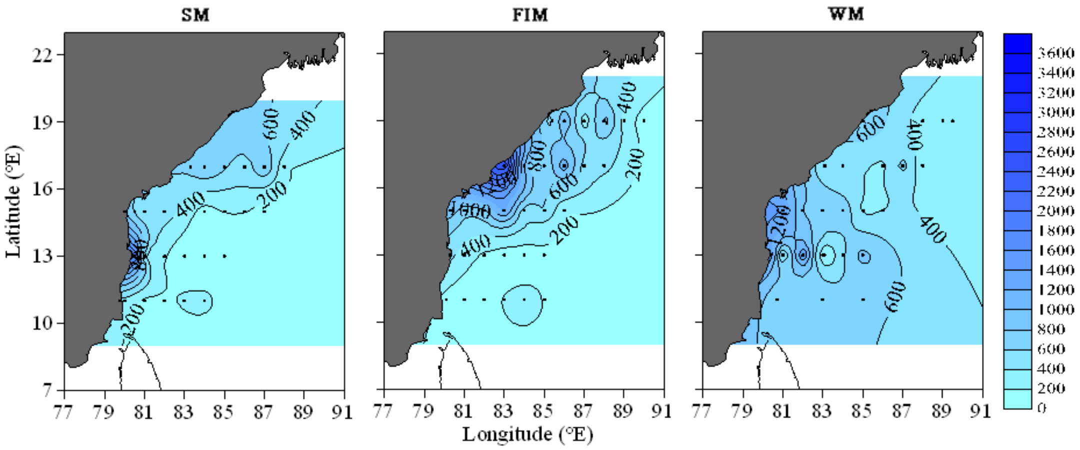

Figure 38. Distribution of mesozooplankton biomass (ml / 1000 m^3) along mixed layer depth in the Bay of Bengal.

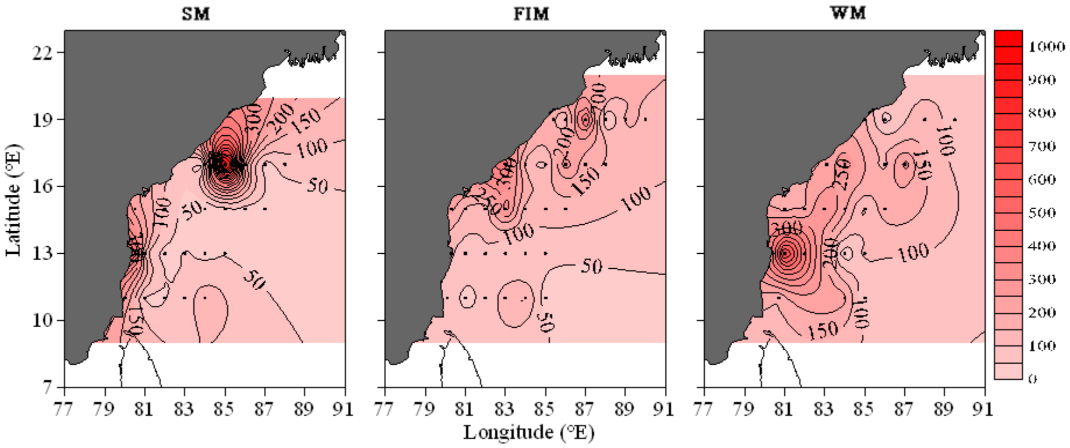

Figure 39. Distribution of mesozooplankton biomass (ml / 1000 m^3) along thermocline in the Bay of Bengal.

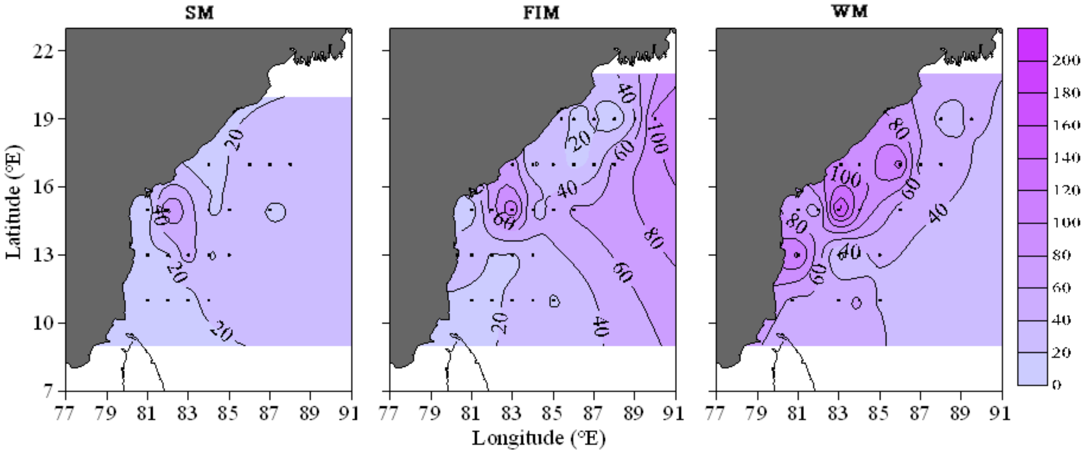

Figure 40. Distribution of mesozooplankton biomass (ml / 1000 m^3) along BT – 300 m depth in the Bay of Bengal.

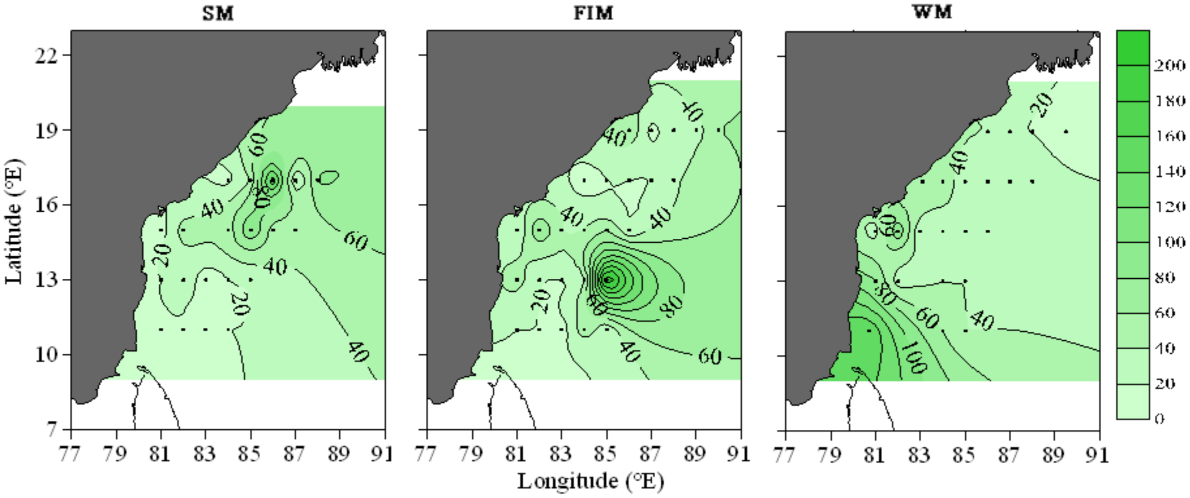

Figure 41. Distribution of mesozooplankton biomass (ml / 1000 m^3) along 300 – 500 m depth in the Bay of Bengal.

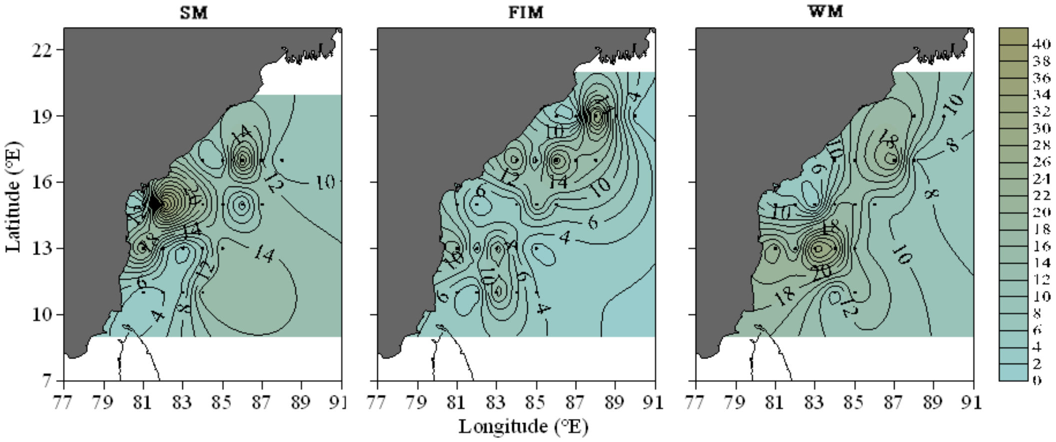

Figure 42. Distribution of mesozooplankton biomass (ml / 1000 m^3) along 500 – 1000 m depth in the Bay of Bengal.

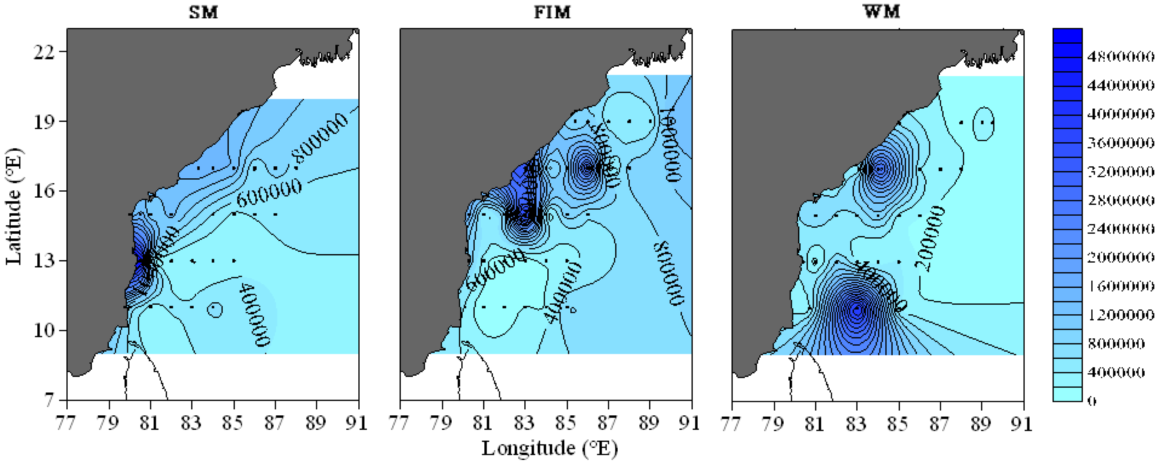

Figure 43. Distribution of mesozooplankton abundance (ind / 1000 m^3) along mixed layer depth in the Bay of Bengal.

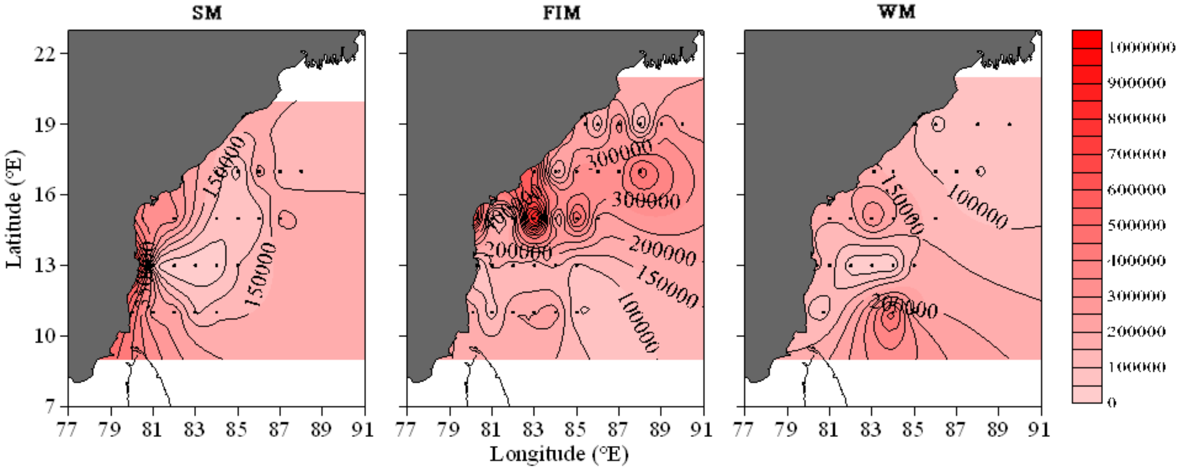

Figure 44. Distribution of mesozooplankton abundance (ind / 1000 m^3) along thermocline in the Bay of Bengal.

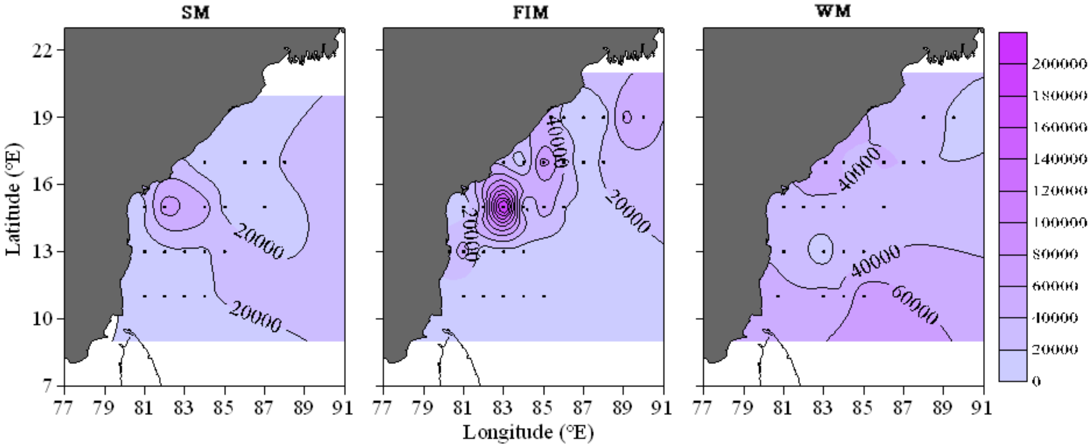

Figure 45. Distribution of mesozooplankton abundance (ind / 1000 m^3) along BT – 300 m depth in the Bay of Bengal.

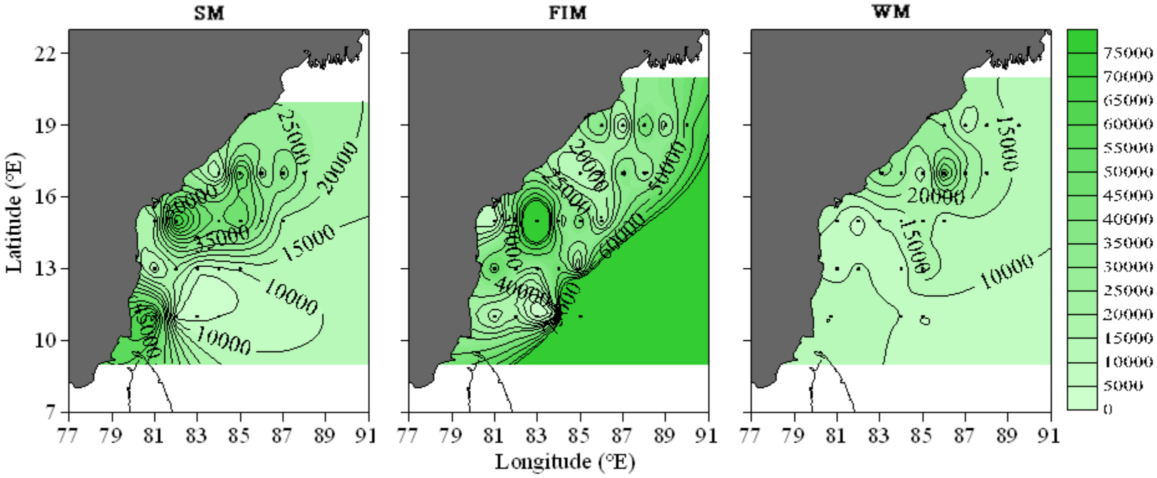

Figure 46. Distribution of mesozooplankton abundance (ind / 1000 m^3) along 300 – 500 m depth in the Bay of Bengal.

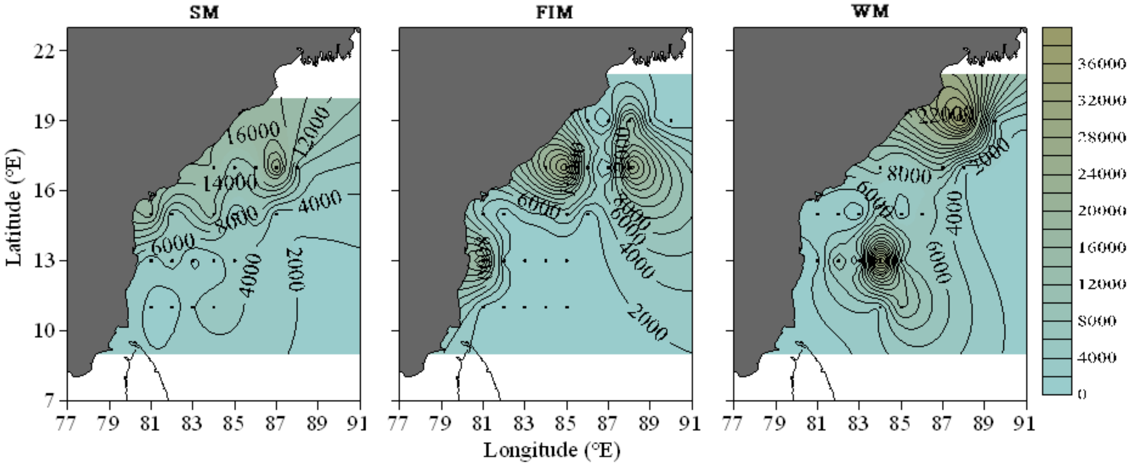

Figure 47. Distribution of mesozooplankton abundance (ind / 1000 m^3) along 500 – 1000 m depth in the Bay of Bengal.

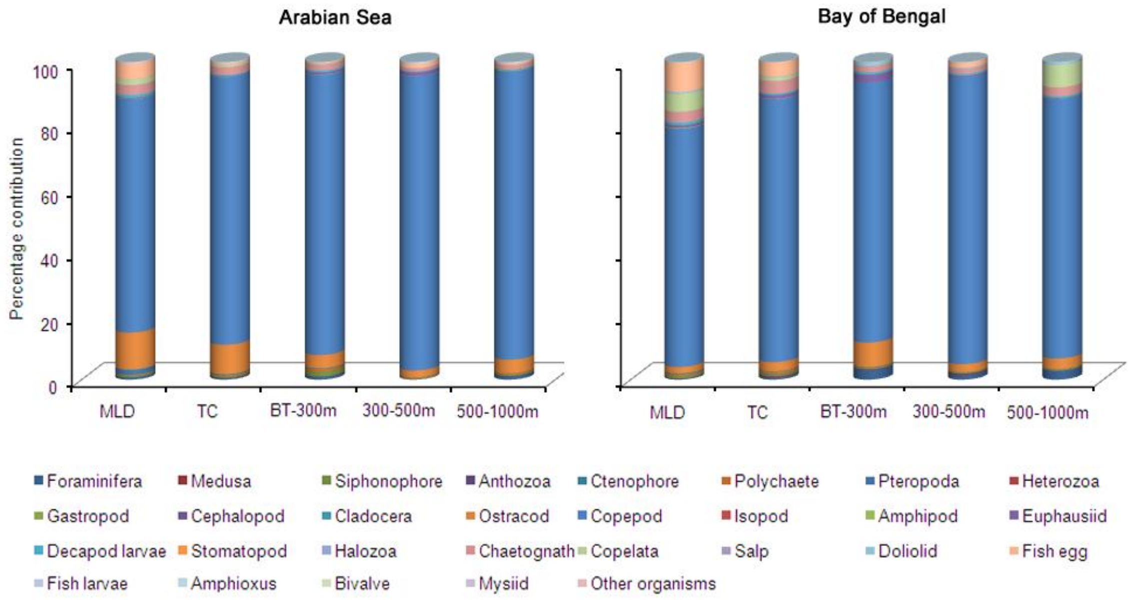

Figure 48. Percentage contribution of different mesozooplankton taxa at different depth strata during summer monsoon.

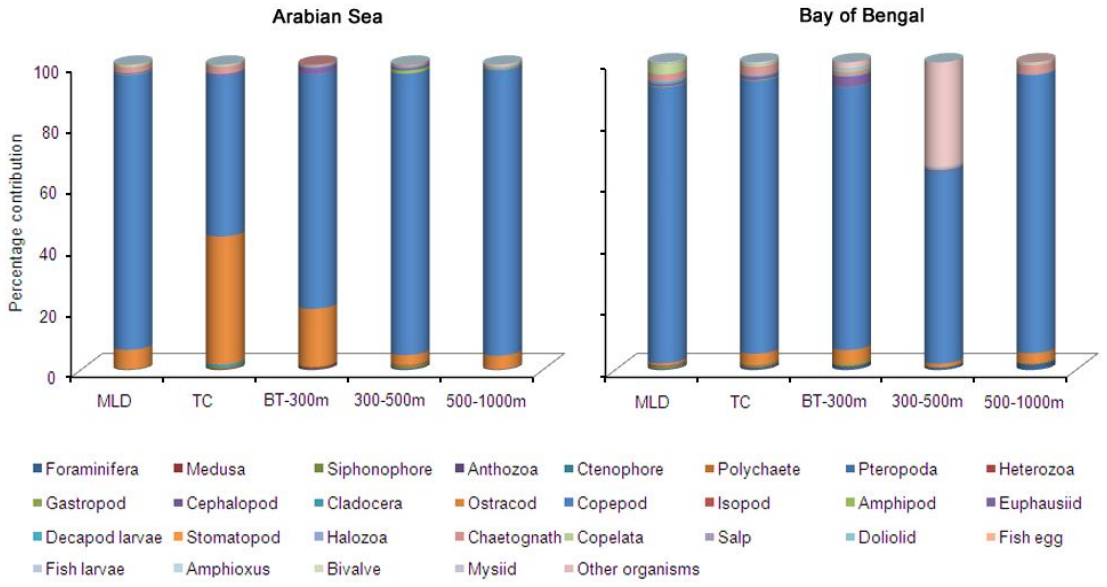

Figure 49. Percentage contribution of different mesozooplankton taxa at different depth strata during fall inter monsoon.

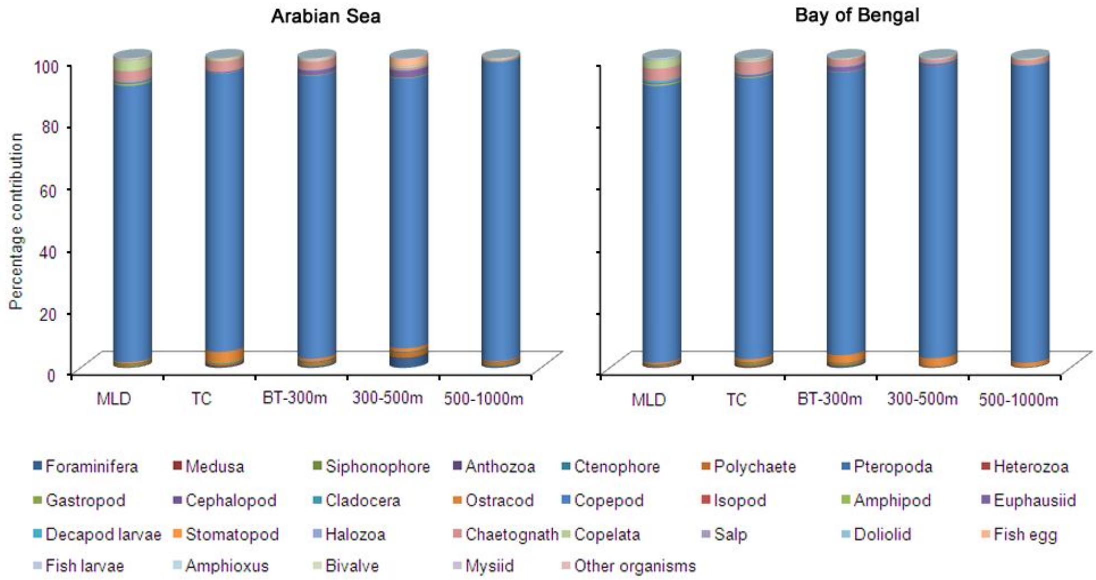

Figure 50. Percentage contribution of different mesozooplankton taxa at different depth strata during winter monsoon.

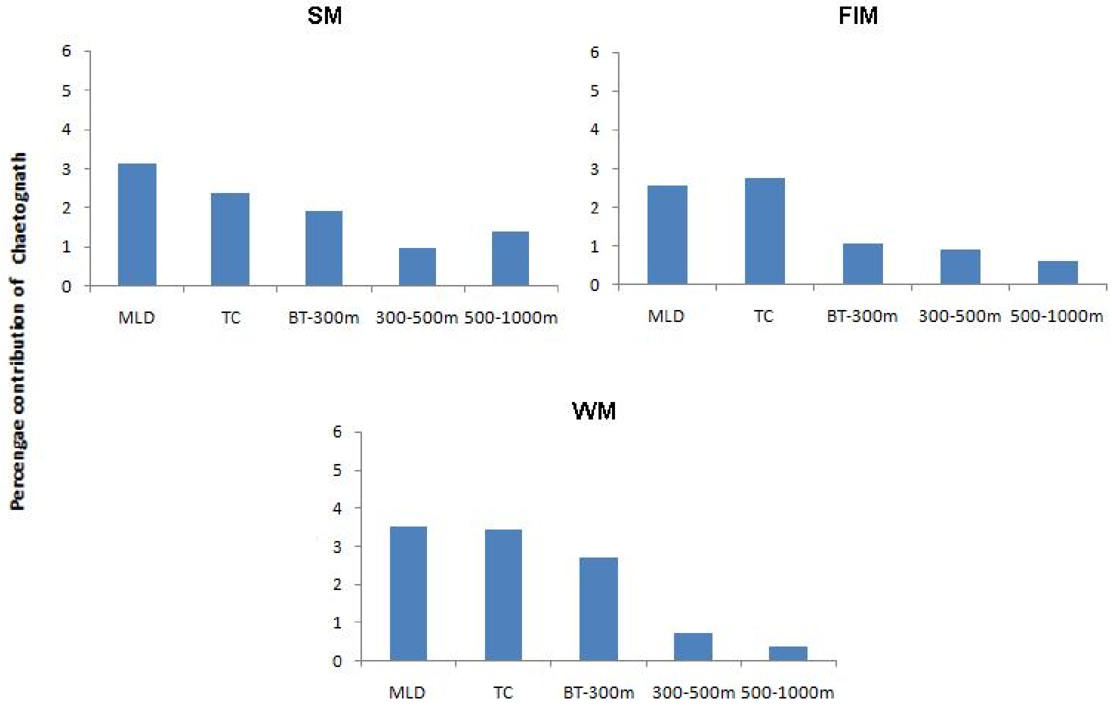

Figure 51. Percentage contribution of chaetognath along different seasons in the Arabian Sea.

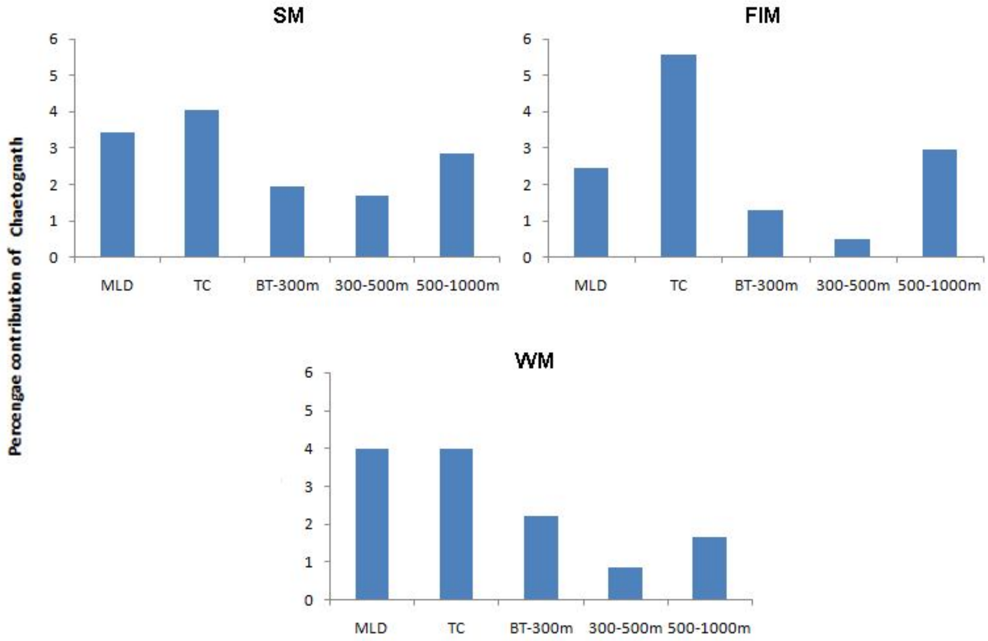

Figure 52. Percentage contribution of chaetognath along different seasons in the Bay of Bengal.

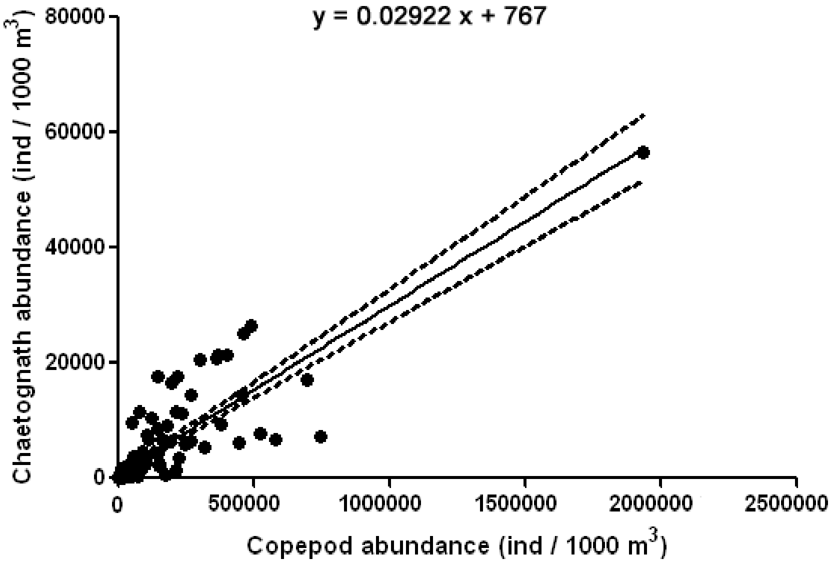

Figure 53. Relationship between copepods and chaetognaths during summer monsoon in the Arabian Sea. The regression equation and the 99% confidence band are shown.

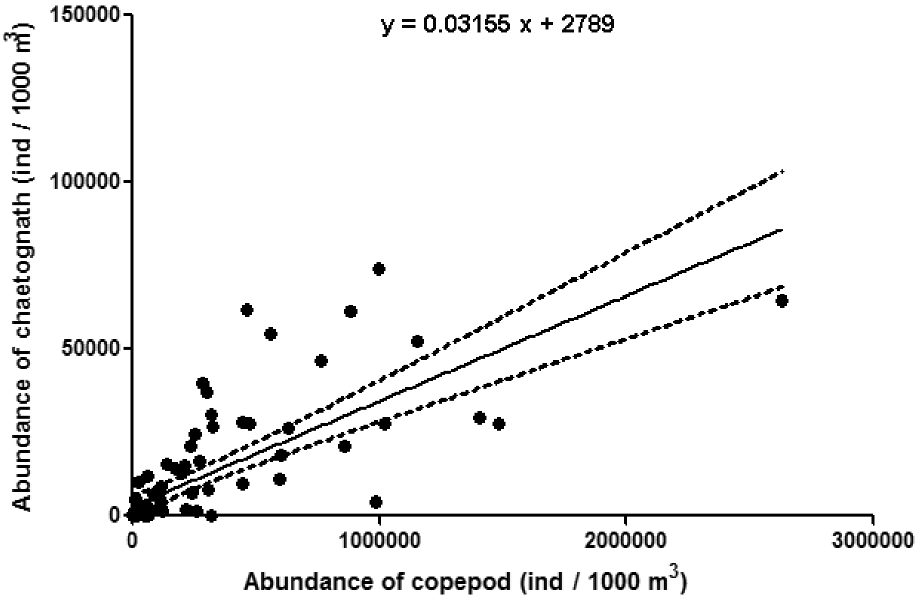

Figure 54. Relationship between copepods and chaetognaths during summer monsoon in the Bay of Bengal. The regression equation and the 99% confidence band are shown.

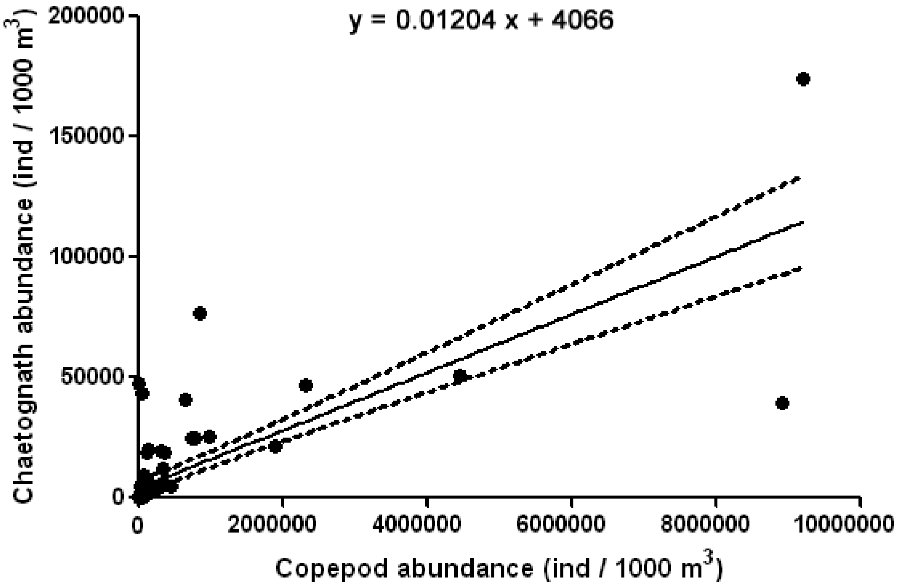

Figure 55. Relationship between copepods and chaetognaths during fall inter monsoon in the Arabian Sea. The regression equation and the 99% confidence band are shown.

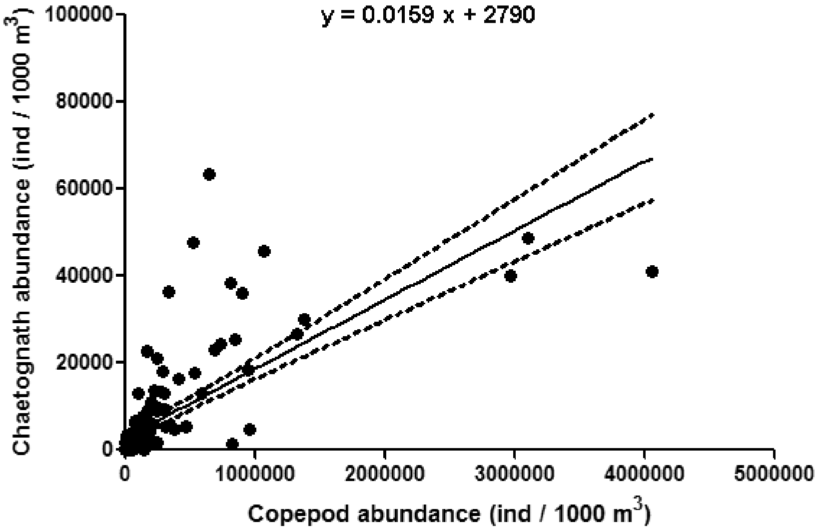

Figure 56. Relationship between copepods and chaetognaths during fall inter monsoon in the Bay of Bengal. The regression equation and the 99% confidence band are shown.

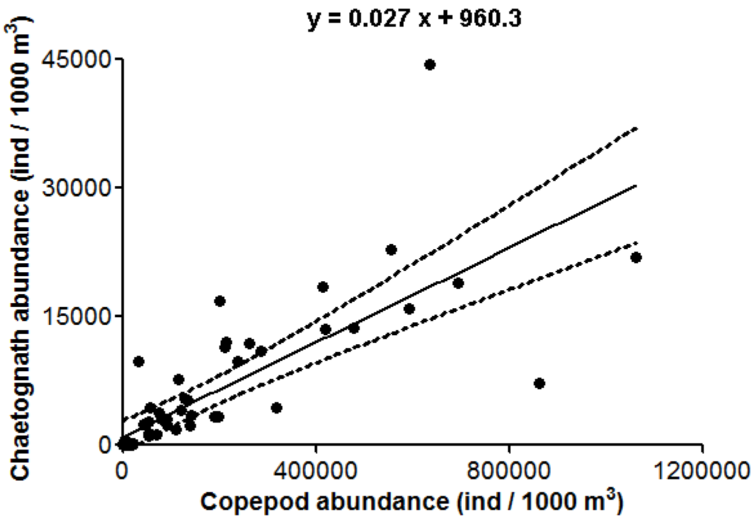

Figure 57. Relationship between copepods and chaetognaths during winter monsoon in the Arabian Sea. The regression equation and the 99% confidence band are shown.

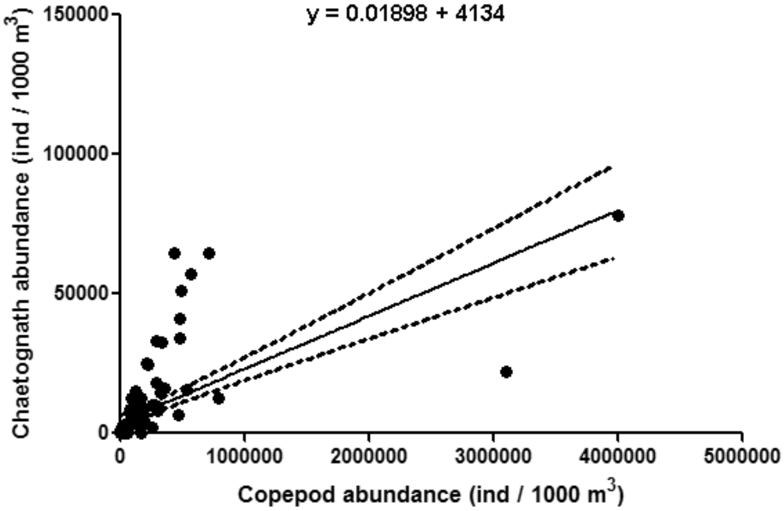

Figure 58. Relationship between copepods and chaetognaths during winter monsoon in the Bay of Bengal. The regression equation and the 99% confidence band are shown.

Chapter 6

Results - Chaetognath distribution and ecology

6.1. Arabian Sea

6.1.1. Summer monsoon

6.1.1.1. Chaetognath abundance

Abundance of chaetognath in MLD was higher (77% of the total collected in the 0 – 1000 m column) and ranged between 121 - 56612 ind / 1000 m^3. Except for the high abundance in the upwelling region (10° N 75.5° E), relatively higher abundance was observed in the northern part of AS (Fig 59). MLD of the upwelling region experienced 5.6 times higher abundance than the non upwelling regions. In TC layer, the abundance ranged between 0 and 11102 ind / 1000 m^3. Chaetognath was absent at some stations in the central and northern transects along 13°, 15° and 17° N. In this depth zone also the effect of upwelling was clearly evident with a 5.1 fold increase of chaetognath abundance when compared to the non upwelling regions (Fig. 60). In BT – 300 m layer, chaetognath was absent at some stations in the northern part of AS and the abundance ranged between 0 and 4465 ind / 1000 m^3 (Fig. 61). The effect of upwelling in the lower subsurface layer (BT – 300 m) was apparent with 11.2 fold higher abundance in the upwelling regions. In 300 – 500 m layer, relatively higher abundance was observed in the southern part of AS and was maximum along 11.5° N- 74° E (160 ind / 1000 m^3) (Fig. 62). This group was absent at some stations in the central and northern parts (11.5° - 19° N). In 500 – 1000 m depth, most of the stations of southern part had relatively higher abundance compared to the northern part (Fig. 63).

6.1.1.2. Species composition

A total of 27 species belonging to 4 genera were recorded from the entire water column (0 – 1000 m) (Table 1) and the genus *Sagitta* dominated (87%) of the total chaetognath population. The percentage contribution of this genus ranged between 62% (500 – 1000 m) and 93% (BT – 300 m). Although the total number of species recorded varied between 10 in 500 – 1000 m layer to 21 in TC layer, the number of species belonging to the genus *Sagitta* ranged from 6 to 16 respectively. Bathyplanktonic species of the genus *Eukrohnia* (4 species) were observed only below 300 m depth except at the upwelling stations. The higher abundance in surface upwelling zone (10° N 75.5° E) was contributed by twelve species of which *Sagitta enflata* dominated (25.9%). The other abundant species were *S. neglecta* (16.5%), *S. ferox* (15.3%), and *Krohnitta subtilis* (10.8%).

Though a total of 18 species were recorded in the upper subsurface upwelling zone (TC), the abundant species were *S. hexaptera*, *S. regularis*, *S. enflata*, *S. decipiens*, *S. neglecta*, *K. pacifica* and *K. subtilis*. The lower subsurface upwelling zones were contributed by 10 species and among them *S. ferox*, *S. regularis* and *S. enflata* dominated. The mesoplanktonic species *E. fowleri* and *E. minuta* shared a lesser percentage of abundance (0.3 – 1.6 %) in lower and upper subsurface upwelling region.

6.1.1.3. Spatial and vertical distribution

Table 1 illustrates the vertical distribution of chaetognath species observed in the upper 1000 m water column. Numerically *S. enflata* dominated in the MLD and TC strata, sharing 34 and 17% of the total population of the respective stratum. In deeper layers also this species contributed moderately to the total chaetognath population. Below TC layer, *S. decipiens* dominated contributing 22% (300 – 500 m) to 47% (500 – 1000 m) of the total population. *S. hexaptera* was abundant in the MLD and TC layer whereas both *S. regularis* and *S. bedfordii* had higher abundance upto 300 m. The epiplanktonic species *Pterosagitta draco*, *Krohnitta pacifica*, *K. subtilis*, *S. bedoti*, *S. ferox* and *S. minima* were more abundant in the upper water column upto 300 m depth. Except *S. decipens*, species like *S. bipunctata* (14%) and *E. minuta* (15%) were dominant in 300 – 500 m layers whereas *E. bathypelagica* (13%) and *E. hamata* (11%) were the other abundant species in 500 – 1000 m layer.

6.1.1.4. Coastal and oceanic variation

In the upper layer, though overall chaetognath abundance along coastal and oceanic stations did not show much variation, most of the species showed a clear preference either for coastal or oceanic waters. *S. bedoti* was observed only in the coastal waters whereas *S. minima, S. tasmanica* and *S. zetesios* were found only in oceanic waters (Fig. 64). Species like *S. bipunctata* and *S. ferox* had comparatively higher abundance in the coastal waters whereas mesoplanktonic species *S. decipiens* was abundant in oceanic region. Among the other dominant species *S. neglecta, S. regularis, S. hexaptera* and *S. robusta* showed a clear preference to the oceanic waters (Fig. 64). S. *oceania, S. pacifica*, *S. bedfordii*, *P. draco* and *K. pacifica* were the other species having relatively higher abundance in the oceanic region. Though *S. enflata* dominated in both coastal and oceanic waters, it was relatively more abundant in the former (Fig. 64).

6.1.2. Fall inter monsoon

6.1.2.1. Chaetognath abundance

During FIM, chaetognath abundance was higher in MLD and gradually decreased towards deeper waters. In MLD the abundance varied widely and ranged from 857 to 174000 ind / 1000 m^3 with an average density of 32390 ± 37442 ind / 1000 m^3. The highest abundance was observed in the Lakshadweep low (LL) region at 10° N 73° E. Except at this station, the abundance gradually decreased from coastal towards oceanic station (Fig. 59). In TC layer, the abundance ranged from 106 to 47203 ind / 1000 m^3 and the highest abundance was observed at 13° N 72° E. In 300 – 500 m layer, the abundance gradually increased towards south (Fig. 62). In the deeper layer (500 – 1000 m), the abundance was relatively less (40 ± 31 ind / 1000 m^3) and the highest abundance (120 ind / 1000 m^3) was observed at 13° N 73° E.

6.1.2.2. Species composition

A total of 24 chaetognath species was observed in the water column (0 – 1000 m) during this season (Table 2). The number of species along different depth layers varied between 13 (500 – 1000 m) and 21 (TC). *Sagitta* was the dominant genus in upper 500 m, contributing to 60% (300 – 500 m) to 91% (MLD) of the chaetognath population. *S. enflata* was the dominant species in the upper two layers (42 and 22% at MLD and TC respectively) whereas *S. decipiens* dominated in the middle layers below TC (42 and 27% at BT – 300 m and 300 – 500 m, respectively). In 500 – 1000 m layer, *Eukrohnia* formed the dominant genus (67%). Two species viz. *E. minuta* and *E. fowleri* (26% each) dominated this layer. The meso and bathyplanktonic species belonging to this genus were found mostly below 300 m depth. Two species belonging to the genus *Krohnitta* and one species belonging to the genus *Pterosagitta* was also observed at varying densities in the water column. In the upper layer of the LL region a total of six species were observed among which *S. enflata* dominated.

6.1.2.3. Stagewise distribution

The maturity stage composition of the total chaetognath population during this season revealed the dominance of Stage I (> 60%) (Fig. 65). Stage II population had a percentage contribution of 5.4% (TC) to 12.2% (BT – 300 m). Stage III population had a lesser contribution to the total population. The minimum occurrence of stage III population (1.9%) was observed in the TC layer (Fig. 65).

6.1.2.4. Spatial and vertical distribution

. A total of seven species were distributed throughout the water column (0 – 1000 m). Among them, the abundance of all three growth stages of *P. draco, S. enflata* and *S. hexaptera* was high in the upper layer (MLD) in (Fig. 66). The immature individuals (stage I) of the mesoplanktonic species *S. decipiens*, dominated in TC whereas the maturing (stage II) and matured (stage III) population had higher abundance in BT – 300 m layer (Fig. 66). Only immature specimens of *S. maxima* were observed during this period. Both immature and mature population of *S. regularis*, dominated in MLD whereas the maturing population dominated in TC (Fig. 66). The immature population of *S. pacifica* was abundant in MLD whereas the other two stages dominated in TC.

The distribution of all three life stages of the epiplanktonic species S*. bedfordii, S. minima, S. oceania* and *P. draco* were restricted to the upper two or three layers. They dominated in MLD except for the maturing stage of *P. draco*, which was abundant in the TC layer (Fig. 66).

Among the mesoplanktonic and bathyplanktonic species of the genus *Eukrohnia*, only the immature individuals of *E. bathypelagica* were observed. Different life stages of *E. hamata*, and *E. fowleri* were also abundant mostly in 500 – 1000 m depth. (Fig. 66).

Species like *K. subtilis*, *S. bipunctata*, *S. ferox*, *S. robusta* and *S. tasmanica* were observed down to a depth of 500 m. The abundance in all three life stages of these species were relatively high in MLD.

6.1.2.5. Coastal and oceanic variation

During this period, abundance of majority of chaetognath species was higher in the coastal region (42935 ind / 1000 m^3) compared to the oceanic region (14170 ind / 1000 m^3) (Fig. 67). Similar to SM, epiplanktonic species *S. bedfordii* dominated in oceanic region. The deep water species *S. maxima* and *S. zetesios* occurred only in oceanic region. But unlike SM, species like *Pterosagitta draco, Krohnitta pacifica, S. decipiens, S. pacifica, S. regularis* and *S. tasmanica* were distributed in higher abundance in the coastal region. Epiplanktonic species, *S. ferox* also showed higher abundance in the coastal region. Though *S. enflata* dominated both in coastal and oceanic waters, their abundance was relatively higher in the former (Fig. 67).

6.1.3. Winter monsoon

6.1.3.1. Chaetognath abundance

Chaetognaths were abundant at MLD (71% of total chaetognaths in 0 – 1000 m water column) and ranged between 2274 and 44444 ind / 1000 m^3. In the upper three depth zones, their abundance was relatively high in the northern region (Fig. 59 - 61). At depths of 300 – 500 m, the highest abundance was observed at 21°N 67°E (129 ind / 1000 m^3), while at depths of 500 – 1000 m, the southern region exhibited relatively higher abundance (Fig. 62 - 63).

6.1.3.2. Species composition

Twenty-two species belonging to four genera were recorded during the present study (Table 3). *Sagitta* was the dominant genus (16 species) in all the depth layers. In MLD, 17 species were observed, and of these two belonged to genus *Krohnitta* (9.9%) and one to genus *Pterosagitta* (1.1%). The TC layer was inhabited by 17 species and the BT – 300 m layer by 10 species. Bathyplanktonic species of the genus *Eukrohnia* (3 species) were sparse and occurred mostly in 500 – 1000 m column (Table 3).

6.1.3.3. Stagewise distribution

The maturity stage-wise abundance showed dominance of Stage I (> 60%) (Fig. 68). In the deeper layer, the less abundant species were represented by higher immature population (84% in 500 – 1000 m). The maximum percentage mature (Stage III) population occurred in MLD (20%) and gradually decreased towards deeper layers (9, 7, 4 and 3% in TC, BT – 300 m, 300 – 500 m and 500 – 1000 m, respectively).

6.1.3.4. Spatial and vertical distribution

Based on their vertical distribution limits, the observed chaetognath species were grouped into four categories.

(I) Species abundant in surface layers with a maximum distribution limit up to 300 m, such as *S. neglecta*, *S. bedfordii*, *S. minima*, *S. pulchra*, *S. bipunctata*, *S. planktonis*, and *P. draco*. *S. neglecta* was one of the major components in upper layers, representing 13, 11 and 10.5% of the chaetognath population in the MLD, TC and BT – 300 m zones, respectively. The immature population had relatively higher abundance (> 80%) in the upper two strata (Fig. 69). *S. bedfordii* comprised 3 – 8% of the population, with maximum abundance in MLD (av. 402 ind / 1000 m^3). Mature specimens of *P. draco* were abundant in the TC layer and immature specimens in MLD, whereas immature specimens of *S. pulchra* were more abundant in the TC layer, and the maturing (stage II) population was mostly distributed in MLD. Regardless of maturity stages, the abundance of most of the other species (except *S. planktonis*) was high in MLD.

(II) Species such as *S. maxima*, *E. bathypelagica*, *E. minuta* and *E. fowleri* were mostly confined to deeper waters (> 500 m). The bathyplanktonic species *S. maxima* was observed only in the southern region at depth of 500 – 1000 m, contributing to 15% of the total chaetognath population of this layer. Most of the species of *Eukrohnia* were restricted to depths below 500 m (Fig. 69). They were mainly observed in the southern region, and only immature stages were encountered during the study.

(III) Species distributed throughout the water column (0 – 1000 m) included *S. enflata*, *S. decipiens*, *S. robusta*, *K. pacifica* and *K. subtilis*. *S. enflata* represented the dominant species up to a depth of 500 m (Table 3). It contributed 5% (500 – 1000 m) to 48.4% (BT – 300 m) of the total chaetognath population. In the upper 300 m, its abundance was relatively high in the northern region, and all three maturity stages were abundant in MLD (Fig. 69), among which stage III constituted 26.1% of the population. Stage I of *S. robusta, K. subtilis* and the mesoplanktonic species *S. decipiens* were distributed throughout the water column.

(IV) *S. hexaptera*, *S. ferox*, *S. pacifica*, *S. regularis*, *S. zetesios* and *S. tasmanica* were the species present in most of the layers, but with a preference for a specific depth stratum. The cosmopolitan species, *S. hexaptera* was abundant in all layers except the BT – 300 m zone (Table 3). The individuals of all three stages dominated in MLD (Fig. 69). *S. zetesios* dominated in BT – 300 m layer whereas all the stages of the abundant species *S. regularis* had higher abundance in MLD.

6.1.3.5. Coastal and oceanic variation

Chaetognath abundance between coastal and oceanic regions did not show much variation though most of the species observed during this period had clear preferences either for coastal or oceanic region. Similar to SM, *K. subtilis* was more abundant in oceanic water (Fig. 70). Epiplanktonic species *S. ferox* and *S. neglecta* had higher abundance in coastal water whereas *S. pacifica* and *S. regularis* were abundant in oceanic water. Abundance of the cosmopolitan species *S. hexaptera* was relatively more in the oceanic waters (Fig. 70). Unlike SM, *S. robusta* was more abundant in coastal region. Though *S. enflata* dominated in both coastal and oceanic waters their abundance was relatively higher in the oceanic waters (Fig. 70).

6.1.4. Diel vertical migration

The Wilcoxon matched pair test was carried out between the day and night abundances of chaetognaths at different depths at the diurnal stations, to determine whether this planktonic group exhibited a significant diel vertical migration. Irrespective of the season, the test revealed insignificant variation ($P > 0.05$) in diel abundance of chaetognath.

6.1.5. Temporal variation

The number of species observed in the water column (0 – 1000 m), was relatively higher during SM period (27, 24 and 22 during SM, FIM and WIM respectively). The upper two layers (MLD and TC) which supported more than 95% of the total population in the total water column, chaetognath abundance was relatively higher during FIM (12610 ± 14425, 32390 ± 37442, 13246 ± 10384 at MLD and 2961 ± 2883, 6475 ± 10337, 4479 ± 6040 at TC during SM, FIM and WM, respectively). During this period, the abundance of *S. enflata*, the dominant species in MLD was markedly higher (Table 2) and was mostly contributed by the immature population (82%). Species like *K. pacifica*, *S. bipunctata*, *S. neglecta*, *S. pacifica*, *S. regularis* and *S. robusta* also had reasonably higher abundance during this season (Table 2). The mesoplanktonic species *E. minuta* and *E. fowleri* were also more abundant during this period in deeper layers. During SM and WM, the overall chaetognath population between coastal and oceanic regions did not show much variation whereas during FIM the coastal population was three times higher than the oceanic population.

6.2. Bay of Bengal

6.2.1. Summer monsoon

6.2.1.1. Chaetognath abundance

In each depth layer chaetognath abundance showed a wide variation between sampling stations (Figs. 71-75). The abundance was relatively higher in MLD, particularly in the coastal upwelling stations (along 13° and 15° N) and ranged between 310 to 73915 ind / 1000 m^3 (Fig. 71). In the northern part, along 17°N, higher abundance was observed in the cold core cyclonic eddy region. Relatively lower abundance was observed at the warm gyre region in the oceanic water along 13° and 15° N transects. In BT – 300 m layer, chaetognath abundance (343 ± 365 ind / 1000 m^3) was relatively less than the layers above (TC, 7116 ± 7186 ind / 1000 m^3) and below (300 – 500 m, 439 ± 996 ind / 1000 m^3). In 300 – 500 m layer, the abundance was relatively higher in the southern part (Fig. 74).

6.2.1.2. Species composition

During this period, a total of 18 species belonging to four genera were observed in the total water column. Along different layers, the number of species varied from 13 (BT – 300 m and 500 – 1000 m, each) to 15 (300 – 500 m). The species of the genus *Sagitta* dominated in the upper 500 m water column. Along different layers their percentage contribution ranged from 46.4% (500 – 1000 m) to 95.9% (TC). In 500 – 1000 m layer the dominant species was *E. fowleri* (52.8%). *K. pacifica* and *K. subtilis* were the two species found under genus *Krohnitta*. Though *K. pacifica* was found in the entire 1000 m water column, *K. subtilis* was restricted in distribution from TC layer to 500 m depth (Table 4).

The higher abundance in the shallow coastal upwelling stations (<75 m depth) were contributed by only six species and among them *S. enflata* (45%), *S. bedoti* (20.3%), *S. neglecta* (10.6%) and *S. bipunctata* (10.6%) were the dominant ones. Seven species were present in the cold core eddy region and the major contributing species were *S. enflata* (53%) and *S. bedoti* (19.7%). Though chaetognath abundance in the warm gyre region was relatively less, a total of twelve species were observed in this region and *S. neglecta* was the dominant species (34%). Other abundant species were *S. enflata* (32%) and *S. regularis* (11.5%).

6.2.1.3. Spatial and vertical distribution

The epiplanktonic species *S. minima* was found only in MLD (Table 4). Another epiplanktonic species *S. ferox* was abundant in the upper two layers. Though it was absent in BT – 300 m layer, a smaller fraction of its population was observed in the 300 – 500 m layer. Of the 18 species observed during this period, 10 were distributed in the entire 1000 m water column, but their abundance varied widely along different depth layers. Cosmopolitan species *S. enflata* dominated in MLD (40%) whereas *S. bipunctata* was abundant in TC layer (45.2%). *P. draco* had maximum abundance in MLD (771 ind / 1000 m^3) and minimum in BT – 300 m layer (< 1 ind / 1000 m^3). Although mesoplanktonic species *S. decipiens* was present at all depths, its abundance was relatively high in the mid-depth and was dominant in both BT – 300 m (63.6%) and 300 – 500 m layers (40.8%). Among the abundant species observed during this period, *S. bedoti, S. neglecta, S. pacifica* and *S. regularis* had maximum abundance in MLD and gradually decreased towards deeper waters. Cosmopolitan species *S. hexaptera* was found in the entire water column with a minimum abundance in BT – 300 m layer. The mesoplanktonic species *S. maxima* was mostly found in the oceanic stations below 300 m.

6.2.1.4. Coastal and oceanic variation

Chaetognath abundance gradually decreased from coastal to oceanic region (Fig. 76). Similar to the observation in AS, most of the species showed preference either for coastal or oceanic waters. *P. draco* and *K.pacifica* had relatively higher abundance in the oceanic region (Fig. 76). Among the epiplanktonic species, *S. bedoti, S. bipunctata, S. ferox, S. neglecta* and *S. pulchra* were abundant in the coastal waters. Cosmopolitan species *S. hexaptera* had higher abundance in the oceanic water. Another cosmopolitan species *S. enflata* was observed in both coastal and oceanic waters, but had higher abundance in the latter.

6.2.2. Fall inter monsoon

6.2.2.1. Chaetognath abundance

Chaetognath abundance was higher in MLD and it gradually decreased towards the greater depth (Figs. 71 - 75). In the MLD and TC layers, the abundance was 21368 ± 28392 and 8514 ± 7790 ind / 1000 m^3, respectively. During this period below TC layer, a sharp decrease in abundance (519 ± 1587, 247 ± 303 and 72 ± 51 ind / 1000 m^3 at BT – 300 m, 300 – 500 m and 500 – 1000 m, respectively) was observed. In MLD, the coastal stations had relatively higher abundance than the oceanic stations (Fig. 71). In upper two layers, the abundance was relatively higher in the northern part while at 300 – 500 m layer the abundance showed an opposite trend (Fig.71 - 74).

6.2.2.2. Species composition

In the present study, a total of 26 species belonging to four genera were observed in the water column. *Sagitta* was the dominant genus in the upper 500 m layer whereas *Eukrohnia* dominated below this depth. The monospecific genus *Pterosagitta* occurred in the upper 500 m whereas species of the genus *Krohnitta* were observed throughout the water column. The number of species varied from 16 (300 – 500 m) to 18 (MLD, TC and BT – 300 m each) (Table 5).

6.2.2.3. Stagewise distribution

The maturity stage composition showed dominance of Stage I (> 80%) population (Fig. 77). In the deeper layer, the less abundant species were represented by a higher percentage of immature population (86% in 500 – 1000 m). The maximum mature (Stage III) population occurred in MLD (7.2%) and it was relatively less in deeper layers (6.3, 1.9, 4.1 and 3.7% at TC, BT – 300 m, 300 – 500 m and 500 – 1000 m, respectively).

6.2.2.4. Spatial and vertical distribution

The epiplanktonic species *S. bedfordii*, *S. bipunctata* and *S. minima* were observed only in the upper 300 m column. The immature stage of *S. bipunctata* was dominant in MLD whereas the maturing and matured ones dominated in TC layer (Fig.78). Irrespective of life stages, abundance of *S. minima* decreased towards the deeper layers (Fig. 78). *S. enflata*, *S. decipiens*, *S. ferox*, *S. hexaptera*, *S. neglecta*, *S. pacifica*, *S. regularis*, *S. robusta*, *K.*

pacifica and *K. subtilis* were the species found throughout the water column in varying density (Table 5). Cosmopolitan species *S. enflata* was dominant in the upper two layers (33.3 and 24.7 % in MLD and TC, respectively) and abundance of all three life stages gradually decreased towards the deeper layers (Fig. 78). Though the immature population of *K. pacifica* were present throughout the water column, the maturing ones were observed in the upper 500 m depth and the matured ones only in the upper two layers. A similar trend was observed in *S. ferox* and *S. neglecta* distribution also. In both cases, the maturing and matured populations were mostly observed in the upper layers only, though the immature were present in the 1000 m water column (Fig. 78). *S. decipiens* dominated in 300 – 500 m layer (36%) and *E. fowleri* below 500 m depth (29%). The meso and bathyplanktonic species of the genus *Eukrohnia* were abundant below 500 m. Only immature individuals of *E. bathypelagica* were found whereas all three stages of *E. minuta* and *E. fowleri* were observed. In the upper two layers, most of the species observed during this period had higher abundance in northern BoB. In 300 – 500 m layer, relatively higher abundance was observed in the southern part.

6.2.2.5. Coastal and oceanic variation

Among the 18 species observed in the upper layer during this period, 12 species had higher abundance in the coastal waters and 6 in the oceanic region (Fig. 79). The coastal stations had relatively higher abundance than the oceanic stations. Similar to SM, *P. draco* showed higher abundance in the oceanic region. *K. pacifica* showed higher abundance in the coastal region whereas *K. subtilis* was more abundant in the oceanic region. Though, *S. enflata* dominated both in coastal and oceanic region, it had relatively higher abundance in the coastal waters. Among other abundant species *S. neglecta* and *S. regularis* showed preference for coastal waters. The epiplanktonic species *S. bipunctata* and *S. regularis* were also mostly abundant in coastal waters. Mesoplanktonic species *S. zetesios* was mostly observed in the oceanic region.

6.2.3. Winter monsoon

6.2.3.1. Chaetognath abundance

The abundance in the upper most layer (MLD) was relatively high when compared to all other layers and ranged between 2133 to 78181 ind / 1000 m^3. The abundance was relatively high in the cold gyre region centering 83°E along 11° to 15°N (Fig. 71). In TC layer, chaetognath abundance was relatively high in the northern part (Fig. 72). In the layer below, the abundance gradually increased towards south and the maximum was observed in an oceanic station along 11°N transect (Fig. 73). In the deeper layer, in 300 – 500 m depth also, chaetognath abundance in the southern BoB was relatively high than the northern part (Fig. 74). The abundance gradually decreased towards the greater depth with an average of 150 ± 190 ind / 1000 m^3 in 500 – 1000 m depth.

6.2.3.2. Species composition

During this period, a total of 25 species belonging to four genera were observed in the study area (Table 6). The number of species varied along different depth layers and it was relatively higher in the upper two layers (23 and 21 in MLD and TC, respectively) than the layers below (17 each in BT – 300 m, 300 – 500 m and 500 – 1000 m). Similar to other seasons, *Sagitta* was the dominant genus in most of the layers and their percentage contribution varied between 36.1% (500 – 1000 m) to 92.4% (BT – 300 m). The number of species belonging to genus *Sagitta* ranged between 11 (500 – 1000 m) to 19 (MLD). *P. draco* was present throughout the water column though their abundance gradually decreased towards deeper waters. *Krohnitta pacifica* and *K. subtilis* were observed throughout the water column whereas the three deeper water species belonging to genus *Eukrohnia* were mostly observed below 300 m.

In the cold gyre region a total of 16 species were observed in the upper depth layers. Though *S. enflata* dominated in this region several other epi- and meso planktonic species also had fair contribution to the chaetognath population in this region. The other abundant species were mesoplanktonic *S. decipiens* (7.3%) and *S. hexaptera* (14%) and the epiplanktonic *K. subtilis* (6.9%), *S. ferox* (9.3%), *S. neglecta* (12.7%), *S. regularis* (7.6%) and *S. robusta* (9.6%).

6.2.3.3. Stagewise distribution

The maturity stage composition (Fig. 80) of the total chaetognath population revealed the dominance of Stage I (> 75%). The maximum percentage contribution of stage I was observed at 300 – 500 m depth (83.6%) whereas the minimum was observed in MLD (75.2%). The stage II population had relatively higher percentage contribution in the upper layers than the deeper layers. The maximum mature (Stage III) population occurred in BT – 300 m (11.8%) and the minimum in 300 – 500 m layer (5.1%).

6.2.3.4. Spatial and vertical distribution

Of the 25 species observed during this period, 12 were distributed throughout the total water column (Table 6) and *S. enflata* dominated in the upper two layers (Table 6). Irrespective of life stages, only a small part of the *S. enflata* population was observed below TC layer (Fig. 81). *S. decipiens* was the dominant species below TC layer down to a depth of 500 m (Table 6). Species like *K. pacifica, K.subtilis, S. hexaptera, S. neglecta, S. regularis and S.robusta* had relatively higher abundance of all the three life stages in MLD (Fig. 81). The immature (stage I) and maturing (stage II) population of *S. ferox* had higher abundance in MLD whereas matured population (stage III) dominated in TC (Fig. 81). Among the mesoplanktonic *S. macrocephala*, the immature and matured population had relatively higher abundance in MLD whereas the maturing population dominated in BT – 300 m layer.

During this period one epiplanktonic group was observed, whose vertical distribution was restricted to upper 300 m. Among this group, *S. bedfordi* had the maximum abundance in all three stages in MLD whereas in *S. bedoti* the maturing and matured population were more abundant in TC layer (Fig. 81). The distribution of mesoplanktonic *S. planktonis* was observed only in the upper 300 m. *S. oceania*, *S. pulchra*, *S. tasmanica* were the other epiplanktonic groups observed during this period. Their immature population was abundant in TC and BT – 300 m layers whereas the matured ones were mostly observed in MLD (Fig. 81).

The meso and bathyplanktonic species of *Eukrohnia* were mostly observed below 300 m depth. In all the three stages, they were mostly abundant in the 500 – 1000 m layer. Only immature and maturing individuals of

E. bathypelagica were observed during this period. Bathyplanktonic species *S. maxima* and *E. fowleri* were found in upper layer at a single station along 15° N transect.

Among other species, *S. zetesios* avoided BT – 300 m layer in the upper 1000 m water column. *S. bipunctata*, though considered as epiplanktonic, a small part of their population was observed at 300 – 500 m depth.

6.2.3.5. Coastal and oceanic variation

The coastal stations experienced higher chaetognath abundance than the oceanic stations (Fig. 82). In the coastal stations a total of 18 species were observed whereas in the oceanic station, the number of species observed was 16. *S. bedoti* was found only in the coastal region whereas *S. tasmanica* and *S. pulchra* were observed only in the oceanic region. *K.subtilis* had higher abundance in the coastal region whereas *K. pacifica* had less variation in the abundance between coastal and oceanic regions. Among the epiplanktonic species, *S. bedfordii* was abundant in oceanic region whereas *S. bipunctata*, *S. neglecta* and *S. minima* had higher abundance in the coastal region (Fig. 82). Similar to other seasons, *S. enflata* was the dominant species in both coastal and oceanic regions. Their abundance in coastal region was 2.5 times higher than the oceanic region (Fig. 82).

6.2.4. Diel vertical migration

The diel vertical migration of the total chaetognath population was studied during each season. A Wilcoxon matched pair test was carried out between the day and night abundances at different depths at the diurnal stations for this purpose. The result was similar to that of AS, showing no significant variation ($P > 0.05$) in their diel abundance during any season.

6.2.5. Temporal variation

During SM, the number of species observed in the total water column was relatively less than both FIM and WM (19, 26 and 25 during SM, FIM and WM, respectively). In the upper layer, the abundance was relatively higher during SM (31829 ± 19593, 22072 ± 28392 and 25596 ± 21648 ind / 1000 m^3 at SM, FIM and WM, respectively). In this layer, species like *S. enflata, S. neglecta, S. bedoti, S. pacifica* and *K. pacifica* had relatively higher abundance during SM (Table 4). In the deeper layer, the number of meso and bathyplanktonic species of the genus *Eukrohnia* was higher during FIM and WM (1, 4 and 3 at SM, FIM and WM respectively).

6.3. Statistical analysis

The Mann-Whitney U test was done between the $\log_e$ transformed abundance values of chaetognaths in AS and BoB to check whether any significant difference existed between these two major parts of the north Indian Ocean. The results of this test did not show any significant difference between the abundance of AS and BoB ($P > 0.05$).

The biplot in the PCA indicated a positive relation of chaetognath abundance with dissolved oxygen (DO) during SM in AS (Fig. 83 - 85). During FIM and WM, a close relationship of chaetognath abundance with both temperature and DO was observed. In BoB also a similar scenario was observed (Fig. 86 - 88).

During SM, species diversity (*H′*) in AS varied between different stations and along different depth strata (Table 7). *H′* was relatively higher in TC (1.7 ± 0.51) than other depth strata (1.6 ± 0.47, 0.96 ± 0.42, 0.93 ± 0.29 and 0.83 ± 0.23 at MLD, BT – 300 m, 300 – 500 m and 500 – 1000 m, respectively). During FIM also, the species diversity (*H′*) was relatively higher in TC (1.79 ± 0.36). Along different depth layers, *H′* was the lowest at BT – 300 m layer (1.01 ± 0.42) and below this layer this value gradually increased (1.04 ± 0.43 and 1.14 ± 0.32 at 300 – 500 m and 500 – 1000 m, respectively). Similar to other seasons, species diversity at WM was relatively higher in TC. It ranged between 1.6 and 2.27 with an average of 1.98 ± 0.23 (Table 7). Below this layer, *H′* gradually decreased (1.05 ± 0.42, 0.94 ± 0.37 and 0.93 ± 0.37 at BT – 300 m, 300 – 500 m and 500 – 1000 m, respectively). Though *H′* was relatively higher in TC during all seasons, between seasons it gradually increased from summer to winter (1.7 ± 0.51, 1.79 ± 0.36 and 1.98 ± 0.23 at SM, FIM and WM, respectively).

In BoB, species diversity (*H′*) at SM was relatively higher in MLD (1.36 ± 0.31) compared to deeper layers (Table 8). This was different from the features observed in AS, where *H′* was higher in TC layer. During FIM, *H′* was relatively higher at TC. In this layer *H′* ranged between 0.64 – 2.51 with an average of 1.74 ± 0.46. Below this layer *H′* gradually decreased (1.24 ± 0.49, 1.07 ± 0.57 and 0.99 ± 0.40 at BT – 300 m, 300 – 500 m and 500 – 1000 m, respectively). During WM, *H′* showed relatively higher value in MLD (2.09 ± 0.19). Below this layer, *H′* gradually decreased upto 500 m depth and after which it increased slightly (Table 8). Among different seasons, *H′* was relatively higher during WM in all depths (Table 8).

In AS the species evenness (J′) in the upper three layers did not show much variation during SM (Table 9). It was relatively higher in the deeper layers with a maximum value at 300 – 500 m depth (0.93 ± 0.8). During FIM, in MLD, it ranged between 0.56 and 0.96. Similar to SM, J′ was relatively higher in deeper layers (Table 9). The maximum value was observed at 500 – 1000 m depth (0.92 ± 0.1). During WM, species evenness was relatively lower in MLD where it ranged between 0.59 – 0.92. Relatively higher values of J′ was found in 500 – 1000 m layer and ranged between 0.81 and 1. In MLD and 300 – 500 m depth, J′ was relatively higher during SM whereas in other layers it was relatively higher during WM (Table 9).

In BoB, the species evenness (J′) ranged between 0.36 and 0.95 in MLD during SM. The layers below (TC and BT – 300 m) had relatively less evenness values (0.67 ± 0.19 and 0.67 ± 0.18 at TC and BT – 300 m, respectively). Relatively higher value was observed in 500 – 1000 m depth (0.75 ± 0.15) (Table 10). During FIM, compared to other layers relatively less evenness value was observed in MLD with a range between 0.58 and 0.97. Among the depth layers, the maximum value was observed in 300 – 500 m depth (0.91 ± 0.11). Below 300 m, the evenness value did not show much variation (Table 10). During WM, J′ value did not show much variation in the upper two layers (0.85 ± 0.04 and 0.84 ± 0.07 at MLD and TC, respectively). In the upper two layers, J′ values were relatively higher during FIM and WM than SM whereas in the deeper layer it was relatively higher in FIM than the other two seasons (Table 10).

In AS the cluster analysis based on the abundance and distribution of chaetognath species at different depth layers revealed some common features during all seasons (Figs. 89 - 91). Based on 60% similarity, the mesoplanktonic *S. maxima* and the meso and bathyplanktonic species of the genus *Eukrohnia* were mostly found in the same cluster. For better understanding of the distribution trend of the chaetognath species 80% similarity level was also checked. The epiplanktonic species *S. bedoti, S. minima, S. bedfordii, S. bipunctata, S. ferox, K. pacifica*, and *K. subtilis* were always found in the same cluster.

In BoB also the clusters of the chaetognath species showed similar features as found in AS. Based on 60% similarity, the species of the genus *Eukrohnia* along with *S. maxima* were mostly found in the same cluster (Figs. 92 - 94). Based on 80% similarity epiplanktonic species of *S. ferox*, *S. bedfordii*, *K. pacifica*, *P. draco* were found along with the cosmopolitan species of *S. enflata* (Figs. 92 - 94).

6.4. Summary

MLD supported a major part of the total chaetognath abundance in both AS and BoB. A tendency of a sharp decline in abundance was observed below TC layer. The spatial variation in abundance was prominent in both AS and BoB. In the upper layers, relatively higher abundance was observed during FIM in AS whereas in BoB it was during SM. During SM in the upper layers the upwelling regions had higher abundance in both AS and BoB whereas during FIM in AS, chaetognath abundance was relatively higher in the Lakshadweep low region. During WM, the BoB experienced relatively higher abundance in the cold core eddy region The PCA biplot showed a close relationship of chaetognath abundance with temperature and dissolved oxygen. Among different depth layers, the species diversity (*H'*) was relatively higher in TC layer in AS whereas in BoB the maximum diversity varied between seasons and was higher either in MLD or TC layer.

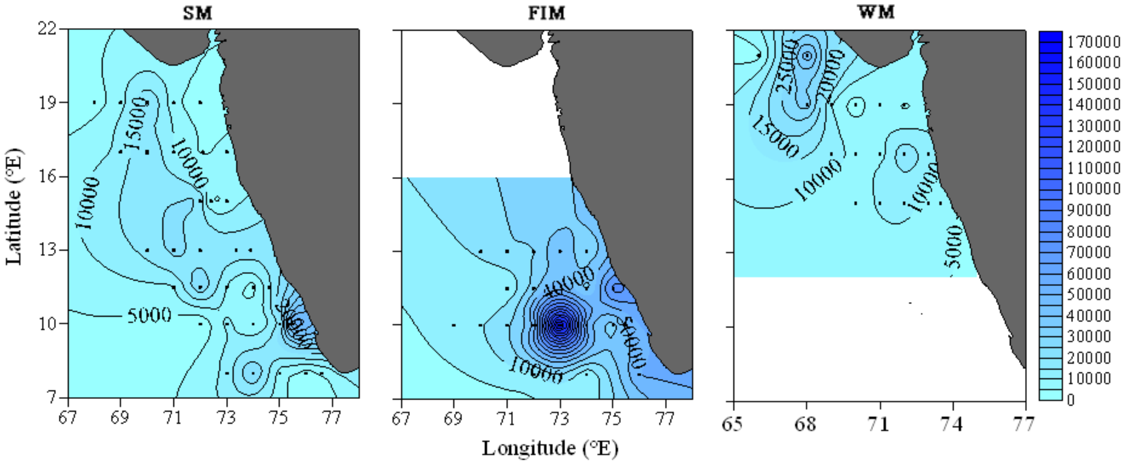

Figure 59. Distribution of chaetognath abundance (ind / 1000 m^3) along mixed layer depth in the Arabian Sea.

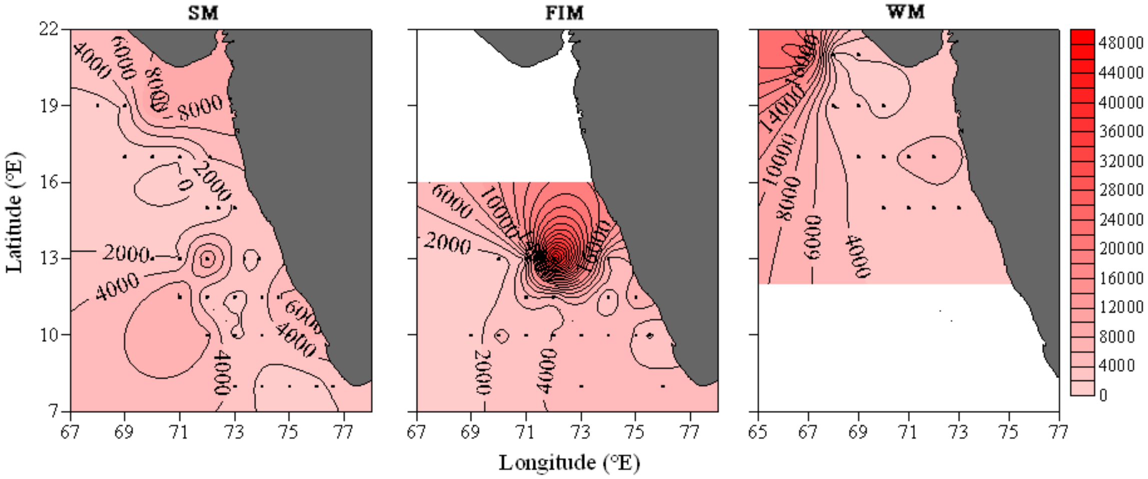

Figure 60. Distribution of chaetognath abundance (ind / 1000 m^3) along thermocline in the Arabian Sea.

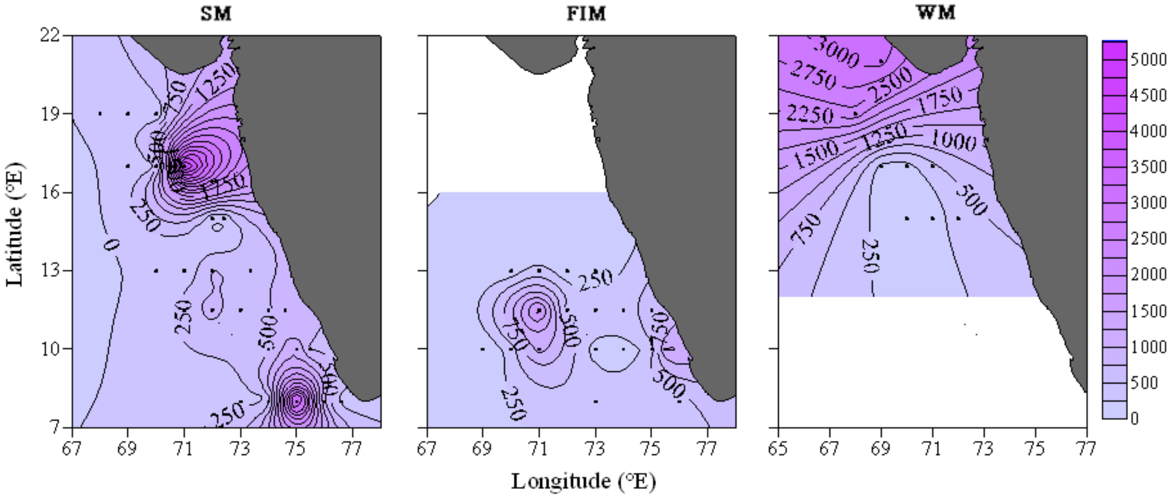

Figure 61. Distribution of chaetognath abundance (ind / 1000 m^3) along BT – 300 m depth in the Arabian Sea.

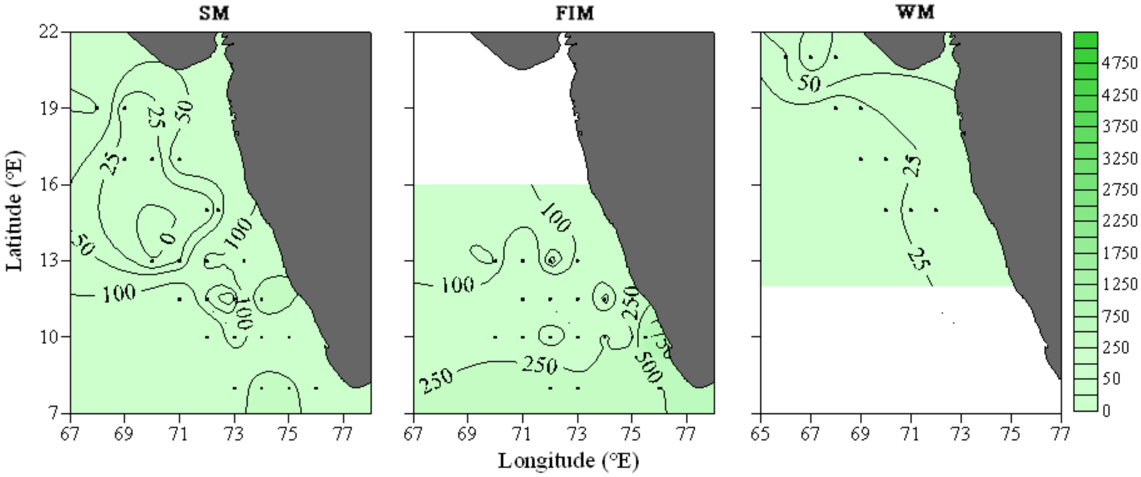

Figure 62. Distribution of chaetognath abundance (ind / 1000 m^3) along 300 – 500 m depth in the Arabian Sea.

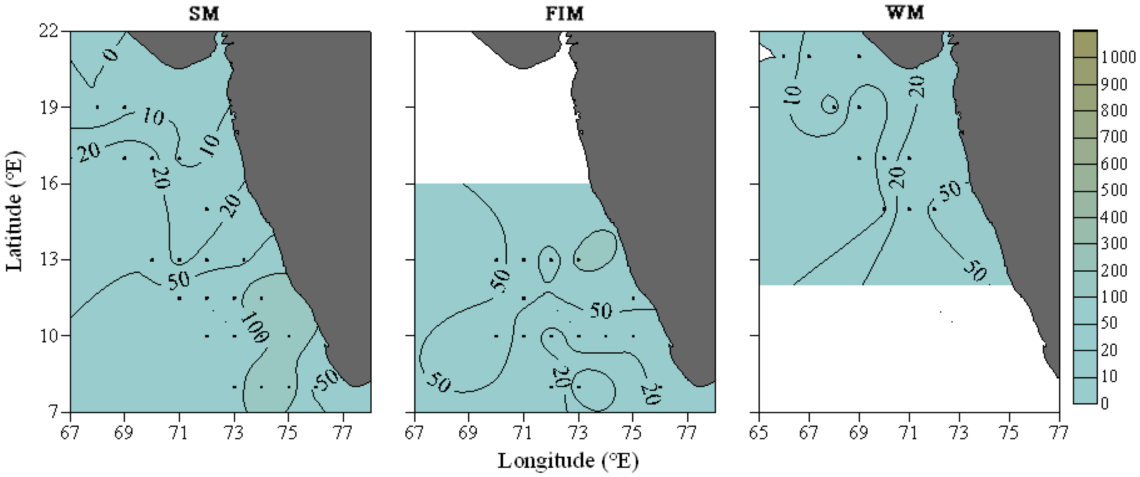

Figure 63. Distribution of chaetognath abundance (ind / 1000 m^3) along 500 – 1000 m depth in the Arabian Sea.

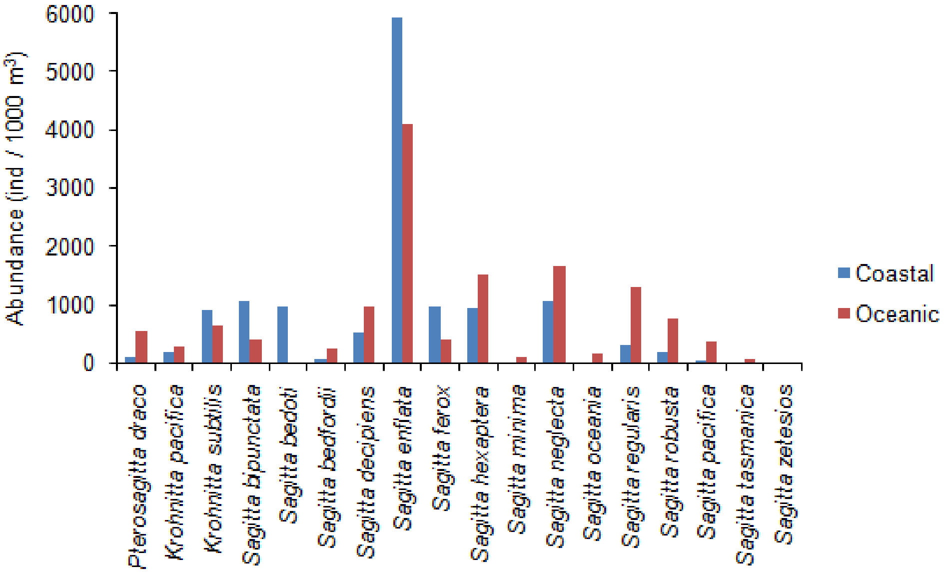

Figure 64. Variation of chaetognath species abundance along coastal and oceanic stations during summer monsoon in the Arabian Sea.

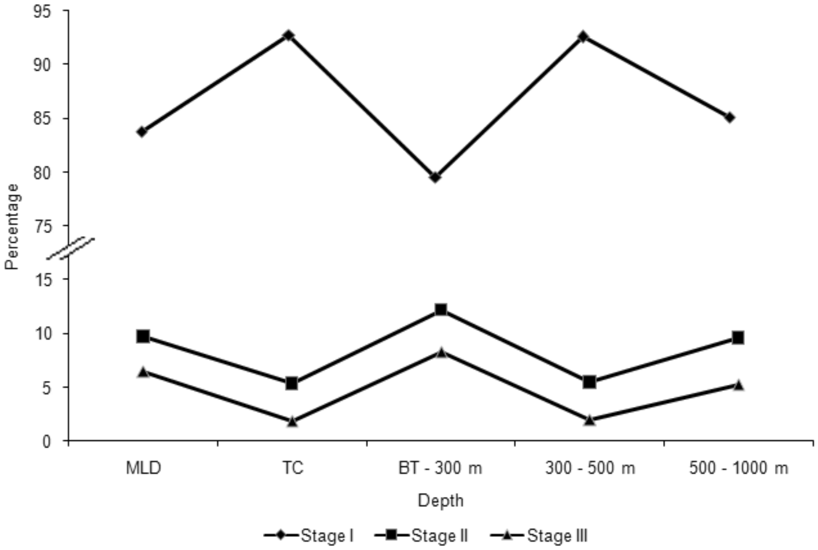

Figure 65. Depth wise percentage composition of different maturity stages of chaetognath population during fall inter monsoon in the Arabian Sea.

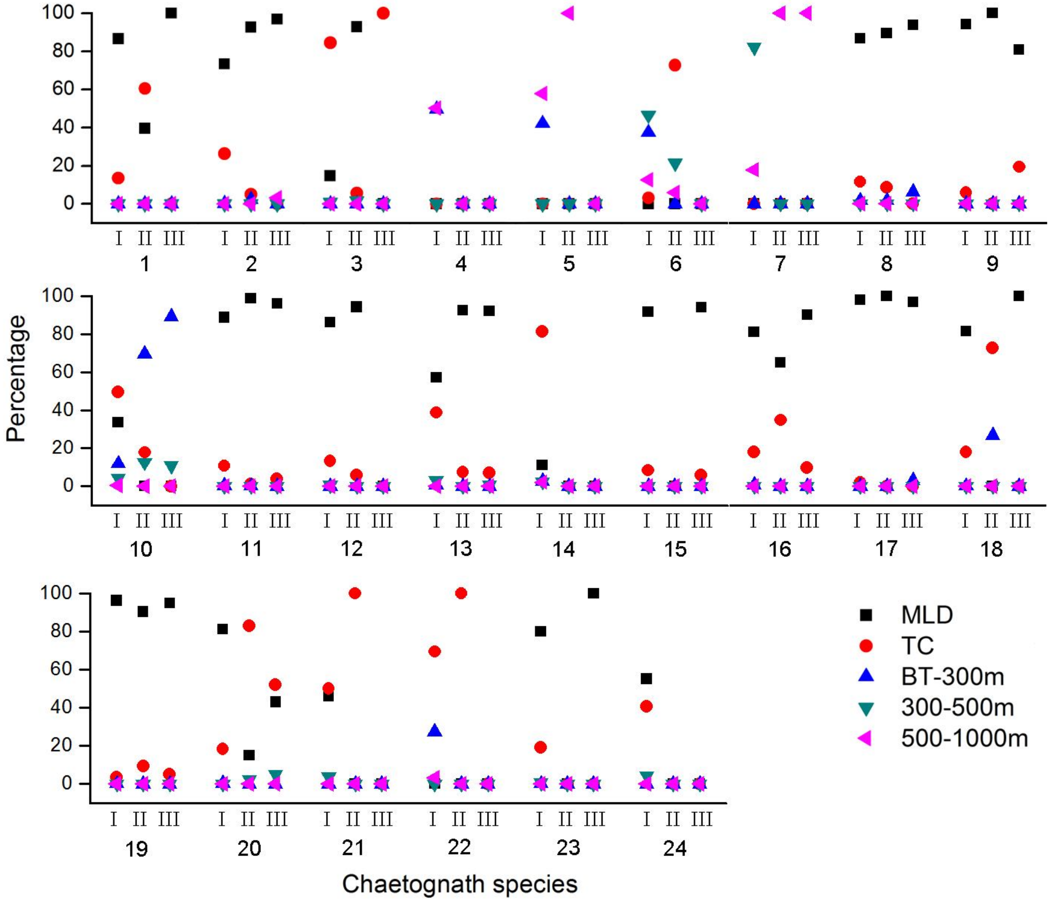

Figure 66. Vertical distribution of different maturity stages of chaetognath species in different depth layers during fall inter monsoon in the Arabian Sea. The numerics in the x-axis corresponds to the following species: 1. *Pterosagitta draco*, 2. *Krohnitta pacifica*, 3. *K. subtilis*, 4. *Eukrohnia bathypelagica*, 5. *E. hamata*, 6. *E. minuta*, 7. *E. fowleri*, 8. *Sagitta bipunctata*, 9. *S. bedfordii*, 10. *S. decipiens*, 11. *S. enflata*, 12. *S. ferox*, 13. *S. hexaptera*, 14. *S. maxima*, 15. *S. minima*, 16. *S. neglecta*, 17. *S. oceania*, 18. *S. regularis*, 19. *S. robusta*, 20. *S. pacifica*, 21. *S. planktonis*, 22. *S. pulchra*, 23. *S. tasmanica*, 24. *S. zetesios*.

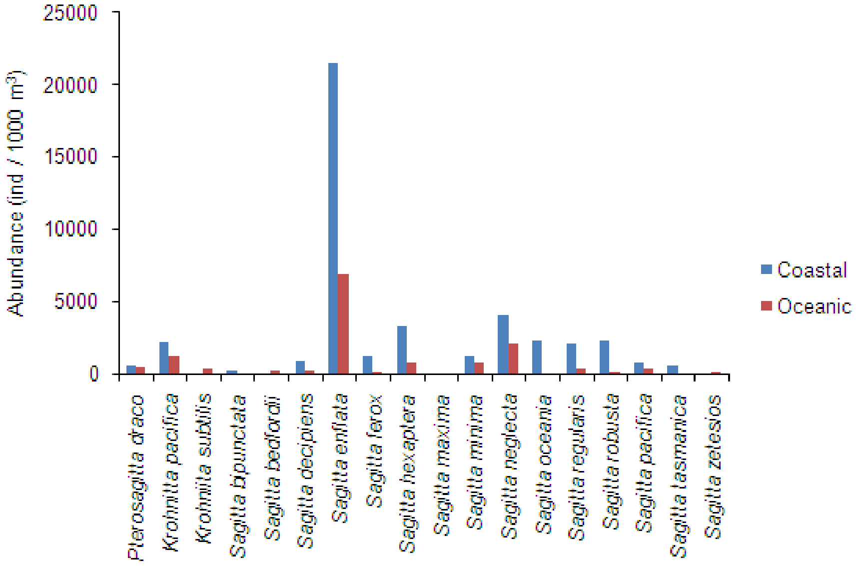

Figure 67. Variation of chaetognath species abundance along coastal and oceanic stations during fall inter monsoon in the Arabian Sea.

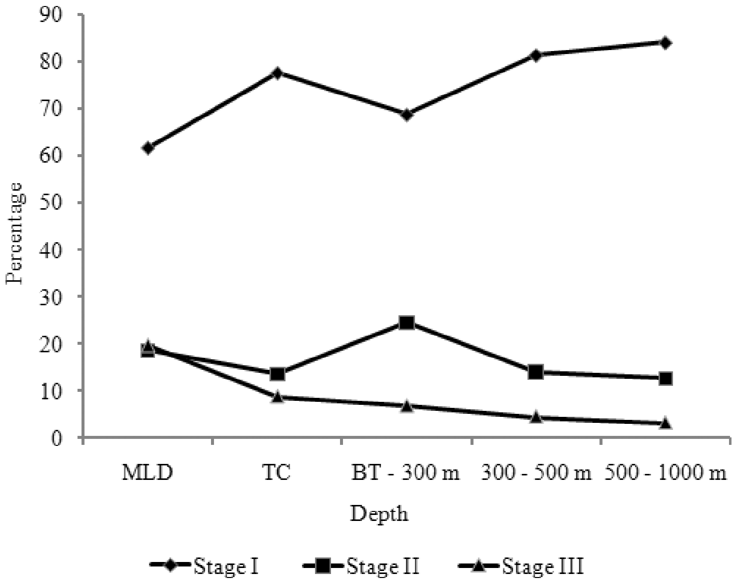

Figure 68. Depth wise percentage composition of different maturity stages of chaetognath population during winter monsoon in the Arabian Sea.

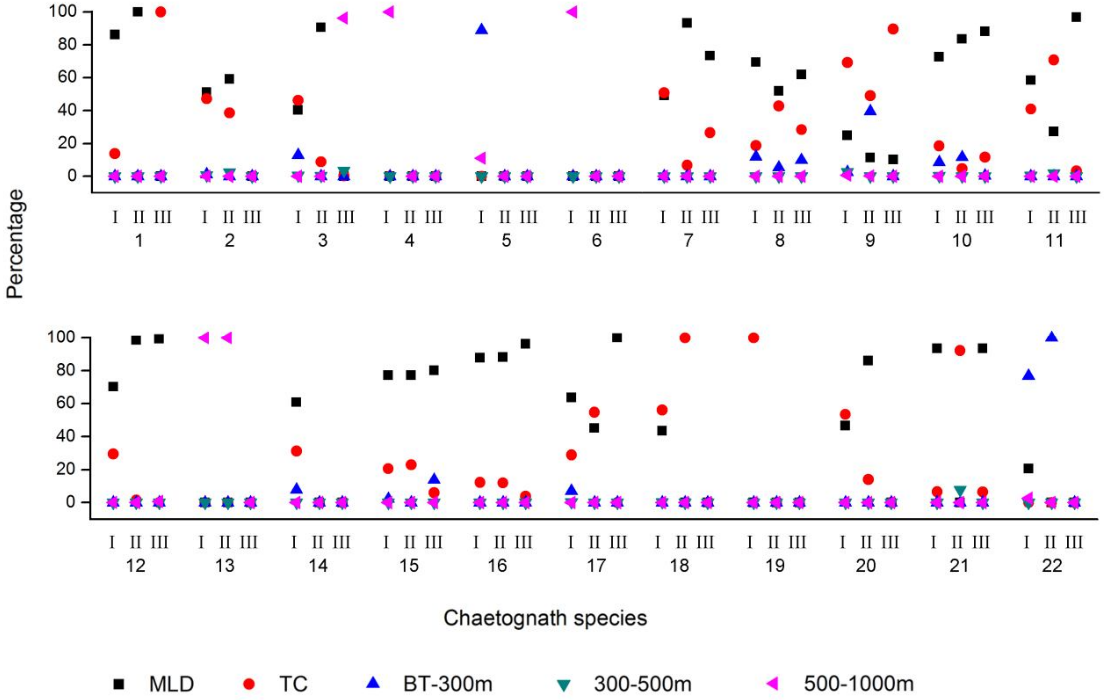

Figure 69. Vertical distribution of different maturity stages of chaetognath species in different depth layers during winter monsoon in the Arabian Sea. The numerics in the x-axis corresponds to the following species: 1. *Pterosagitta draco*, 2. *Krohnitta pacifica*, 3. *K. subtilis*, 4. *Eukrohnia bathypelagica*, 5. *E. minuta*, 6. *E. fowleri*, 7. *Sagitta bipunctata*, 8. *S. bedfordii*, 9. *S. decipiens*, 10. *S. enflata*, 11. *S. ferox*, 12. *S. hexaptera*, 13. *S. maxima*, 14. *S. minima*, 15. *S. neglecta*, 16. *S. regularis*, 17. *S. robusta*, 18. *S. pacifica*, 19. *S. planktonis*, 20. *S. pulchra*, 21. *S. tasmanica*, 22. *S. zetesios*.

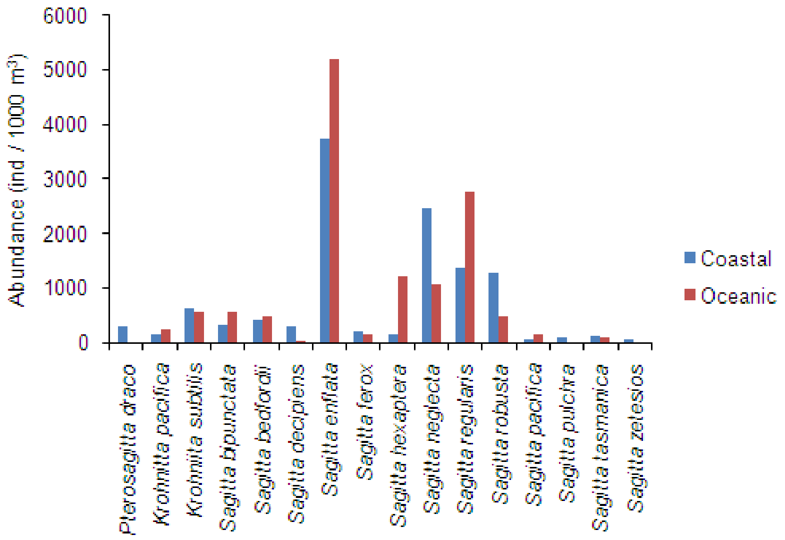

Figure 70. Variation of chaetognath species abundance along coastal and oceanic stations during winter monsoon in the Arabian Sea.

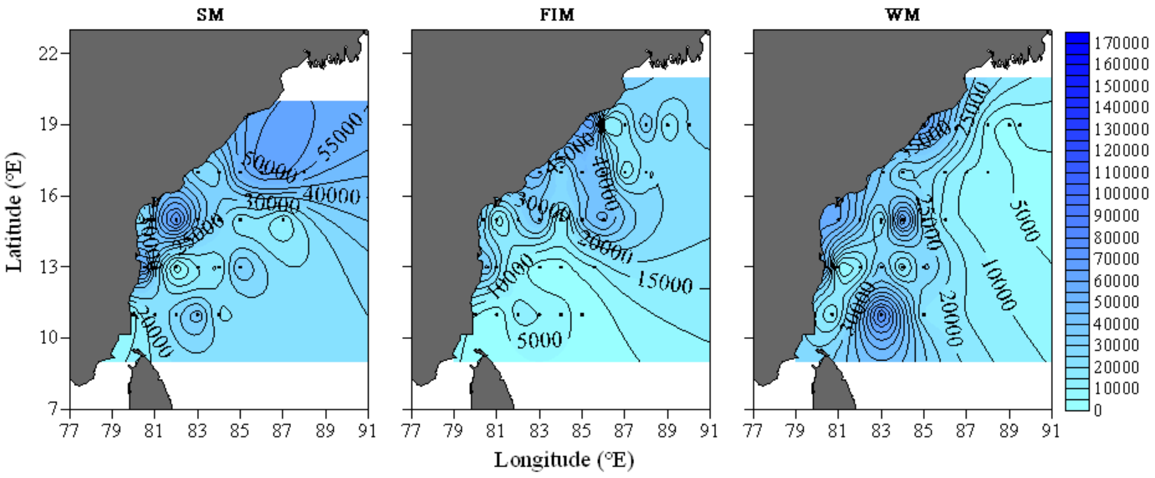

Figure 71. Distribution of chaetognath abundance (ind / 1000 m^3) along mixed layer depth in the Bay of Bengal.

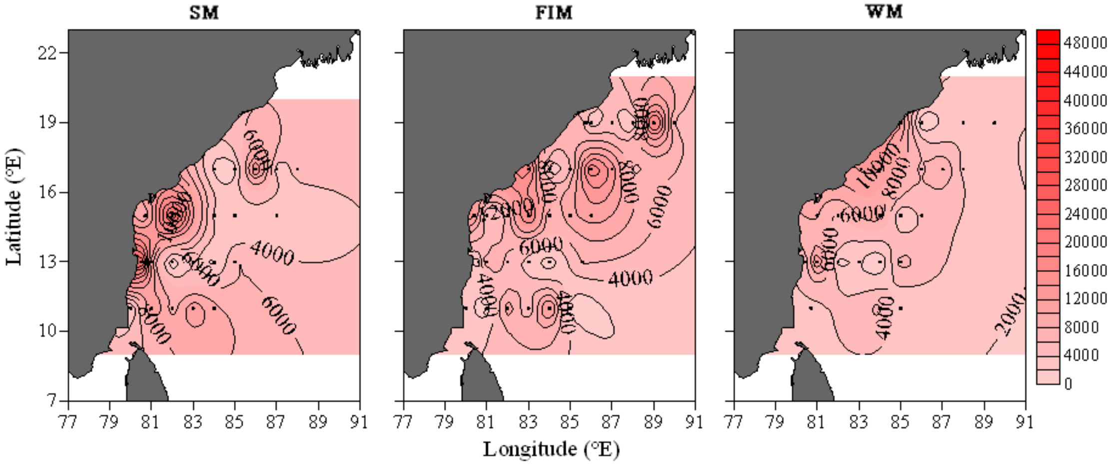

Figure 72. Distribution of chaetognath abundance (ind / 1000 m^3) along thermocline in the Bay of Bengal.

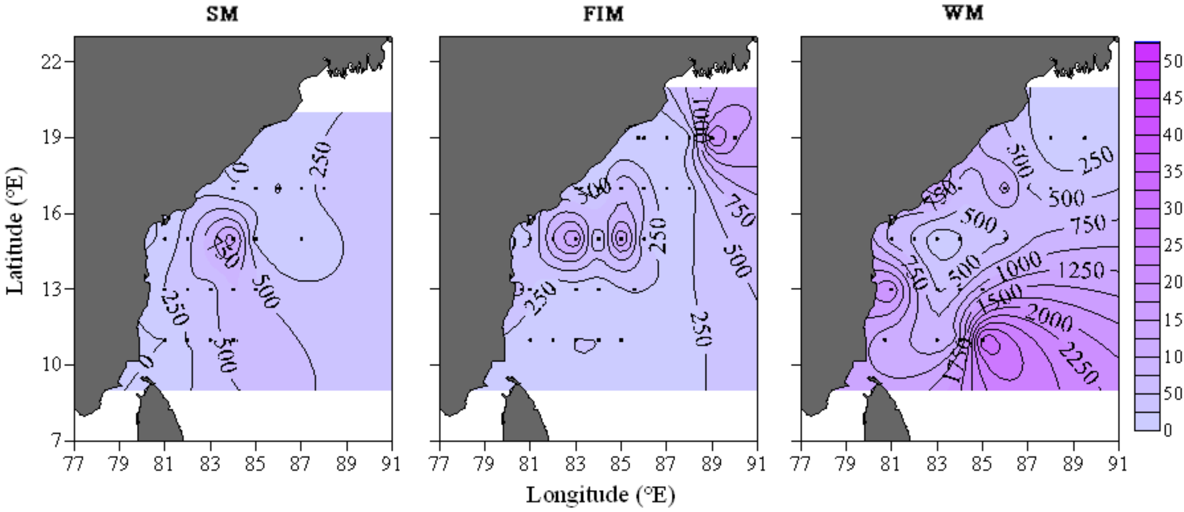

Figure 73. Distribution of chaetognath abundance (ind / 1000 m^3) along BT – 300 m depth in the Bay of Bengal.

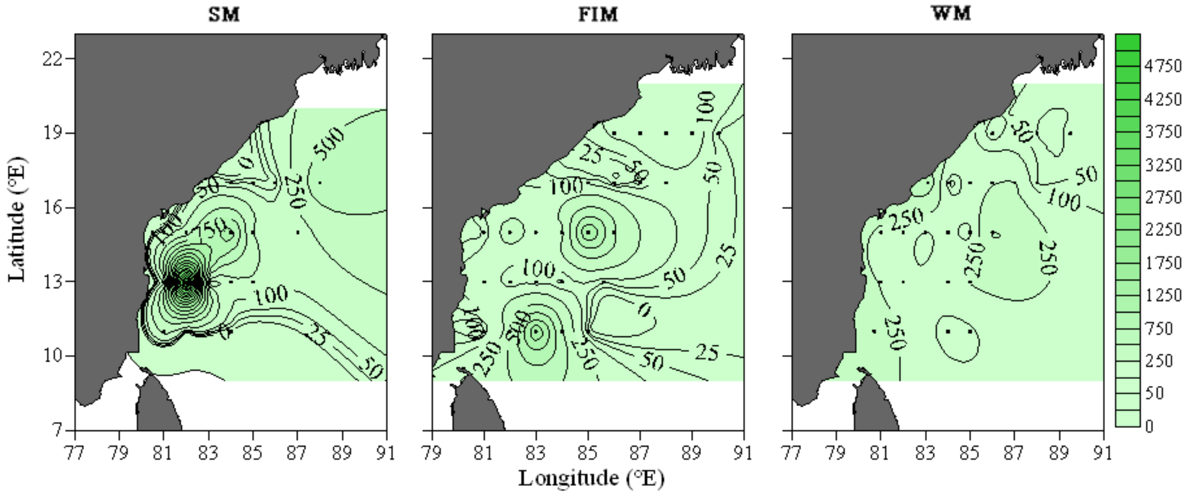

Figure 74. Distribution of chaetognath abundance (ind / 1000 m^3) along 300 – 500 m depth in the Bay of Bengal.

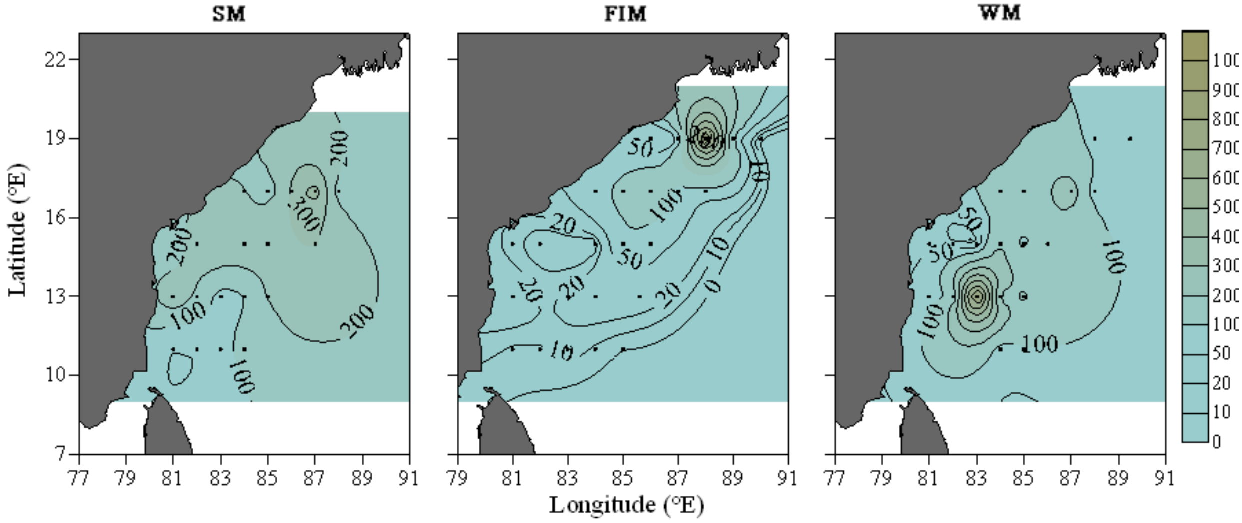

Figure 75. Distribution of chaetognath abundance (ind / 1000 m^3) along 500 – 1000 m depth in the Bay of Bengal.

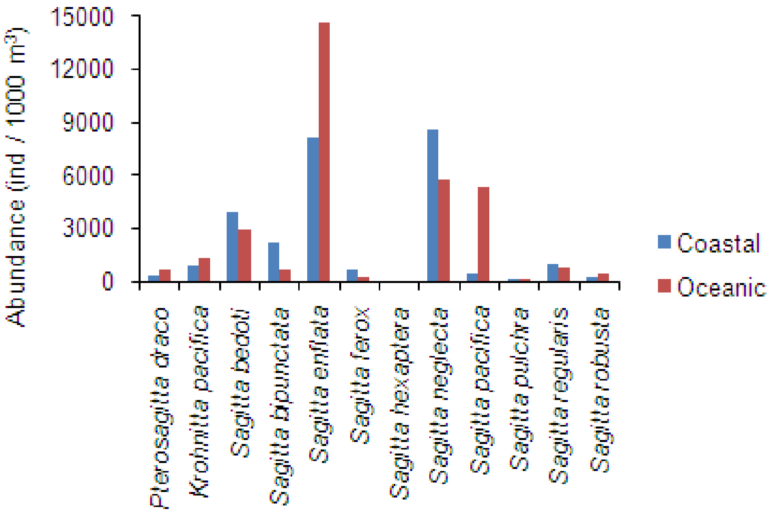

Figure 76. Variation of chaetognath species abundance along coastal and oceanic stations during summer monsoon in the Bay of Bengal.

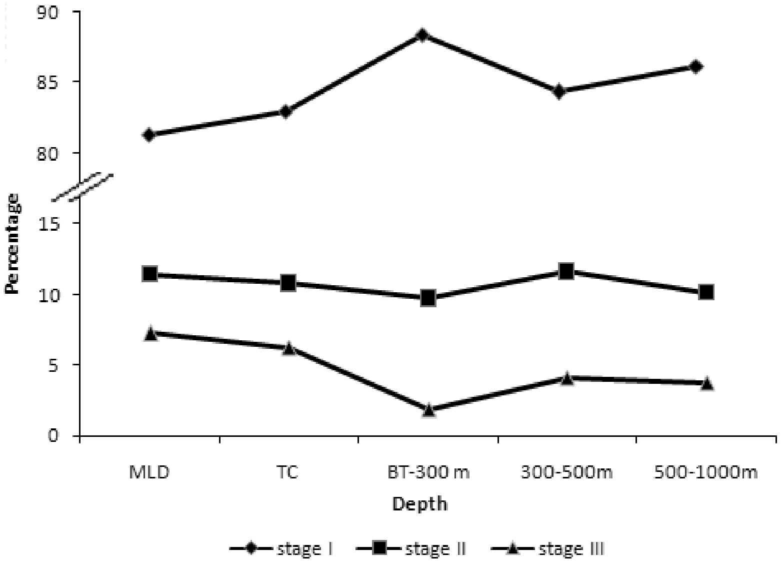

Figure 77. Depth wise percentage composition of different maturity stages of chaetognath population during fall inter monsoon in the Bay of Bengal.

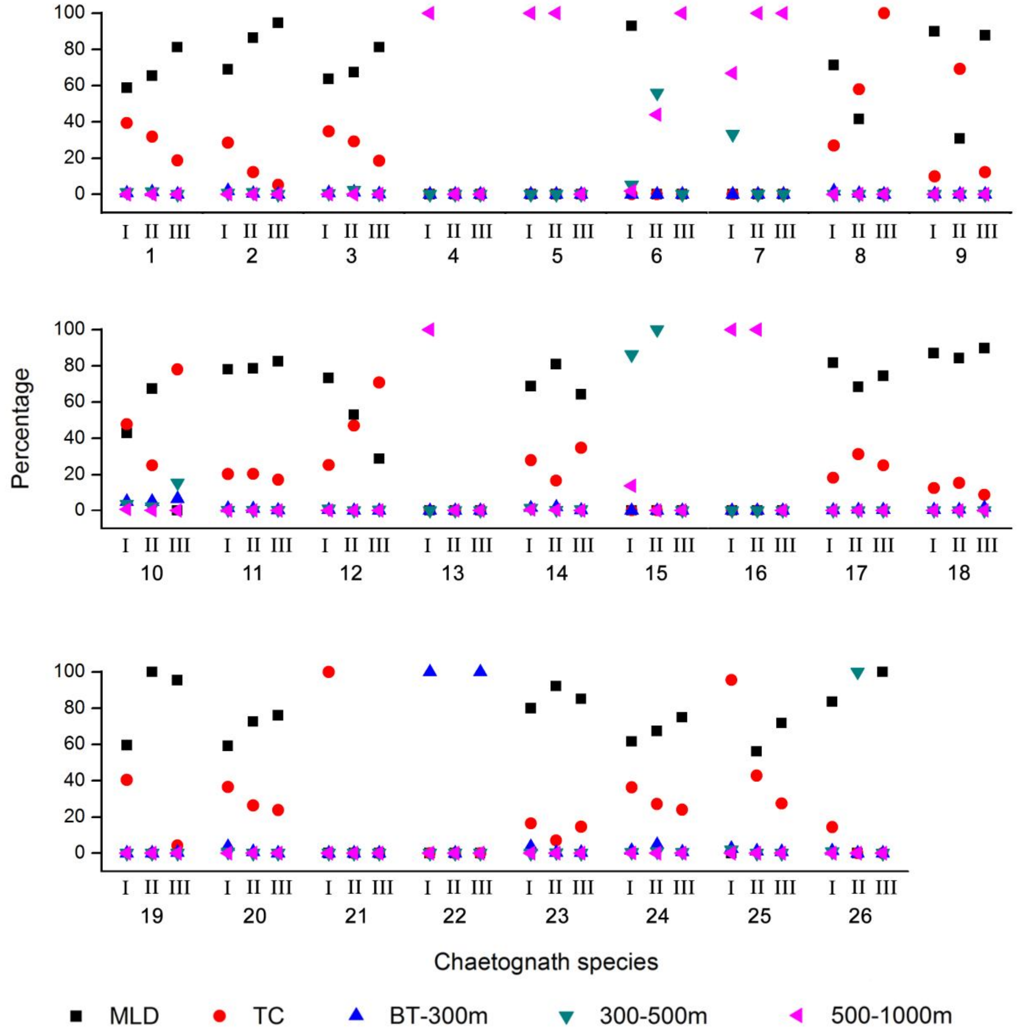

Figure 78. Vertical distribution of different maturity stages of chaetognath species in different depth layers during fall inter monsoon in the Bay of Bengal. The numerics in the x-axis corresponds to the following species:1. *Pterosagitta draco*, 2. *Krohnitta pacifica*, 3. *K. subtilis*, 4. *Eukrohnia bathypelagica*, 5. *E. hamata*, 6. *E. minuta*, 7. *E. fowleri*, 8. *Sagitta bipunctata*, 9. *S. bedfordii*, 10. *S. decipiens*, 11. *S. enflata*, 12. *S. ferox*, 13. *S. gazellae*, 14. *S. hexaptera*, 15. *S. macrocephala,* 16. *S. maxima*, 17*. S. minima*, 18. *S. neglecta*, 19. *S. oceania*, 20. *S. pacifica*, 21. *S. planktonis*, 22. *S. pulchra*, 23. *S. regularis*, 24. *S. robusta*, 25. *S. tasmanica*, 26. *S. zetesios*.

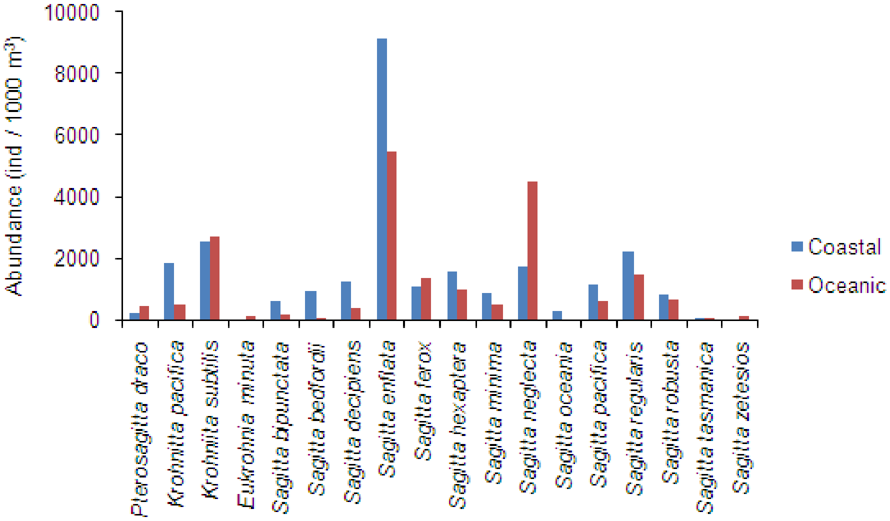

Figure 79 Variation of chaetognath species abundance along coastal and oceanic stations during fall inter monsoon in the Bay of Bengal.

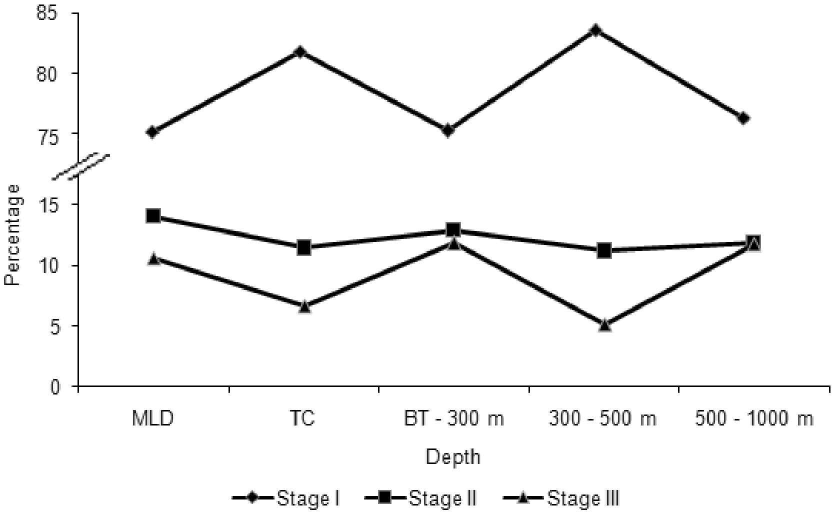

Figure 80. Depth wise percentage composition of different maturity stages of chaetognath population during winter monsoon in the Bay of Bengal.

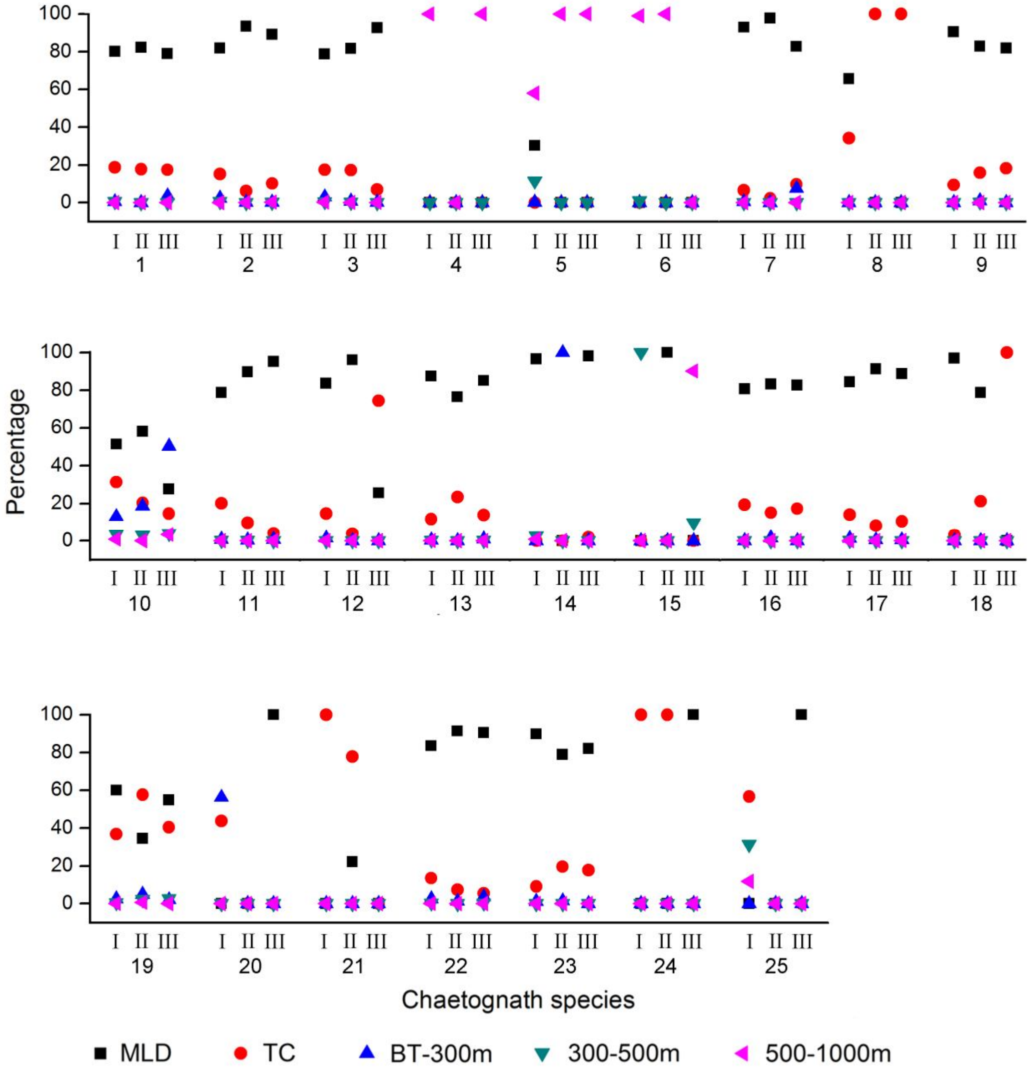

Figure 81. Vertical distribution of different maturity stages of chaetognath species in different depth layers during winter monsoon in the Bay of Bengal. The numerics in the x-axis corresponds to the following species: 1. *Pterosagitta draco*, 2. *Krohnitta pacifica*, 3. *K. subtilis*, 4. *Eukrohnia bathypelagica*, 5. *E. fowleri*, 6. *E. hamata*, 7. *S. bedfordii*, 8. *S. bedoti*, 9.*Sagitta bipunctata*, 10. *S. decipiens*, 11. *S. enflata*, 12. *S. ferox*, 13. *S. hexaptera*, 14. *S. macrocephala* 15. *S. maxima*, 16. *S. minima*, 17. *S. neglecta*, 18. *S. oceania*, 19. *S. pacifica,* 20. *S. planktonis*, 21. *S. pulchra*, 22. *S. regularis*, 23. *S. robusta*, 24. *S. tasmanica*, 25. *S. zetesios*.

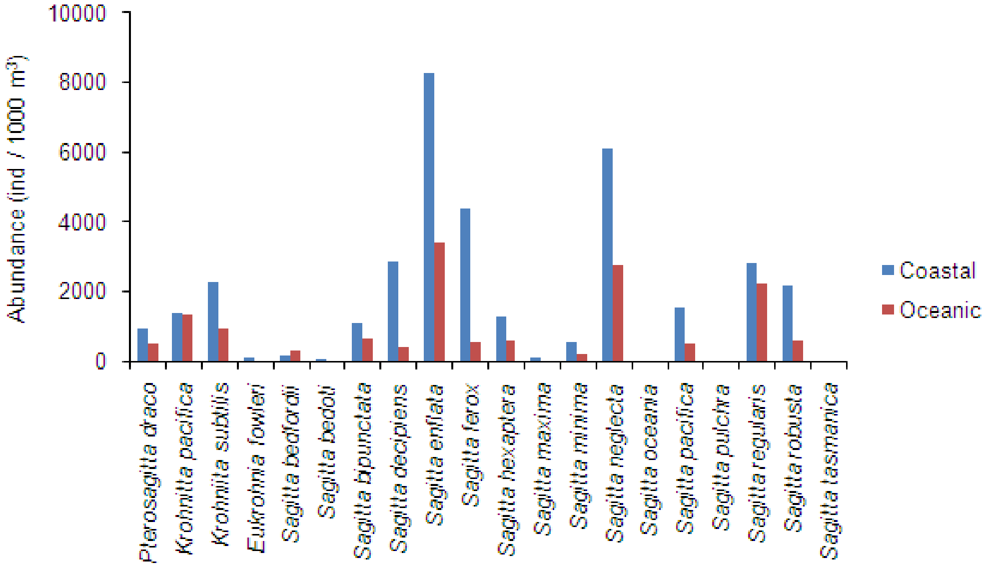

Figure 82. Variation of chaetognath species abundance along coastal and oceanic stations during winter monsoon in the Bay of Bengal.

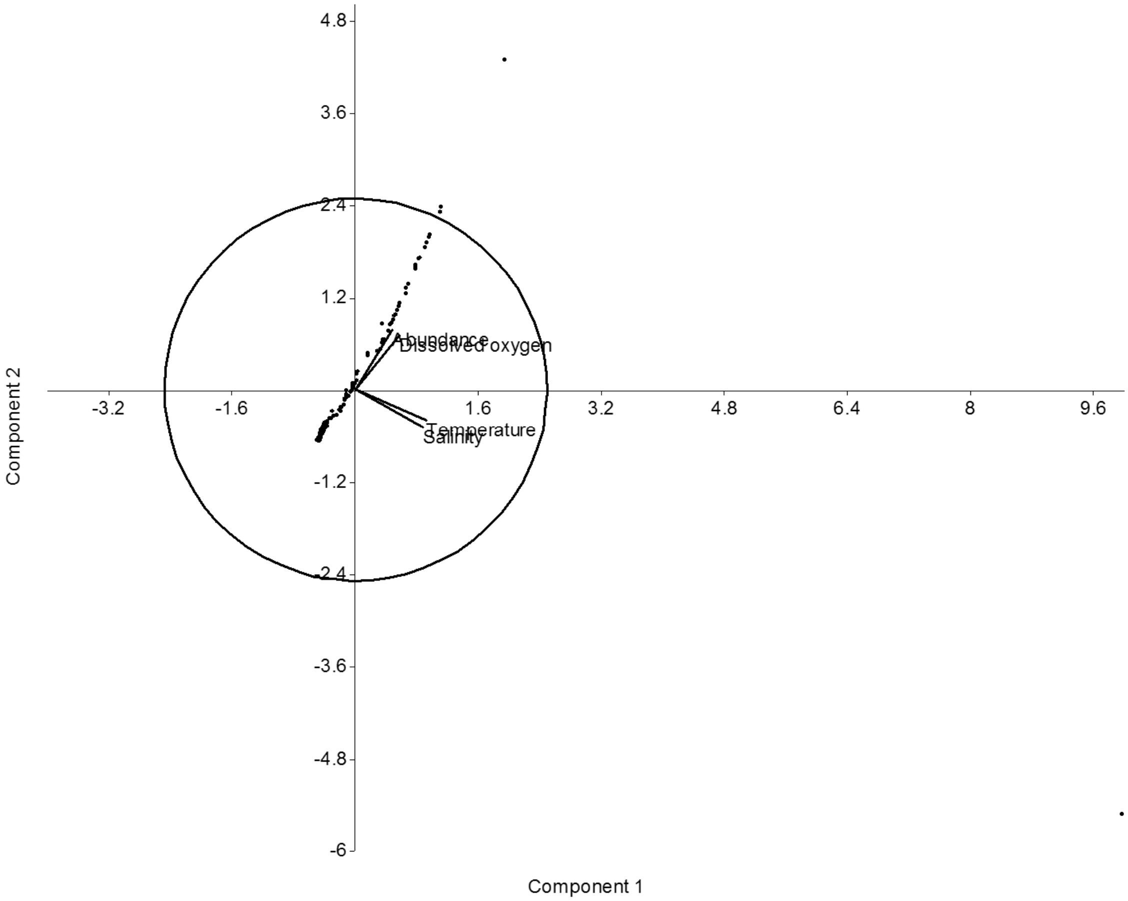

Figure 83. PCA biplot showing the internal relationships of biotic and abiotic parameters during summer monsoon in the Arabian Sea.

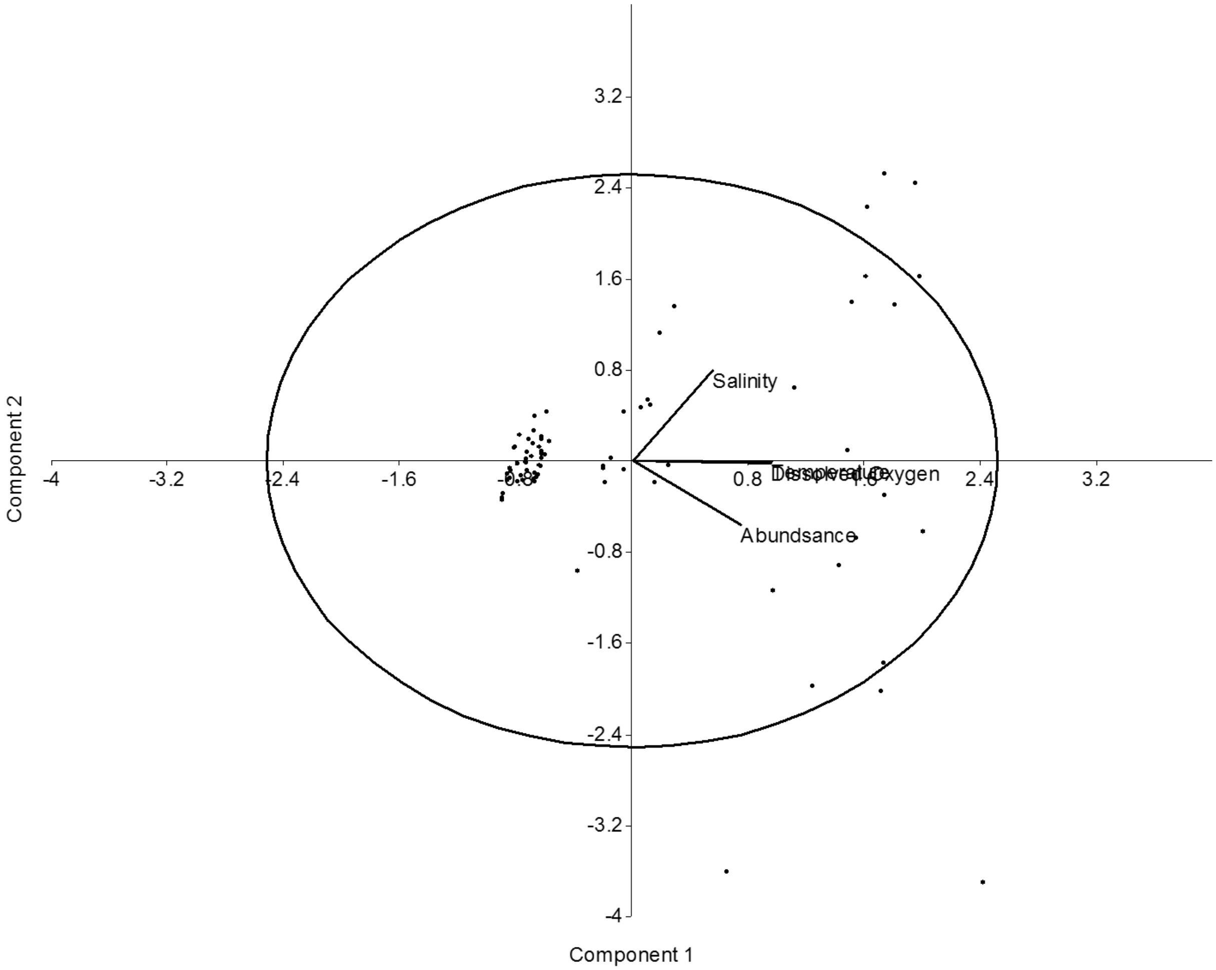

Figure 84. PCA biplot showing the internal relationships of biotic and abiotic parameters during fall inter monsoon in the Arabian Sea.

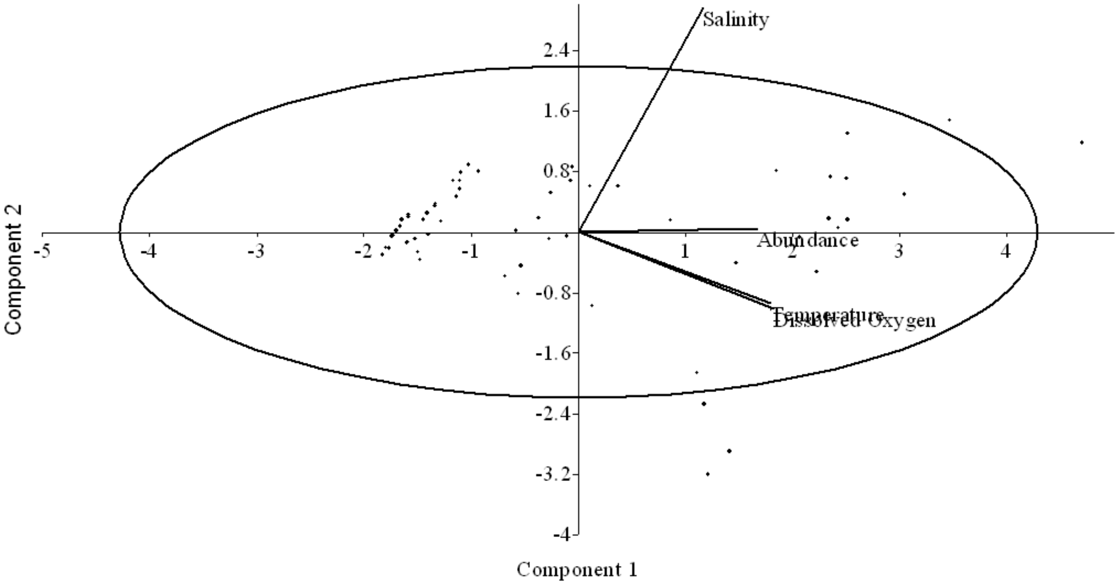

Figure 85. PCA biplot showing the internal relationships of biotic and abiotic parameters during winter monsoon in the Arabian Sea.

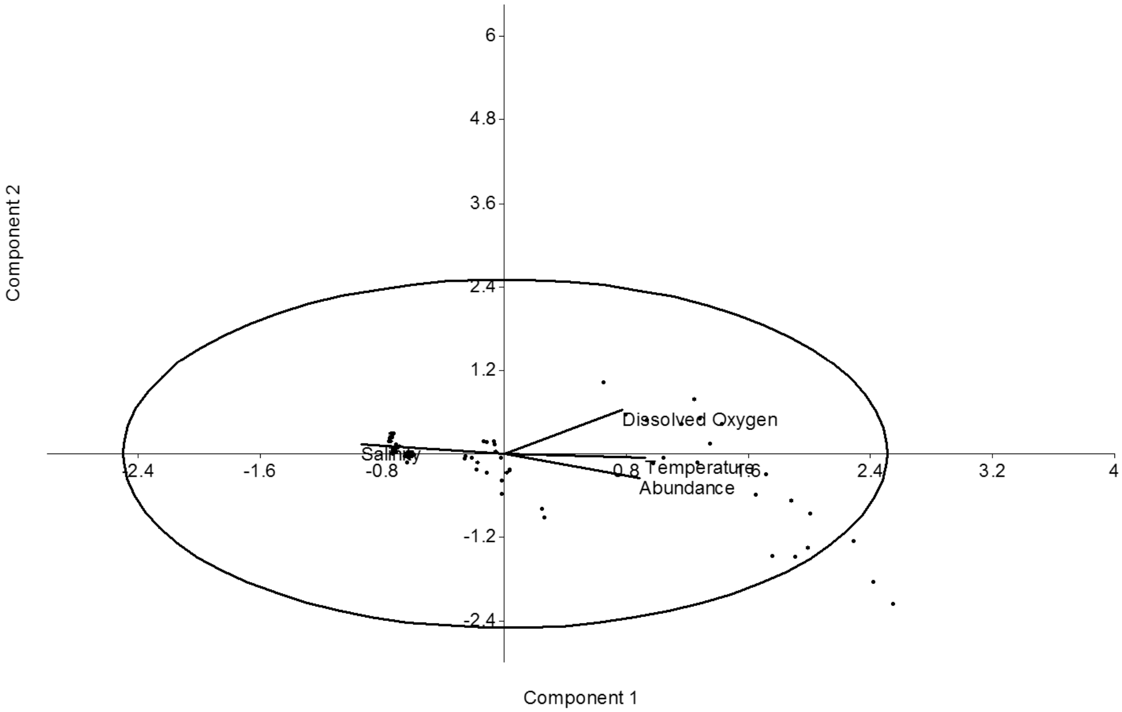

Figure 86. PCA biplot showing the internal relationships of biotic and abiotic parameters during summer monsoon in the Bay of Bengal.

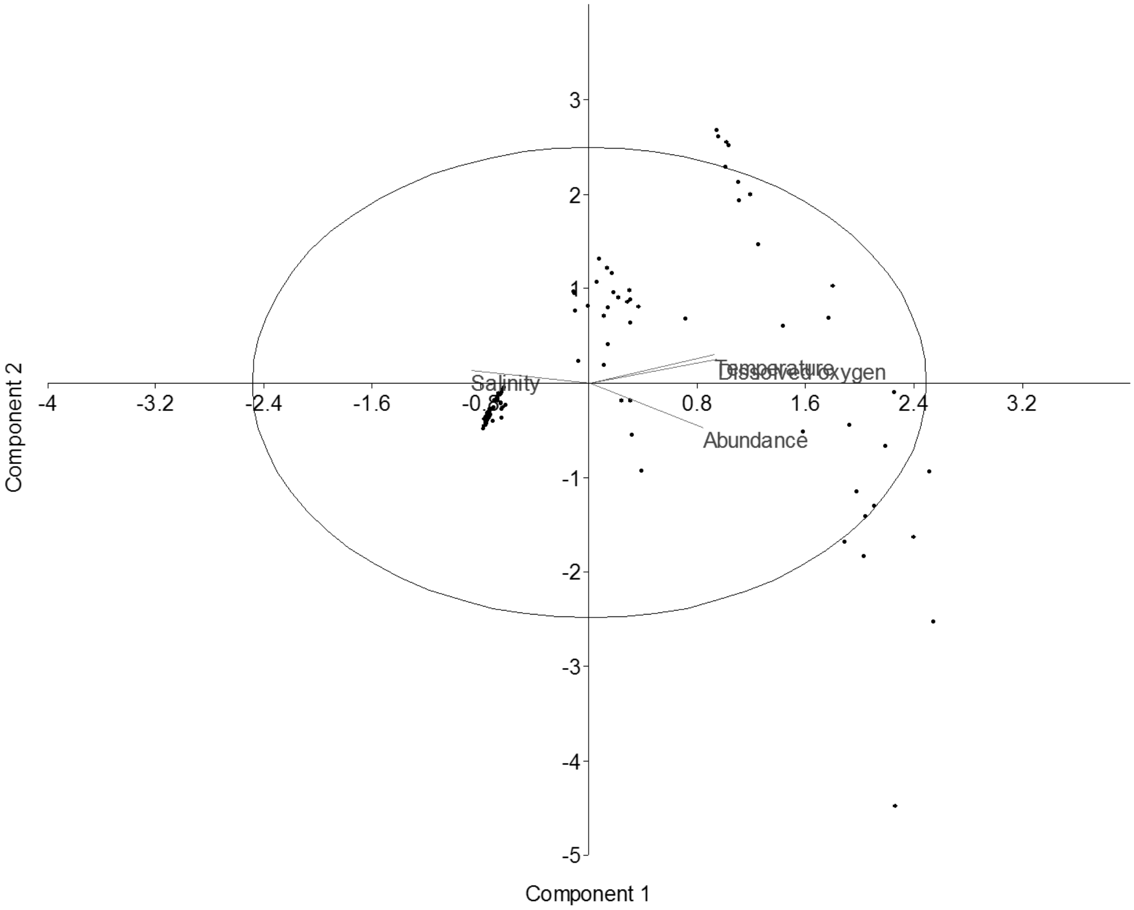

Figure 87. PCA biplot showing the internal relationships of biotic and abiotic parameters during fall inter monsoon in the Bay of Bengal.

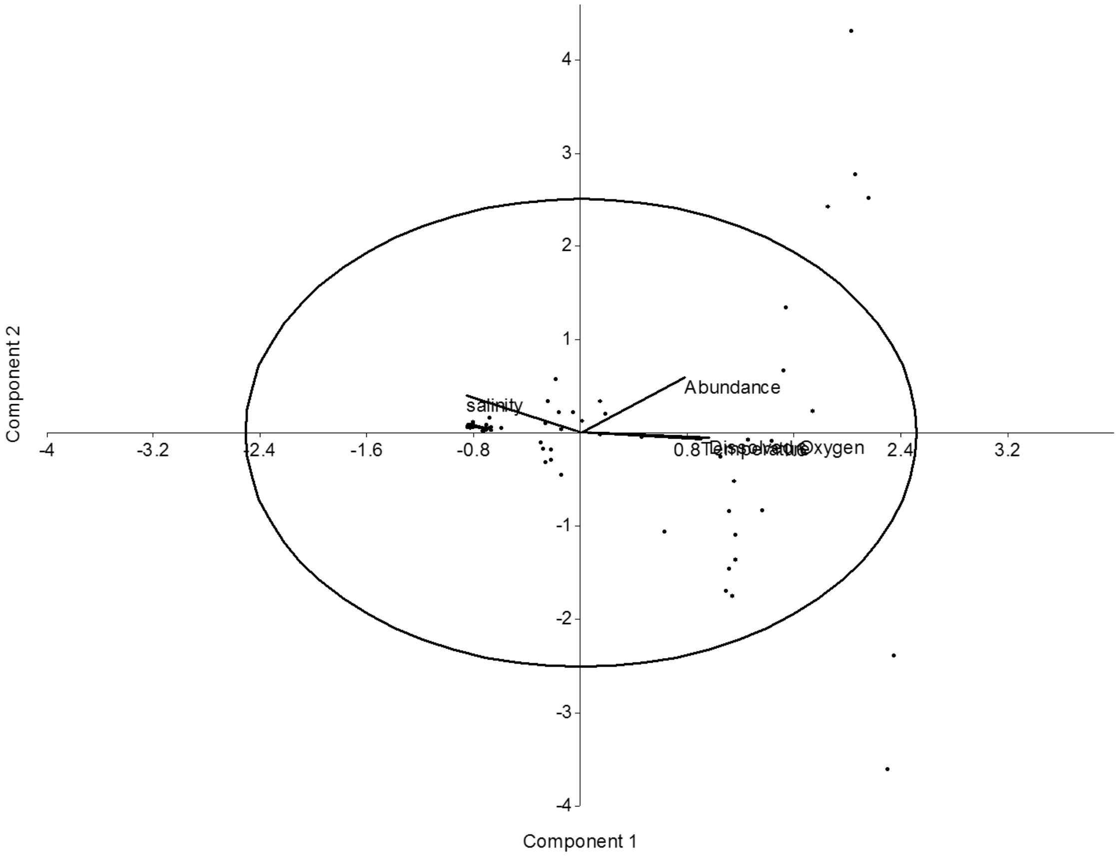

Figure 88. PCA biplot showing the internal relationships of biotic and abiotic parameters during winter monsoon in the Bay of Bengal.

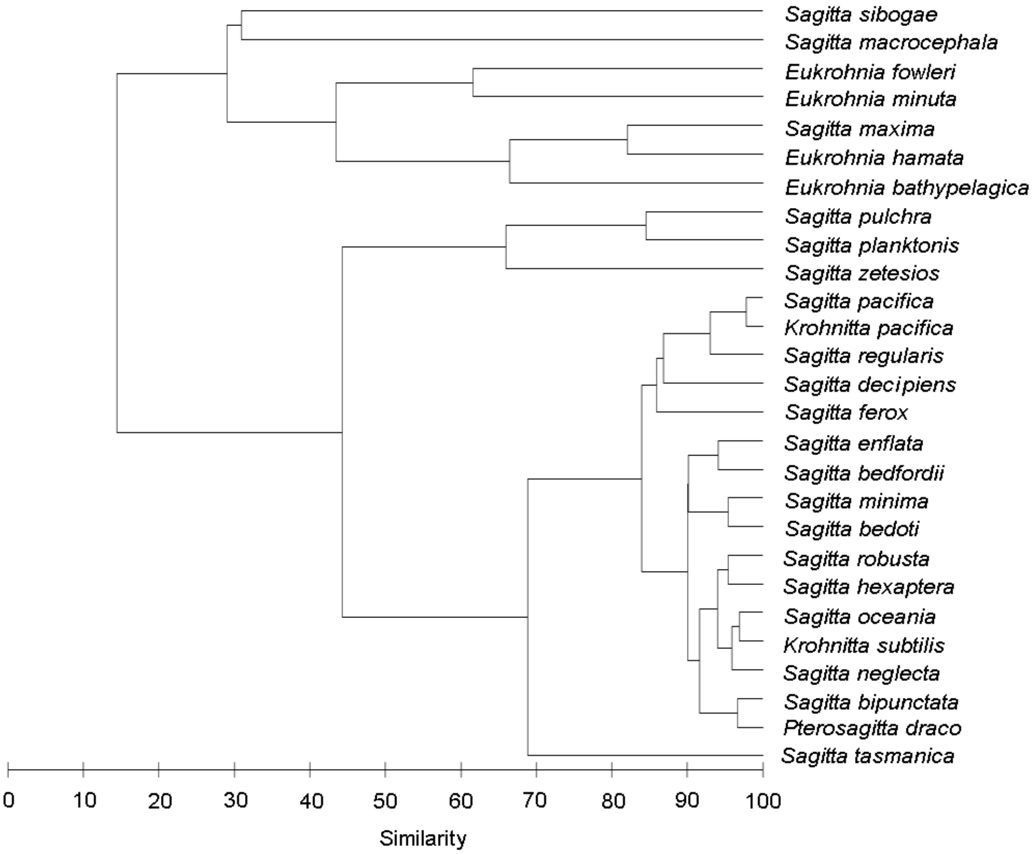

Figure 89. Cluster plot displaying the affinity between different chaetognath species based on their habitat preferences during summer monsoon in the Arabian Sea.

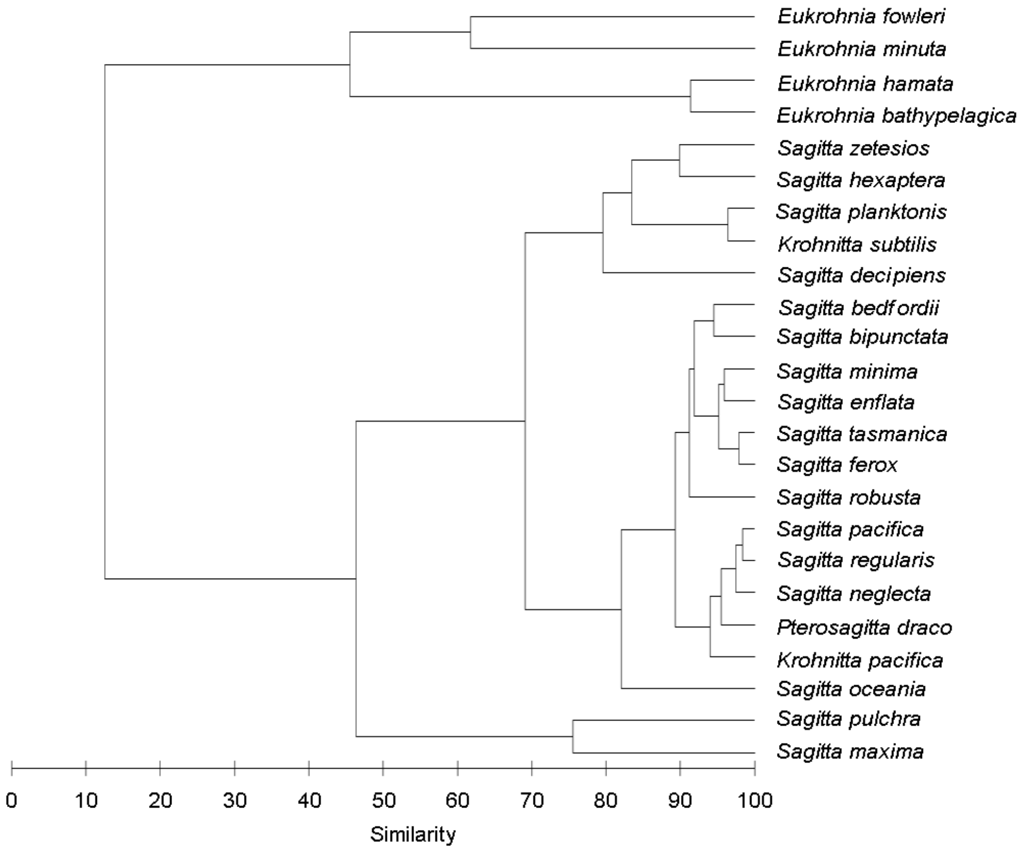

Figure 90. Cluster plot displaying the affinity between different chaetognath species based on their habitat preferences during fall inter monsoon in the Arabian Sea.

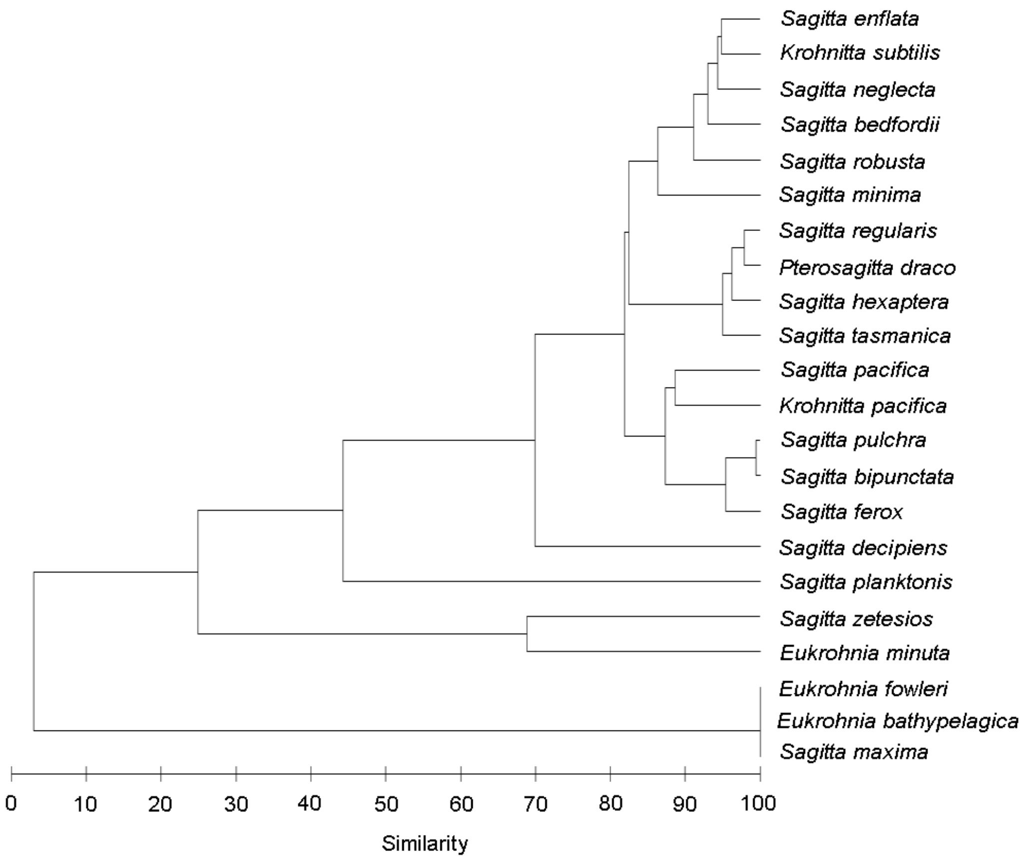

Figure 91. Cluster plot displaying the affinity between different chaetognath species based on their habitat preferences during winter monsoon in the Arabian Sea.

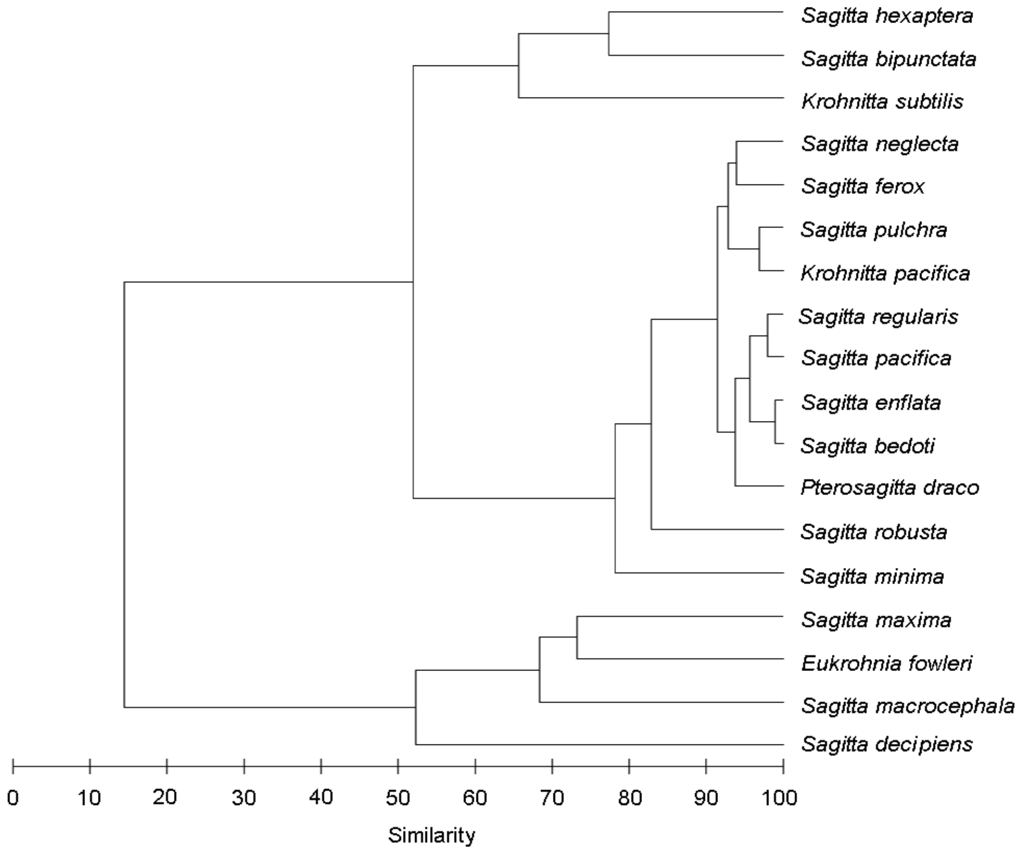

Figure 92. Cluster plot displaying the affinity between different chaetognath species based on their habitat preferences during summer monsoon in the Bay of Bengal.

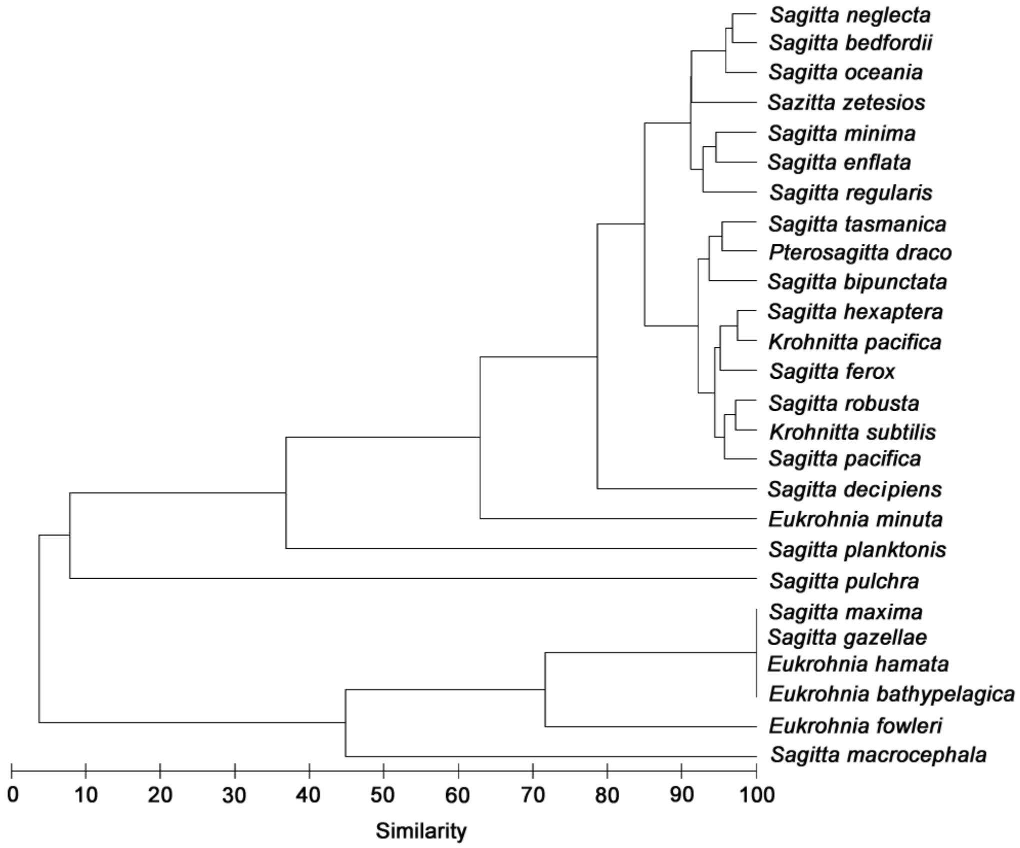

Figure 93. Cluster plot displaying the affinity between different chaetognath species based on their habitat preferences during fall inter monsoon in the Bay of Bengal.

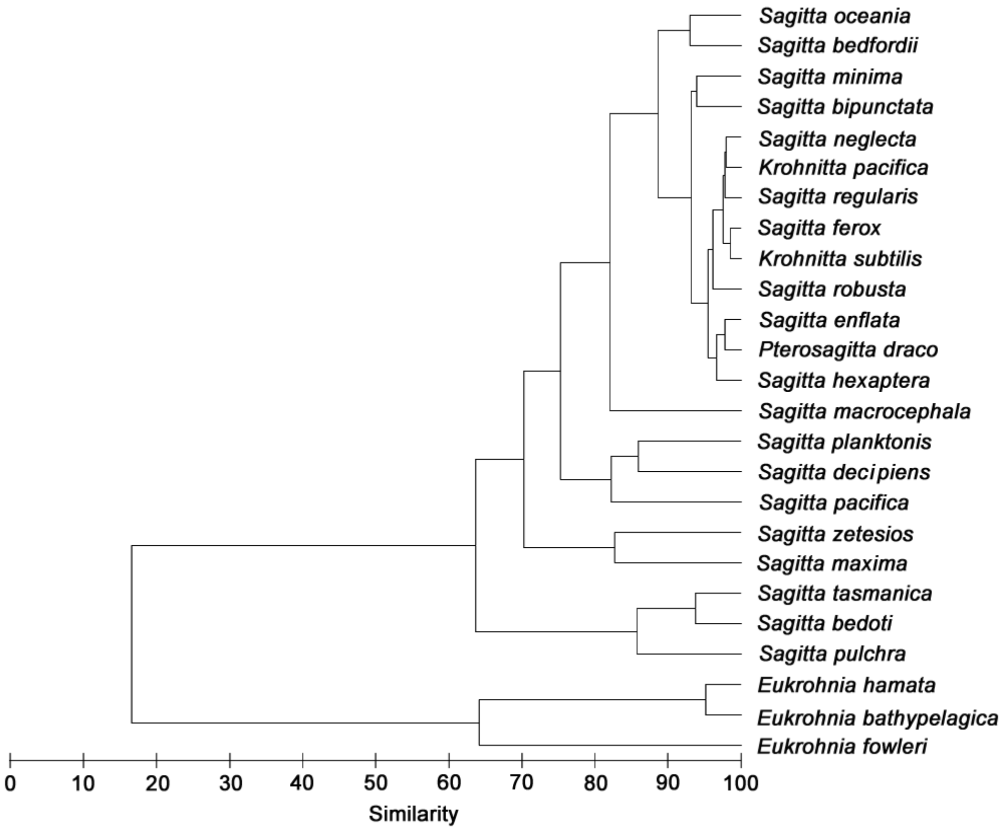

Figure 94. Cluster plot displaying the affinity between different chaetognath species based on their habitat preferences during winter monsoon in the Bay of Bengal.

Table 1. Average abundance of chaetognath species (ind / 1000 m^3) in different depth strata during summer monsoon in the Arabian Sea.

Species	MLD	TC	BT-300m	300-500m	500-1000m
Pterosagitta draco	430	153	2	4	0
Krohnitta pacifica	313	147	22	1	0
K. subtilis	802	146	14	1	0
Eukrohnia bathypelagica	0	0	0	0	8
E. hamata	0	0	0	8	7
E. minuta	0	5	3	17	4
E. fowleri	0	3	5	0	4
Sagitta bipunctata	533	170	3	16	0
S. bedoti	359	58	0	0	0
S. bedfordii	181	28	4	2	1
S. decipiens	680	320	166	25	28
S. enflata	4243	505	113	5	3
S. ferox	567	82	118	6	0
S. hexaptera	1146	303	4	6	1
S. macrocephala	0	0	7	1	0
S. maxima	0	0	0	1	4
S. minima	137	21	0	2	0
S. neglecta	1420	392	38	1	0
S. oceania	150	31	4	0	0
S. regularis	897	298	99	6	1
S. robusta	524	126	3	0	0
S. pacifica	183	100	16	<1	0
S. planktonis	0	30	3	0	0
S. pulchra	0	12	0	0	0
S. sibogae	0	0	0	8	0
S. tasmanica	37	0	0	0	0
S. zetesios	8	31	3	3	0

Table 2. Average abundance of chaetognath species (ind / 1000 m^3) in different depth strata during fall inter monsoon in the Arabian Sea.

Species	MLD	TC	BT-300 m	300-500 m	500-1000 m
Pterosagitta draco	394	88	0	0	0
Krohnitta pacifica	2336	814	9	2	2
K. subtilis	139	270	0	4	0
Eukrohnia bathypelagica	0	0	3	0	2
E. hamata	0	0	3	0	4
E. minuta	0	9	35	46	11
E fowleri	0	0	0	35	11
Sagitta bipunctata	1269	156	29	1	0
S. bedfordii	308	21	10	0	0
S. decipiens	390	592	200	60	6
S. enflata	13747	1420	47	5	<1
S. ferox	422	53	<1	2	0
S. hexaptera	1473	697	14	54	1
S. maxima	5	34	1	1	1
S. minima	727	88	0	0	0
S. neglecta	3245	728	31	0	<1
S. oceania	713	4	15	0	0
S. regularis	2692	614	13	3	1
S. robusta	1882	78	4	1	0
S. pacifica	2376	601	17	2	1
S. planktonis	9	18	0	1	0
S. pulchra	0	28	6	0	1
S. tasmanica	173	26	<1	1	0
S. zetesios	33	25	0	3	0
Unidentified	58	111	39	2	0

Table 3. Average abundance of chaetognath species (ind / 1000 m^3) in different depth strata during winter monsoon in the Arabian Sea.

Species	MLD	TC	BT - 300m	300 - 500m	500 - 1000m
Pterosagitta draco	139	27	0	0	0
Krohnitta pacifica	257	270	6	6	1
K. subtilis	1047	369	86	3	1
Eukrohnia bathypelagica	0	0	0	0	1
E. minuta	0	0	11	0	2
E. fowleri	0	0	0	0	3
Sagitta bipunctata	357	215	0	0	0
S. bedfordii	402	169	54	0	0
S. decipiens	142	471	65	7	3
S. enflata	4704	991	417	11	1
S. ferox	190	132	0	3	0
S. hexaptera	701	148	0	1	1
S. maxima	0	0	0	0	3
S. minima	48	45	11	0	0
S. neglecta	1718	494	91	0	0
S. regularis	2415	391	0	0	1
S. robusta	788	458	55	5	1
S. pacifica	148	238	-	1	-
S. planktonis	-	9	-	-	-
S. pulchra	35	22	-	-	-
S. tasmanica	128	30	-	1	-
S. zetesios	27	-	66	-	2

Table 4. Average abundance of chaetognath species (ind / 1000 m^3) in different depth strata during summer monsoon in the Bay of Bengal.

Species	MLD	TC	BT-300 m	300 - 500 m	500 - 1000 m
Pterosagitta draco	771	84	1	15	1
Krohnitta pacifica	1789	180	1	1	<1
K. subtilis	0	30	<1	2	0
Eukrohnia fowleri	0	0	52	37	114
Sagitta bedoti	2801	395	4	15	<1
S. bipunctata	1068	3213	18	68	8
S. decipiens	3	95	218	179	68
S. enflata	12743	1720	22	78	6
S. ferox	278	16	0	3	0
S. hexaptera	20	18	<1	8	1
S. lyra	0	0	0	0	0
S. minima	39	0	0	0	0
S. neglecta	8043	431	11	4	7
S. pacifica	2643	507	7	19	2
S. pulchra	98	11	0	0	0
S. regularis	1106	211	7	6	3
S. robusta	427	205	2	0	0
S. macrocephala	0	0	0	<1	1
S. maxima	0	0	0	4	4

Table 5. Average abundance of chaetognath species (ind / 1000 m^3) in different depth strata during fall inter monsoon in the Bay of Bengal.

Species	MLD	TC	BT-300m	300-500m	500-1000m
Pterosagitta draco	333	209	5	7	0
Krohnitta pacifica	1202	448	33	13	2
K. subtilis	1909	908	28	24	6
Eukrohnia bathypelagica	0	0	0	0	5
E. hamata	0	0	0	0	7
E. minuta	60	0	0	5	3
E. fowleri	0	0	0	8	21
S. bipunctata	395	218	10	0	0
S. bedfordii	408	61	<1	0	0
S. decipiens	932	961	122	89	13
S. enflata	7125	1803	122	36	2
S. ferox	1131	480	6	17	1
S gazellae	0	0	0	0	<1
S. hexaptera	1211	432	27	22	7
S. macrocephala	0	0	0	4	1
S. maxima	0	0	0	0	1
S. minima	672	175	2	0	0
S. neglecta	2382	337	14	2	<1
S .oceania	216	22	<1	0	0
S. pacifica	874	488	51	10	1
S. planktonis	0	3	0	0	0
S. pulchra	0	0	1	0	0
S. regularis	1680	322	73	1	<1
S. robusta	710	373	22	7	2
S. tasmanica	48	38	1	<1	0
S. zetesios	80	13	1	2	0

Table 6. Average abundance of chaetognath species (ind / 1000 m^3) in different depth strata during winter monsoon in Bay of Bengal.

Species	MLD	TC	BT-300m	300-500m	500-1000m
Pterosagitta draco	666	153	6	5	<1
Krohnitta pacifica	1314	202	26	8	2
K. subtilis	1473	250	29	5	4
Eukrohnia bathypelagica	0	0	0	0	9
E. fowleri	24	0	<1	9	67
E. hamata	0	0	0	<1	13
Sagitta bedfordii	258	19	8	0	0
S. bedoti	10	18	0	0	0
S. bipunctata	1039	130	2	1	0
S. decipiens	1471	831	444	94	27
S. enflata	5209	1089	48	13	6
S. ferox	1986	331	32	2	5
S. hexaptera	1437	245	8	4	1
S macrocephala	112	1	5	1	<1
S. maxima	24	0	0	2	4
S. minima	321	70	1	0	0
S. neglecta	4617	713	64	10	5
S. oceania	98	7	0	0	0
S. pacifica	998	662	45	11	3
S planktonis	8	4	5	0	0
S. pulchra	1	5	0	0	0
S. regularis	2761	412	81	8	3
S. robusta	1502	212	16	<1	1
S. tasmanica	12	13	0	0	0
S. zetesios	9	1	0	1	<1
Unidentified	246	125	1	3	3

Table 7. Species diversity (H′) along different depths in the Arabian Sea.

	SM	FIM	WM
MLD	1.6 ± 0.47	1.47 ± 0.4	1.57 ± 0.32
TC	1.7 ± 0.51	1.79 ± 0.36	1.98 ± 0.23
BT - 300 m	0.96 ± 0.42	1.01 ± 0.42	1.05 ± 0.42
300 - 500 m	0.93± 0.29	1.04 ± 0.43	0.94 ± 0.37
500 - 1000 m	0.83 ± 0.23	1.14 ± 0.32	0.93 ± 0.37

Table 8. Species diversity (H′) along different depths in the Bay of Bengal.

	SM	FIM	WM
MLD	1.36 ± 0.31	1.7 ± 0.35	2.09 ± 0.19
TC	1.17 ± 0.4	1.74 ± 0.46	1.99 ± 0.24
BT - 300 m	0.92 ± 0.51	1.24 ± 0.49	1.29 ± 0.42
300 - 500 m	1.01± 0.49	1.07 ± 0.57	1.23 ± 0.5
500 - 1000 m	0.89 ± 0.45	0.99 ± 0.4	1.44 ± 0.47

Table 9. Species evenness (J′) along different depths in the Arabian Sea.

	SM	FIM	WM
MLD	0.83 ± 0.9	0.76 ± 0.12	0.8 ± 0.09
TC	0.83 ± 0.1	0.87 ± 0.07	0.9 ± 0.03
BT - 300 m	0.84 ± 0.2	0.82 ± 0.17	0.93 ± 0.08
300 - 500 m	0.93 ± 0.8	0.89 ± 0.12	0.89 ± 0.09
500 - 1000 m	0.89 ± 0.11	0.92 ± 0.1	0.94 ± 0.08

Table 10. Species evenness (J′) along different depths in the Bay of Bengal.

	SM	FIM	WM
MLD	0.71 ± 0.13	0.85 ± 0.09	0.85 ± 0.04
TC	0.67 ± 0.19	0.88 ± 0.07	0.84 ± 0.07
BT - 300 m	0.67 ± 0.18	0.91 ± 0.11	0.74 ± 0.11
300 - 500 m	0.72 ± 0.21	0.89 ± 0.13	0.77 ± 0.16
500 - 1000 m	0.75 ± 0.15	0.89 ± 0.15	0.84 ± 0.12

Chapter 7

Long term monitoring

7.1. Physico-chemical variables

In AS, long term changes in sea surface temperature (SST) for the period 1960 – 2005 was determined on the basis of the data extracted from Prasanna Kumar et al. (2010b). This data was based on the 5 year running mean of the monthly mean SST of AS (0 - 25° N and 45 - 80° E), using the International Comprehensive Ocean Atmospheric Data Set (ICOADS). There was an increasing trend in the SST distribution during this period (Fig. 95) and the rate of increase was relatively higher after 1995 in comparison with the previous years.

In BoB, the long term monitoring of SST for the period of 1901–2000 was determined based on the monthly mean SST data in Jadhav and Munot (2009) which was originally derived from the global sea ice sea surface temperature (GISST) dataset (version 2.3 b, Rayner et al.,1996). The decadal mean SST data of the BoB (2.5 – 22.5° N and 79.5 – 95.5° E) showed an increasing tendency from 1901 to the present period (Fig. 96).

Unlike SST, long term data sets on salinity and dissolved oxygen in both AS and BoB are not available due to lack of continuous monitoring of these parameters. But the recent reports (Stramma et al., 2008) on dissolved oxygen distribution clearly indicate the expansion of oxygen minimum zone (OMZ) in the tropical Oceans.

7.2. Long term changes in abundance

Chaetognath abundance in the upper 202 m in AS (7657 ind / 1000 m^3) recorded during the present study was much higher than that recorded earlier from the upper 200 m (5272 ind / 1000 m^3) during IIOE (1960 – 65). In the present study a total of 23 chaetognath species were observed in contrast to the 14 species recorded earlier during the IIOE period (Fig. 97). Most of the epiplanktonic species (*K. pacifica, K. subtilis, S. neglecta, S. regularis, S. ferox, S. minima, S. pacifica*) showed relatively higher abundance in the present study (Fig. 97). *S. enflata*, which is the dominant species in the upper layers, was relatively less abundant in the present collections compared to the earlier ones. The mesoplanktonic species *S. decipiens, S. planktonis* and *S.maxima* which were not recorded in upper 200 m during the IIOE period, was observed in the present study though in small numbers. Similarly, a few individuals of two mesoplanktonic species of genus *Eukrohnia* (*E. minuta* and *E. fowleri*) were found only in the present samples. However, most of the species recorded presently had relatively higher abundance in the northern part of the AS than its southern counterpart (Fig. 98).

More or less a similar scenario in abundance pattern was observed in BoB also. The abundance in the upper 168 m during the present period (11250 ind / 1000 m^3) was relatively higher than that recorded during IIOE programme (9748 ind / 1000 m^3). In the present study though the abundance observed in the northern BoB (13056 ind / 1000 m^3) was higher than that of IIOE period (9748 ind / 1000 m^3), in the southern BoB (9228 ind / 1000 m^3) it was less than the values recorded earlier. In the IIOE collections, 14 species of chaetognath were recorded from BoB whereas in the present study 24 species were collected (Fig. 99). In the northern BoB all 24 species were observed, but in the southern part only 21 species prevailed. Though most of the species showed relatively higher abundance compared to earlier period, the most dominant species *S. enflata* was less in abundance in the present samples (almost half that of IIOE) (Fig. 99). *P. draco* and *S. pacifica* were the two species which were relatively less abundant. The mesoplanktonic species *S. decipiens, S. macrocephala, S. maxima, E. minuta, and E. fowleri* which were not recorded earlier were observed during the present study but in less numbers. Two species belonging to genus *Krohnitta* (*K. pacifica* and *K. Subtilis*) had relatively higher abundance in the present study (Fig. 99). As in the Arabian Sea, most of the species exhibited relatively higher abundance in the northern Bay of Bengal (Fig. 100). The abundance of *S. enflata, S. decipiens* and *S. pacifica* in both northern and southern BoB was comparatively less than that recorded during IIOE period.

7.3. Summary

Unlike Pacific Ocean and Atlantic Oceans, continuous monitoring of physicochemical variables is lacking in Indian Ocean. The few available data on physicochemical variables indicate some notable changes in the climatic conditions over the years. In the SST distribution an apparent increase was observed in both AS and BoB. Though a continuous monitoring on DO profile was absent from this region, results from several studies carried out in global ocean in the recent years clearly indicated the spreading of OMZ layer in the mid-depth region of the tropical ocean, restricting the habitable zone of pelagic organisms. In the present study, it was observed that both in AS and BoB, the northern region exhibited relatively higher abundance of chaetognaths and the abundance was comparatively much higher when compared to IIOE period. The species recorded were also more in the present sampling period. In AS and BoB, almost all species exhibited relatively higher abundance compared to IIOE, but the abundance of *S. enflata* and *P. draco* showed a decreasing pattern.

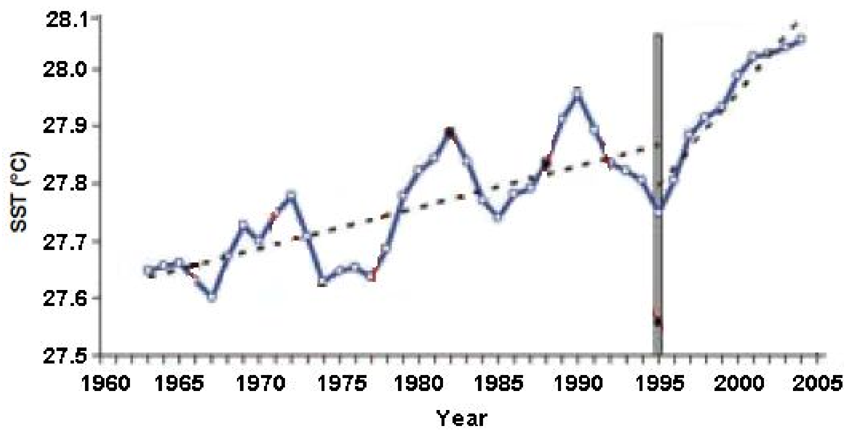

Figure 95. Sea surface temperature (SST, °C) of the Arabian Sea averaged over the basin (0° - 25° N, 45° - 80° E) during 1960 – 2005 (Redrawn from Prasannakumar et al., 2010).

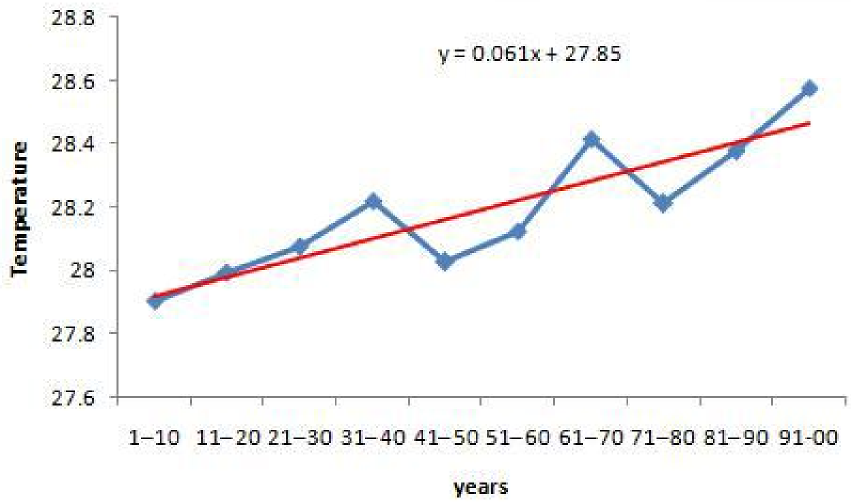

Figure 96. Sea surface temperature (SST, °C) of the Bay of Bengal averaged over the basin (2.5° - 22.5° N, 79.5° - 95.5° E) during 1901 – 2000 (Drawn from the data set of Jadhav and Munot, 2009).

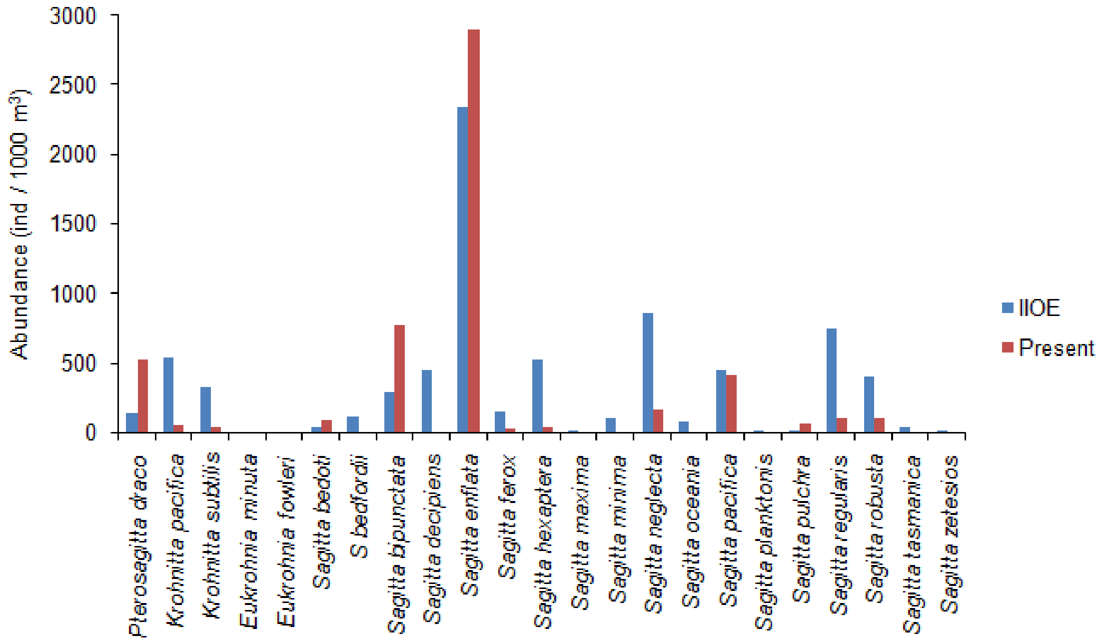

Figure 97. Comparative account of chaetognath species abundance between International Indian Ocean Expedition sampling and present period in the Arabian Sea.

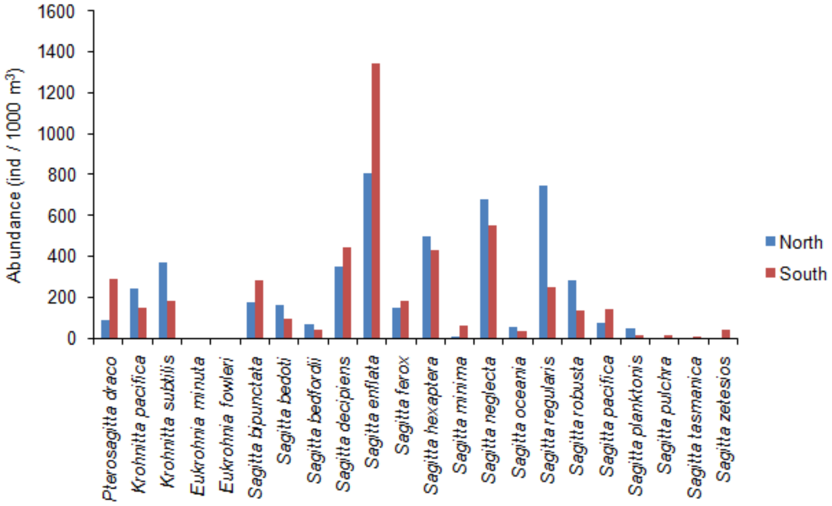

Figure 98. Comparative account of chaetognath species abundance between the upper 202 m of northern and southern part of the Arabian Sea in the present study.

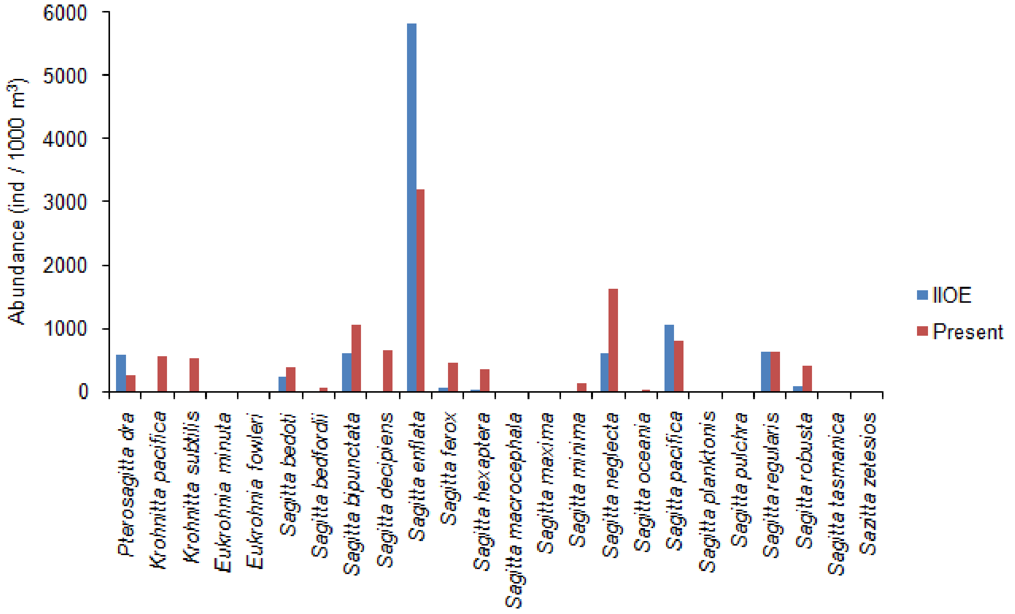

Figure 99. Comparative account of chaetognath species abundance between International Indian Ocean Expedition and present study in the Bay of Bengal.

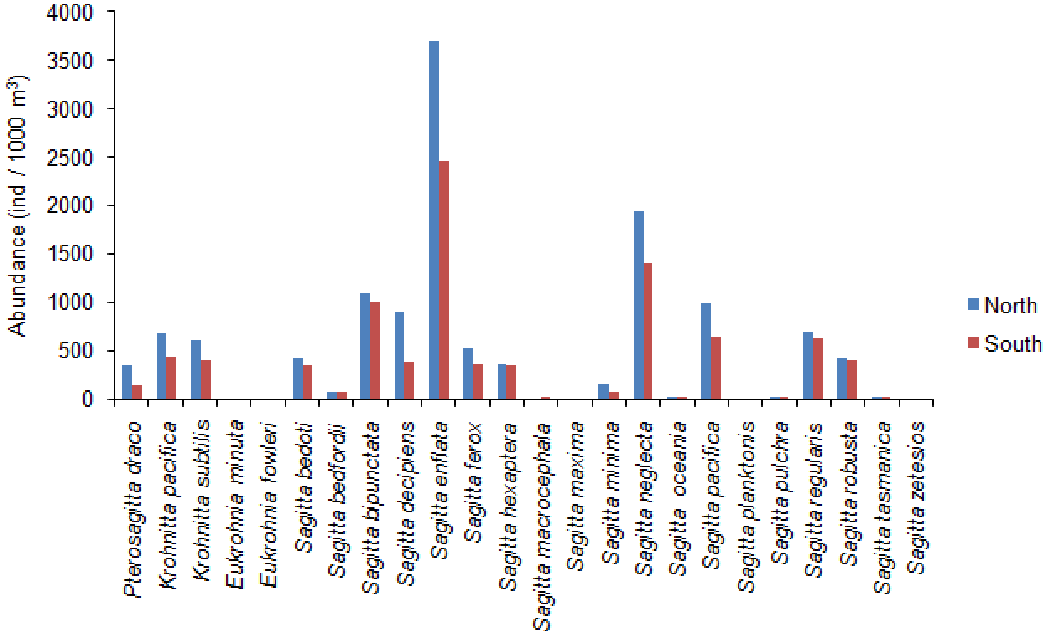

Figure 100. Comparative account of chaetognath species abundance between 168 m of northern and southern part of the Bay of Bengal in the present study.

Chapter 8

Discussion

The Arabian Sea and the Bay of Bengal, encompassing the eastern and western boundaries of the Indian subcontinent share some common characteristics in their geographic and oceanographic features. They are geographically postioned in the tropical low latitude region and have their northern boundary landlocked by Asian landmasses. Both these major ocean basins are characterized by strong monsoonal wind that reverses semiannually during southwest and northeast monsoons (Cutler and Swallow, 1984; Hasternath and Greischar, 1989; Shankar et al., 2002; McCreary et al., 2009). Soalr radiation reaching the top of the troposphere is also similar in these two ocean basins (Shenoi et al., 2002). In spite of these prominent similarities several conspicuous differences also exist among these two major ocean basins. Winds over AS, are much stronger than BoB, as this ocean basin is being bounded on its west by the highlands of East Africa (Shankar et al., 2002). This difference in the geographical features inturn leads to strong differences in the heat budget in the near surface waters of AS and BoB (Shenoi et al., 2005). A profound SST variation is reported between these two ocean basins which is often the consequence of the differences existing in the heat budget in the near surface waters of AS and BoB. In the present study, though a slight variation in the SST values was observed along different transects between AS and BoB, the difference was not statistically significant.

The average SST recorded during the SM in the AS was much higher than previously observed by Shenoi et al (2002). The AS is characterized by excessive evaporation over precipitation which is in contrast to the feature observed in BoB where precipitation exceeds evaporation. The river influx into BoB ($1.6\times10^{12}m^3y^{-1}$) is also immense when compared to AS ($0.3\times10^{12}m^3y^{-1}$). The distribution of this fresh water, predominantly seen near the riverine outlets, is largely controlled by density driven flows and prevailing winds over the bay .This surface layer low saline cap in BoB leads to a significant difference in surface salinity of AS and BoB with a range of 3 to 7 (Prasanna Kumar et al., 2002; Shenoi et al., 2002). Higher surface salinity values observed in AS during the present study also clearly supports the earlier observations. The significant difference observed between the surface salinity of AS and BoB ($P< 0.05$) further corroborates this view.

Summer monsoon

In AS, pronounced north–south variation observed in the SST and SSS distribution during the present study supports views of a prevalent north south gradation of oceanographic parameters described earlier (Wyrtki, 1971; Naqvi, 2008). This is further strengthened by the gradual increase in the thickness of OMZ from 8° to 19° N. Upwelling is a well known phenomenon during summer monsoon along the west coast of India which significantly influences the biological productivity (Banse, 1959, 1968; Ramamirtham and Jayaraman, 1960; Sharma, 1978; Muraleedharan and Prasanna Kumar, 1996; Smitha et al., 2008). In the present study also clear signatures of upwelling was evident along five stations from 8° to 19° N. Pronounced higher abundance of zooplankton observed in the upwelling areas further signifies the influence of upwelling on the zooplankton community. Similar reports on higher zooplankton standing stock associated with upwelling in this region by Haridas et al., (1980) and Madhupratap et al., (1990) also are in support of our observation.

It was observed during this study that chaetognath population formed a major share of the zooplankton community in the upwelling region. Higher chaetognath abundance in the surface and subsurface layers in upwelling stations (5.1 – 11.2 times higher than non upwelling stations) in both the northern and southern regions of AS futher signifies the role of this temporal scale physical process on the spatial abundance. The higher abundance of chaetognaths in the upwelling regions might have resulted by the horizontal aggregation of epiplanktonic chaetognath species around the upwelling centers. The higher abundance of the epiplanktonic species like *S. enflata*, *S. bipunctata*, *S. bedoti*, *S. ferox*, *S. neglecta* and *K. subtilis* along with *S. hexaptera* in the upwelling zone further strengthens the view of horizontal aggregation of the chaetognath species rather than the contribution by vertical mixing associated with upwelling. Similar report on the horizontal aggregation of copepod species in upwelling regions of Chile (Escribano and Hidalgo, 2000) also further substantiates the present observation. The ecological and biogeochemical significance of this temporal physical phenomenon is remarkable as it leads to the horizontal aggregation of organic matter towards the center of the upwelling regions.

Earlier*, E. fowleri* was reported to be mesoplanktonic in the Indian Ocean (Nair, 1978) and the Pacific Ocean (Bieri, 1959) and *E. minuta* was identified as mesoplanktonic in the Arabian Sea (Silas and Srinivasan, 1969) which was also evident in the present observation. Because of their mesoplanktonic characteristics (Nair, 1978) and also their abundance in the subsurface layers of upwelling stations, they can be considered as ideal indicators of the upwelling phenomena. The upward displacement of the deeper waters during the upwelling process might have resulted in the higher abundance of these species in subsurface waters. Similar record on chaetognath associated with upwelling was from the coastal upwelling water of Chile, where *E. hamata* was identified as the upwelling indicator (Ulloa et al., 2000, 2004). Of the total 27 species collected during the study, the dominance of only some chaetognath species (*S. enflata*, *S. ferox*, *S. hexaptera*, *S. neglecta*, *S. regularis* and *K. subtilis*) in the upwelling stations might be due to their well adaptability in the upwelling environments. As some of the upwelling stations (17° N 71° E) were located in lower sub-surface layer, which were within OMZ, the abundant chaetognath population observed in this region (*S. ferox*, *S. regularis* and *S. enflata*) might have been able to cope up with the low oxygen conditions prevailing in the environment (Longhurst, 1967; Escribano et al., 2009). In the present study, *S. bedoti* dominated in the surface upwelling region and as per earlier reports this species is known to occur in the near shore area and also in the estuarine regions (Nair, 1974). Thus, their higher abundance in the off-Cochin coastal upwelling station indicates their affinity towards the coastal upwelling event.

The strong impact of OMZ and ODW on the vertical distributional limits of chaetognath species was a significant feature observed during this study. Difference observed in the abundance of chaetognaths in the northern and southern parts of AS, except in the upwelling region, further signifies the impact of OMZ on their vertical distribution. In the northern part of AS, due to the presence of thick OMZ in the entire water column below ~ 150 m, the chaetognath community congregated mainy in the upper layers (mostly in MLD). Excluding the high abundance observed in the upwelling region, the low abundance recorded in the southern part in MLD (8261 ± 6673 ind / 1000 m^3) compared to the higher abundance in the northern part (11903 ± 7168 ind / 1000 m^3) also corroborates this view.

. The vertical distribution ranges exhibited by different chaetognath species in the study area give a better insight on the impact of OMZ on their distribution. The cosmopolitan species *S. hexaptera* has been reported as the dominant species in 200 – 500 m depth, mostly in the non OMZ region at north of 10° S in the Indian Ocean (Nair, 1978). However, the higher abundance of this species observed in the MLD during the present study might have resulted due to its tendency to avoid the oxygen deficient mid depth waters. Higher abundance of mesoplanktonic species, *S. decipiens* in MLD and TC layers also corroborates this view. Alvariño (1964a) recorded this species mostly between 150 – 900 m depth along different regions of the Pacific Ocean. In the Indian Ocean, the earlier observation (Fig. 6 in Nair, 1978,) reporting the maximum abundance of this species in the upper layer along 15° N and in the mesopelagic layers at different parts of the non OMZ region along 8° to 35° S further strengthen the view of the tendency of this species to avoid oxygen deficient water. The restricted distribution of bathyplanktonic species *S. maxima* and four other species of genus *Eukrohnia* mostly in deeper waters of southern AS except during the upwelling event, might have resulted due to their reluctance to inhabit the oxygen deficient deeper waters of northern region of AS.

The insignificant variation observed in day and night abundance of chaetognaths might be due to their limited vertical migration in the presence of the thick OMZ. This is similar to the distribution pattern of several species of zooplankton in the OMZ region at northern Chile (Escribano and Hidalgo, 2000; Escribano et al., 2009). The significant reduction in the abundance of chaetognath with depth supports the view that the epiplanktonic chaetognaths were either avoiding the OMZ layer below or were reluctant to migrate towards the food scarce deeper layers. Similar observations of insignificant diel variation made along the coast of Chile (Hidalgo et al., 2010; Ulloa et al., 2004) and also in Andaman waters (Madhu et al., 2003) further strengthen this view.

Though chaetognaths were highly abundant in MLD, they had their maximum diversity in TC layer. The mixing of epiplanktonic and mesoplanktonic species in the TC layer might have faciliatated in the higher diversity in this layer, thus corroborating the earlier observation of maximum species diversity in 125 – 250 m depth in the Indian Ocean (Nair, 1978). This was evident from the abundance seen in the upper layers as most of the mesoplanktonic species showed preference to inhabit the MLD, thus avoiding the OMZ in the middle and deep layers. Though, abundance in the upwelling stations was much higher compared to other stations, the diversity remained moderate as only a few species contributed to the abundance in the upwelling stations.

During the SW monsoon, three concomitant physical processes like coastal upwelling, cold core eddy and warm gyre were observed along three different parts of BoB (Muraleedharan et al., 2007). Coastal upwelling region was characterized by the upsloping of the isolines of temperature and salinity leading to the formation of a low temperature and high saline watermass. In the northern part, coastal upwelling might have been suppressed by the southward moving low salinity plume originated by the high fresh water inflow in the upper part (Gopalakrishna and Sastry, 1985). During the summer monsoon, similar to AS, coastal upwelling is a common process in BoB also (LaFond, 1957; Shetye et al., 1991; Naidu et al., 1999; Rao, 2002). The uplifting of cool subsurface nutrient rich water leading to high biological production is the chacterisitic feature of this phenomenon (Bhavanarayana and La Fond, 1957; Achuthankutty et al., 1980; Madhu et al., 2002). The upwelling zone characterized by “new production” triggers the growth of phytoplankton community as they can directly utilize the abundant nitrate (Muraleedharan et al., 2007) surfaced through the uplifting waters. High transfer efficiency between the trophic levels is also a unique feature of the upwelling zone.The higher biomass and abundance of zooplankton observed in the coastal area along 15° - 19° N clearly supports this view. Higher abundance of chaetognath observed in this zone compared to the oceanic region indicates their quick response to the upwelling phenomenon. Similar to AS, higher abundance of epiplanktonic chaetognath species in the upwelling zone might have resulted by the horizontal aggregation from the surrounding regions. Of the six species observed in this region, *S. enflata*, *S. neglecta*, *S. bedoti* and *S. bipunctata* had relatively higher abundance and thus indicate their higher affinity towards this coastal physical process. The absence of mesoplanktonic species might be the result of the shallowness (<75 m) of the the upwelling stations.

Occurrence of a high saline cold core cyclonic eddy along 17°N 84° E was a prominent feature observed during this period. During south west monsoon the occurrence of cyclonic eddy along 17° N 85°E was reported earlier by Babu et al., (1991) and Prasanna Kumar et al., (1992, 1994). In BoB cyclonic eddy also facilitated in the enhancement of biological production (Falkowski et al., 1991; Seki et al., 2001; Prasanna Kumar et al., 2004, 2007). When compared to the warm gyre region the cyclonic eddy zone had relatively higher zooplankton biomass and abundance. Of the three physical processes, coastal upwelling contributed the most towards the enhancement of secondary production in BoB. Similar to upwelling region the higher abundance of chaetognath in the cold core eddy region indicates their strong response to this mesoscale physical event. Among the abundant species in upwelling zone, *S. enflata*, *S. bedoti* and *S. bipunctata* were abundant in this environment also. But, *S. neglecta* which was abundant in the MLD and also in the upwelling region had meager abundance in the eddy region. The occurrence of only seven species of chaetognath in this eddy region indicates the affinity of a few species towards this meso scale physical process.

Warm gyre, another important physical process was also observed during this period in the oceanic stations of the central BoB. Occurrence of anticyclonic warm cell is common to this region (Somayajulu et al., 2003). Generally it forms in spring inter monsoon and continues it course throughout the summer monsoon. This anticyclonic warm cell deepens the isothermal layer, resulting in increasing the thickeness of the barrier layer and thus preventing vertical mixing. This in turn results in an oligotrophic condition leading to low secondary productivity in this region.The low zooplankton biomass and abundance were the resultant effect of this oligotrophic environment (Muraleedharan et al., 2007).In this region though chaetognath abundance was relatively less it supported the existence of a higher number of species (13) compared to upwelling zone (6) and cyclonic eddy region (7). Johnson and Terazaki (2003) reported similar low abundance in the warm core ring in Oyashio water. The dominance of *S. neglecta* (34%) over *S. enflata* (32.6%) in the warm gyre region clearly indicates the former's affinity towards the warm oligotrophic waters. The contrasting nature observed in the abundance of *S. enflata* and *S. neglecta* in cool cyclonic eddy and warm gyre region provide clear indication on their temperature preferences. Cosmopolitan species *S. enflata*, which was dominant in the upper layer of AS and BoB showed preference for relatively low SST whereas *S. neglecta*, which is often the second dominant species observed in the upper layer of this region inhabited waters with relatively higher temperature also.

A sudden decline in chaetognath abundance was seen below TC layer (Table 4). A slight increase in abundance was again observed in the 300 - 500 m layer. The presence of thick ODW occupying most of the BT – 300 m layer might have forced the chaetognath population to avoid this uninhabitable zone.The only species that had relatively higher percentage contribution (63%) in this layer was *S. decipiens* and thus indicated their adaptability to survive in the oxygen deficient environment.

Species diversity was relatively high in MLD during this period. Compared to other layers, markedly high chaetognath abundance in MLD with more number of species resulted in the high diversity value. In spite of high abundance, the species evenness in MLD was lower than 500 – 1000 m layer.

Though MLD supported higher abundance and high number of species, in many locations a few species dominated which in turn might have resulted in the less eveness value.

The large cluster formed between epiplanktonic and cosmopolitan species and also the cluster formed by three mesoplanktonic species *S. maxima, S. macrocephala and E. fowleri* (60% similarity) indicated their preference for a similar habitat (Fig. 92).

The insignificant ($P > 0.05$) diel variation observed among the chaetognath population indicated the restricted vertical migration of this major zooplankton group. The restricted vertical migration in the low productivity warm gyre environment might have resulted due to the high physiological cost for performing DVM whereas in the productive coastal upwelling and eddy region, the existence of thick OMZ might have restrained the chaetognatha population from actively migrating to deeper layers.

Fall inter monsoon

In AS during the transitional FIM period, the average SST was lower than the SM period but higher than WM period. The Lakshaweep low (LL), characterized by low sea surface height, low SST and anticlockwise geostrophic current, was observed centering around 10° N 73° E with a width of 1° longitude and length of 3° latitude (Fig. 7). This LL is created by the Rossby waves radiated by the Kelvin waves along the south west coast of India (Shetye, 1998). Generally it forms to the east of Lakshadweep islands in July – August. Then it gradually stretches towards the oceanic region along west. Finally at the end of October it has no separate existence as negative anomalies in the sea level spreads all over the AS (Shetye, 1998). Thus LL which is formed at the midsummer period continues in the system throughout the FIM period.

Markedly higher mesozooplankton biomass and abundance observed in the upper layer at LL region indicated the strong influence of this physical event on secondary production. Similar higher biomass and abundance of mesozooplankton in MLD have been reported in the cold core eddy of BoB during fall intermonsoon (Fernandes, 2008). The higher abundance of copepod (96.7%) followed by chaetognatha (1.8%) in this region supports the fact that these two planktonic groups are most suitable for this environment. Earlier observation on higher abundance of copepod and chaetognath along with fish larvae in the eddy region of Hawaiian water (Lobel and Robinson, 1988) further substantiates this observation.

In MLD chaetognath abundance (32390 ± 37442 ind / 1000 m^3) was markedly higher than SM and WM. During this period, the relatively higher abundant copepod community might have helped in the sustenance of chaetognath population in this layer. The role of copepod as main prey of chaetognath is well established in different parts of the marine system (Fiegenbaum and Maris, 1984; Alvariño, 1985; Terazaki, 2000) and the positive correlation observed between these groups in the present study ($P < 0.01$, $r = 0.76$) further corroborates this view. In the LL region, the markedly high chaetognath abundance was contributed by only six species. This clearly indicates the affinity of these species towards this meso scale physical event. *S. enflata* predominated in this environment indicating its preferences for relatively cool water.

During this period except along 13° N, the thickness of OMZ was very less when compared to other seasons. The acute oxygen deficient ODW layer was absent throughout the study region and has consequently led to differences in the vertical distribution pattern of chaetognath species compared to SM and WM. The deeper water species of the genus *Eukrohnia* had relatively higher percentage composition in 300 – 500 m (36.3%) and 500 – 1000 m (67.2%) depth layers compared to SM (22 and 37.7% at 300 – 500 m and 500 – 1000 m, respectively) and WM (0 and 31% at 300 – 500 m and 500 – 1000 m, respectively). These deeper water species might have migrated towards the mid-depth water due to the relatively higher oxygen content during this period. During this season as deeper waters were relatively well oxygenated when compared to the WM period, the distribution of different life stages of chaetognath population did not exhibit any particular trend (Fig. 65).

Though the abundance was much higher in MLD, the species diversity index (H′) was relatively higher in TC. The mixing of epipelagic and mesopelagic species in this layer might have led to this high diversity index. In MLD, species evenness (J′) was quite less than all deeper layers (Table 9). In this food rich environment, the '*r'* selected species might have preferences over other species resulting in the less evenness value in this layer.

During this period, the cluster formed among the different species of chaetognath gave a clear indication on their habitat preferences. Among the species of genus *Eukrohnia*, based on 60% similarity, mesoplanktonic *E. minuta* and *E. fowleri* formed one cluster whereas bathyplanktonic *E. hamata* and *E. bathypelagica* were grouped in another cluster, thereby indicating their differential habitat preferences. The clusters formed based on 80% similarity level further added information regarding this aspect. All the mesoplanktonic species of genus *Sagitta* (*S. decepiens*, *S. planktonis* and *S. zetesios*) were found in a single cluster denoting the similarity in their distribution (Fig. 90).

The insignificant diel vertical migration (P> 0.05) observed during this period gives significance to the biological control on vertical distribution. The food rich environment with higher abundance of their main prey copepod in MLD can be a probable reason for the observed reluctance to migrate to deeper waters.

During the fall inter monsoon (FIM), BoB experienced some unique features in both physicochemical and biological characteristics. Warm surface water prevailed throughout BoB and the SST also exibited a gradual increasing trend from north to south. Higher average SST during this period compared to that of SM may be the result of less cloud cover than SM period. The east India coastal current which is generally driven by interior Ekman pumping (Shetye et al., 1993), local along shore winds adjacent to the east coast of India and Srilanka (McCreary et al., 1993), remote alongshore winds (McCreary et al., 1993) and remote forcing from the equator (Yu et al., 1991; Potemra et al., 1991) flows northward during February to September and southward during October to January (McCreary et al., 1996). This current might have influence on the secondary production during this period as the southward flow carrying the high nutrient load water from the northern part might help in the enhancement of biological production along the coastal waters, gradually spreading from north to south. The low surface salinity observed during this period (32.6 ± 1.5) compared to other seasons, indicated that the high rainfall and subsequent river influxes which are characteristics of SM is continued up to FIM in BoB. The SSS gradually increased towards south as the riverine input in this region is quite less than the northern part. A pronounced north south variation in the distribution of dissolved oxygen (DO) was also observed. Though along north the mid-depth oxygen deficient water was thicker; a thin well oxygenated layer was prominent in the surface waters of BoB. The mixed layer depth which supported a major part of the total zooplankton community in this region had varying thickness along different transects.The thickness in the northern part (17 m) was quite less than its southern counterpart (28.4 m). Thus an overall difference in the hydrological and physicochemical characteristics was observed along these two parts of BoB.

The relatively higher biomass and abundance in the coastal region of northern BoB might have resulted by the enhanced biological production due to the influence of nutrient rich southward flowing coastal current. Higher abundance of chaetognath observed in the northern part further strengthened this view. The thick oxygen deficient mid-depth water might have prevented downward migration resulting in the congregation of chaetognath in surface layers leading to the higher abundance towards upper layer in the northern part.

The percentage contribution of different life stages of total chaetognath species along different depth zones showed low population of matured individuals towards depth. This may be due to avoidance of the oxygen deficient layers by the matured population. A total of ten species (*S. enflata*, *S. decipiens*, *S. ferox*, *S. hexaptera*, *S. neglecta*, *S. pacifica*, *S. regularis*, *S. robusta*, *K. pacifica* and *K. subtilis*) were found distributed in the entire water column, but irrespective of growth stages their higher abundance was seen mostly in the upper layers, indicating their preference for epipelagic layers (Fig. 78). All the above species except *S. decipiens*, have been recorded as epiplanktonic in this region (Nair, 1978) and thus supports our observation. The occurrence of mesoplanktonic *S. decipiens* in the upper layers might have resulted either to the easy accessibility of prey in food-rich upper layers or to avoid the oxygen deficient mid depth waters. In BoB, the mesoplanktonic *E. minuta* was observed only during this season. In AS, it was observed during all the seasons and the abundance was also higher than that in BoB. Silas and Srinivasan (1969) first recorded this species in AS, but no record of its occurrence is available from BoB. This is the first report of its occurrence in BoB. *E. fowleri* formed a dominant species in deeper layers. It has been reported as one among the two bioluminescent species of chaetognaths recorded so far (Thuesen et al., 2010). Bioluminescence is often considered as an adaptive strategy exhibited by organisms of bathypelagic environments, which can be an advantage to locate their prey in aphotic environment.

The occurrence of more number of species in the food rich and oxygenated surface layers might have resulted in the higher species diversity (H′) in the upper two layers compared to deeper layers (Table 8). The higher species evenness (J′) throughout the water column indicated FIM as a favourable environment for the sustenance of higher number of species.

The clusters based on 80% similarity helped in the better understanding of the species with similar habitat preferences. Two clusters were found during this period. Most of the meso and bathy-planktonic species of the genus *Sagitta* and *Eukrohniia* were found in a single cluster due to their affinity towards deeper waters. The occurrence of some mesoplanktonic species such as *S.*

zetesios and *S. hexaptera* in the large cluster along with epiplanktonic species might be due to their tendency to migrate towards the upper layer avoiding the oxygen deficient mid depth watersr.

The insignificant diel vertical migration observed during this period might have been resulted due to the reluctance of the epiplanktonic chaetognath population to migrate into oxygen deficient deeper layer from the oxygenated food-rich surface waters.

Winter monsoon

In AS during winter monsoon, relatively low SST prevailed compared to other seasons. The profound OMZ (< 0.5 ml l^{-1}) and ODW (< 0.2 ml l^{-1}) in major part of the water column below the subsurface layer signified the existence of a pronounced oxygen-deficient water mass. The thickness of these layers was relatively higher than that of SM and FIM. This thick OMZ and ODW layers had a strong impact on the zooplankton abundance and biomass in this region. A north – south gradation in the temperature profile resulted in deepening of thermocline layer (217 ± 29 and 297 ± 12 m at 15° and 21° N, respectively) from south to north. In the northern region, the thick ODW extending between depths of 200 - 800 m might have been responsible for the zooplankton groups congregating mainly in the upper layers. The relatively higher abundance of chaetognaths in the upper layers (< 300 m) of the northern AS indicates their preference for oxygenated water. The higher abundance of chaetognaths (16217 ind. / 1000 m^3) observed in MLD of the northern region compared to the average abundance (< 4500 ind. / 1000 m^3) recorded in the upper layer of the entire Indian Ocean (Fig. 2 in Nair, 1978) is also in support of this view.

Compared to the northern region, the relatively higher abundance of chaetognaths in deeper layers in the southern region might have resulted from the absence of the ODW in most of the deeper layers (> 400 and 775 m along 15°N and 17° N, respectively). In contrast to the characteristics observed in the northern AS, a relatively high abundance of chaetognaths was observed at depths of 300 – 500 m at 21° N 67° E, and this was mostly contributed by the immature stages of *K. pacifica*, *S. enflata* and *S. robusta*. Besides, the chaetognath abundance in the TC layer at this station was not only high but was mainly contributed by the immature population. The higher abundance in the 300 – 500 m layer might have resulted from the downward migration of a portion of the population to avoid competition.

Compared to deeper waters, the relatively high percentage composition of mature chaetognaths (mainly epiplanktonic) in upper layers suggests that mature stages of some species are more sensitive to the ODW layer than the immature stages. However, this observation contrasts with that of Zo (1973), who reported higher abundance of immature *S. elegans* in upper layers of relatively shallow oxygenated basin areas, and that of Johnson and Terazaki (2004), who reported a higher incidence of immature individuals of deeper water species, such as *S. gazellae*, *S. marri* and *E. hamata*, in a relatively oxygenated (> 3 ml l^{-1}) Australian sector of the Antarctic Ocean. Wishner et al., (2000) opined that the oxygen demands of mature organisms are higher than those of immature individuals due to egg and sperm production and this might be the prime reason for avoiding the oxygen-depleted water. The higher abundance of mature populations of the epiplanktonic species *K. subtilis*, *S. ferox* and *S. regularis* observed in MLD in the present study (Fig. 69) also provides credence to the above mentioned view. Due to the presence of a thick ODW below the subsurface layer, immature individuals showed a relatively stronger and more active migratiory tendency than mature individuals. The occurrence of only immature stages of epiplanktonic species, such as *S. regularis*, *S. robusta* and *K. pacifica*, at depths of 500 – 1000 m also corroborates this view.

The existence of the ODW appears to have a strong impact on the distributional limit of the four groups of chaetognaths recognised based on their vertical distribution pattern in the study region. Among the species abundant in surface layers, *S. bedfordii*, *S. neglecta* and *S. pulchra* have generally been reported in the upper 200 m of the water column (Nair, 1978), which is also in agreement with the present observations. However, species such as *P. draco, S. bipunctata* and *S. minima* that have previously been recorded up to depths of 500 m in the non-OMZ region of the southern Arabian Sea and other parts of the Indian Ocean (Nair, 1978) were found to be restricted to the upper 300 m of the water column in the present study, thus indicating the possibility of avoiding the oxygen-deficient waters below. Similarly, the mesoplanktonic species *S. planktonis*, which has been previously recorded as mesoplanktonic in the non-OMZ southern part of the Indian Ocean (Nair and Madhupratap, 1984) and off the coast of Chile (Ulloa et al., 2000), was found to be confined to the thermocline layer in the present investigation, thereby avoiding the oxygen-depleted mid-depth waters.

Deep water species, such as *S. maxima* and all three species of *Eukrohnia*, were restricted in distribution mainly to depths greater than 500 m and were dominated by immature stages, as observed by Duró and Gili (2001) for the Weddell Sea. A likely reason for such a scenario may be that matured individuals of these species are distributed in relatively highly oxygenated waters in deeper layers, below the present depth of sampling (i.e. > 1000 m).

As regards the third group, the presence of *S. enflata* and *S. decipiens* throughout the water column might have resulted from the vertical migration of a part of their population. *S. enflata* is a cosmopolitan species and is considered epiplanktonic, although it has been found in deeper layers (Alvariño, 1965a; Furnestin, 1979). Vertical migration of *S. enflata* has been reported in different parts of the world ocean, mostly within the upper layers (Pearre, 1974; Pierrot-Bults, 1982), whereas the depth range found in the present study was relatively greater. The difference in the thickness of ODW appears to play a key role in influencing the variation in the abundance and vertical distribution of *S. enflata* in the northern and southern AS. In the southern region, where the ODW was thinner, this species was abundant throughout the water column, whereas in the northern region, where the thickness of the ODW was greater, its abundance was restricted to the upper layers. The relatively similar patterns of abundance shown by most species in this group point to the effect of ODW on their vertical distribution.

Among the fourth group, *S. tasmanica*, which has previously been recorded mostly at depths of 200 – 1000 m in the non-OMZ region of the central and southern Indian Ocean (Pierrot-Bults and Nair, 1991), showed higher abundance in the upper two layers in the present study (Fig. 69), suggesting that this species might be avoiding the oxygen-deficient waters at deeper layers. Similarly, *S. hexaptera*, which has been reported to occur mostly in the 200 – 500 m depth stratum in the non-OMZ region of the southern

Arabian Sea (Nair, 1978), was found in greater abundance in the upper two layers in the AS in the present study (Table 3). Both these examples suggest that these species have a tendency to avoid the ODW layer. The presence of mature individuals of the latter species both in upper (MLD) and deeper (500 – 1000 m) layers shows that it is an actively migrating species, but the low oxygen content in the middle layer might be hampering its abundance at mid-depths. This is also supported by earlier reports on the restricted vertical migration of zooplankton groups between the upper and lower interface of the OMZ in the tropical Pacific Ocean (Wishner et al., 1995).

Based on 60% similarity the small cluster comprising two mesoplanktonic species *S. zetesios* and *E. minuta* indicates similarity in their habitat preference (Fig. 91). Another similar cluster was found with mesoplanktonic *E. fowleri*, *S. maxima* and bathylanktonic *E. bathypelagica*. Due to the presence of oxygen deficient middle layers, the restricted vertical migration and confined abundance in the upper layer resulted in a large cluster consisting of most of the epiplanktonic species along with the cosmopolitan species.

The PCA biplot indicates a tendency for higher chaetognath abundance associated with high dissolved oxygen and water temperatures, (Fig. 85). The insignificant relationship ($P > 0.05$) observed between the day and night abundance of chaetognaths might have resulted from the restricted vertical migration of some species in the presence of the thick ODW layer. Similar observations have been made by Fernandes and Ramaiah (2008) with respect to the mesozooplankton biomass and density pattern in the OMZ of the Bay of Bengal. The observed greater species richness and diversity in the thermocline layer suggest that this niche is suitable for many chaetognath species. Similar reports of maximum species diversity existing at 125 – 250 m water depths in the Indian Ocean (Nair, 1978) and maximum zooplankton biomass and density being found in the TC layer in the Pacific Ocean (Saltzman and Wishner, 1997) are also consistent with the present observations. As suggested by Pierrot-Bults and Nair (1991), the mixing of mesoplanktonic and epiplanktonic species in TC layer might have contributed to the high species richness and diversity in this region. The existence of the intense ODW layer has also been playing a prominent role in species diversity by controlling the vertical migration of the investigated species towards deeper layers. The high evenness in distribution (> 0.6) throughout the water column indicates that strong oxygen deficiency plays a key role in influencing the distribution of most of these species, as none of them dominated at any station.

In BoB, during winter monsoon the average temperature was quite less than other seasons. The surface salinity was higher in the southern part compared to the northern part. In the north the MLD was also deeper. Thus practically two different environments were found to exist in the northern and southern part of BoB. Relatively high fresh water influx in the northern part led to stratification in this region (Shetye et al., 1996). Though, compared to SM, riverine runoff is lower during WM (Varkey et al., 1996), the fresh water induced surface layer stratification is common in the northern BoB (Shetye et al., 1996). The salinity stratification plays an important role by obstructing the mixing of water column. Though the average SST is relatively low due to the decreasing atmospheric temperature (winter cooling), it does not lead to convective mixing due to the stratification in the upper layer. The temperature inversion mostly observed in the northern part of BoB was also the result of this surface water cooling. In the southern part mostly centering along 83° E, a cold gyre was observed along 11° to 15° N. which inturn lowered temperature in the southern part. The relatively high zooplankton biomass and abundance observed in the upper layer of the southern part was clearly the resultant effect of these two different physical environments along northern and southern BoB. The biomass and abundance distribution recorded during this season was in contrast with that observed during SM and FIM. Similarly, chaetognath abundance in this layer was also relatively high in the southern part. One striking feature observed during this period was the different trend in chaetognath species composition. Though *S. enflata* remained the dominant species in upper two layers, its percentage contribution was quite less than both SM and FIM. Several other species (10 and 9 at MLD and TC, respectively) were abundant in these layers (>3.5% of the total abundance). During this period, the total number of species in upper two layers (23 and 21 in MLD and TC, respectively) was also relatively higher than SM (14 each in MLD and TC) and FIM (18 each in MLD and TC). The physicochemical environment during this period might have been favourable for the existence of higher number of species.

In the upper layer of cold gyre region a total of 16 species were observed. The winter monsoonal cold gyre region acted as a suitable habitat for higher number of species compared to three concomitant physical processes active during SM. The number of species in upwelling (6), cold core eddy (7) and warm gyre region (13) during SM was quite less than the observed number of species in cold gyre region (16). *S. enflata* remained the dominant species whereas *K. subtils*, *S. bipunctata*, *S. decipiens*, *S. ferox*, *S.*

hexaptera, *S. neglecta*, *S. pacifica*, *S. regularis* and *S. robusta* showed their affinity towards this physical event as observed from their high abundance.

The effect of oxygen deficient layer in the mid-depth waters of the study region was prominent during this season also. The thickness of OMZ varied along different transects with a gradual increase towards north. In general, the upper boundary of OMZ was below TC layer and extended to a maximum limit of 775 m. Compared to the upper layers (25596 ± 21648 and 5493 ± 3507 ind / 1000 m^3 in MLD and TC, respectively), the low abundance in middle layers (821 ± 785 and 177 ± 163 ind / 1000 m^3 in BT – 300 m and 300 – 500 m, respectively) clearly indicate the reluctance of the chaetognath species to live in the oxygen deficient water. The dominance of *S. decipiens* in BT – 300 m and 300 – 500 m (54 and 53%, respectively) clearly shows that this species is the most suitable for oxygen deficient mid-depth water. The bioluminescent chaetognath, *E. fowleri* (Thuesen et al., 2010) was observed as the dominant species in 500 – 1000 m depth layer in BoB irrespective of season.

The cluster of meso and bathyplanktonic species of the genus *Eukrohnia* (60% similarity) clearly indicate their preference for similar habitat. Based on 80% similarity several clusters were identified which categorized the chaetognath species according to their habitat preferences. Mesoplanktonic, *S. zetesios* and *S. maxima* were found in one cluster whereas *S. planktonis* and *S. decipiens* were grouped in another cluster.

There was a reduction in the evenness value in the oxygen deficient middle layers (BT – 300 m and 300 – 500 m) compared to the upper (MLD and TC) and deeper layers (500 – 1000 m). The higher abundance of a single species, *S. decipiens* (54 and 53% in BT – 300 m and 300 – 500 m, respectively) might have resulted in the low evenness values in these layers.

The physical features of BoB played an important role in the insignificant diel vertical migration ($P > 0.05$) during the WM. The stratification of the upper layers and thermal inversion in the subsurface layer have caused the formation of different physicochemical environment in the upper and middle layers. As a consequence the organisms showed reluctance to traverse through these layers as this demands high physiological energy. The presence of thick oxygen deficient layers in the mid-depth waters might be another reason for the avoidance of active vertical migration to these layers.

Copepods have been well established as the major prey of chaetognath in different parts of the global ocean (Feigenbaum and Maris, 1984; Øresland, 2000, Terazaki, 2000). In the present study, a significant positive correlation between chaetognaths and copepods abundance was observed during all seasons in both AS and BoB. Although gut contents of chaetognaths were not analyzed in this study, the significant correlation ($P < 0.001$) along with the magnitude of the regression equation and the least squares line indicated the strong trophic relationship that exists between these two major prey and predator groups.

Based on the effect of different physical forces in surface layer and variations in physicochemical variables, some differences were seen in zooplankton biomass and abundance between AS and BoB. But the results of the Mann-Whitney U test showed that these variations were not statistically significant. Similarly, the abundance of chaetognath in these two major ocean basins did not show any significant variation. Though some differences in the physicochemical control on the biotic community were observed in AS and BoB, these two sister basins share several common physicochemical and environmental characteristics and these might have led to the insignificant variation in the biotic community of AS and BoB.

Chapter 9

Summary and Conclusion

The present study, in general, deals with the distribution pattern of mesozooplankton biomass and abundance with special reference to the detailed ecology of the important carnivorous planktonic group, the chaetognath, in the two major ocean basins of the Indian EEZ, the Arabian Sea (AS) and the Bay of Bengal (BoB). Prior to the International Indian Ocean expedition (IIOE, 1960 – 1965), comprehensive studies on chaetognath in the Indian waters were very limited and was confined mostly to some coastal and oceanic regions. The IIOE, for the first time, provided an extensive systematic account of chaetognath and its distribution in the Indian Ocean region, but most of it was limited to upper 200 m water column. However, not much emphasis was given on the influence of physico-chemical factors on community structure and distribution pattern of this important planktonic group. Similarly, the recently carried out two major eco-biological programmes, like the Joint Global Ocean Flux study-India (JGOFS, 1994 - 2000) and the Bay of Bengal Process Studies (BoBPS, 2000-2006) in these two ocean basins, specific information on the ecology of zooplankton, particularly related to chaetognath was lacking. In view of this, the present study gains utmost significance as it deals in detail with the ecology of the major planktonic predator group chaetognath and also the general distribution pattern of mesozooplankton in upper 1000 m of both AS and BoB covering a major part of the Indian EEZ. The present study, for the first time also describes the growth stage wise distribution of the chaetognath community in this region and further analyzes the varied responses of different life stages to physico-chemical variables.

All the samples were collected onboard FORV Sagar Sampada, under the research project Marine Research on Living Resources funded by the Department of Ocean Development (presently the Ministry of Earth Sciences, Govt. of India). In both AS and BoB sampling locations were fixed along different latitudinal transects within the EEZ covering the summer monsoon (SM, June – September), fall inter monsoon (FIM - October) and winter monsoon (WM, November - February). The stations were set apart by 1° longitude and 2° latitude covering the coastal and oceanic regions. One coastal and one oceanic station along each transect were sampled on a diurnal basis to have a better understanding on the ecological and behavioral aspects of this important carnivorous community. Mesozooplankton samples were collected by vertical haul using a multiple plankton net of 200 µm mesh size and the nets were closed at the desired depths by means of electric sensors onboard the ship. The samples were obtained from five distinct depth strata form surface layer to 1000 m, based on the temperature and density characteristics of the water column viz., Mixed layer depth (MLD), Thermocline layer (TC), Bottom of thermocline - 300m (BT-300m), 300-500m and 500-1000 m. The environmental parameters, i.e. temperature, salinity and dissolved oxygen, were also monitored simultaneously. Temperature and salinity profiles were taken at each station up to 1000 m using a CTD. Dissolved oxygen was estimated from standard depths up to 1000 m, by collecting water samples using a rosette sampler attached to CTD.

The study revealed a profound influence of different physical process on the abundance of chaetognath community. The significant influence exerted by different physico-chemical factors on the vertical distribution of chaetognath species was also evident. In both AS and BoB, the prominent north-south variation observed in most of the physicochemical variables corroborated well with the earlier hypothesis that a pronounced north-south gradation prevails in the oceanographic parameters compared to the east-west axis (Wyrtki, 1971; Naqvi, 2008). Globally, the basins at the west coasts of continents in tropical and subtropical latitudes, supported by offshore winds and strong eastern boundary current, form strong upwelling zones, and, therefore represent one of the most productive regions (Ryther, 1969). During SM, a prominent upwelling zone was evident in the surface and subsurface layers of AS. From Holocene period onwards biological production associated with upwelling has been reported in AS (Sirocko et al., 1991). The observed higher biomass and abundance of mesozooplankton in the upwelling regions during the present study also support the significant role of this physical event on secondary productivity. This upwelling phenomenon also played a crucial role in the higher spatial abundance of the chaetognath community as evidenced from the wide variations observed between the abundance at upwelling and non upwelling areas (>5 times in upwelling region). As the food chain observed in the upwelling region is considered to be very efficient and short compared to oceanic regions, the higher chaetognath abundance in this region signifies its trophic efficiency in this dynamic system. The horizontal aggregation of the epiplanktonic chaetognaths from the neighbouring areas towards the upwelling zone might have been responsible for contributing to higher abundance in this region. The occurrence of mesoplanktonic, *Eukrohnia fowleri* and *E. minuta* along with the abundance of epiplanktonic species in the upper layers of the upwelling region characterize them as the indicator species of upwelling event in this region. The vertical distribution of chaetognath community was immensely influenced by the extreme changes observed in the vertical profiles of most of the physico-chemical parameters within few 100 meters. During the SM, the thick OMZ and ODW layers observed below the sub-surface layer greatly affected their vertical distribution pattern as most of the chaetognath species avided the oxygen deficient mid depth waters.

Strong signatures of upwelling was also observed in BoB during SM. Upwelling was more prominent in the shallow coastal stations along 15° to 19° N. Besides upwelling, two other mesoscale physical processes (cyclonic eddy and warm gyre) were also prominent during this period. These three concomitant processes played a significant role on the secondary production and also on the abundance and distribution of chaetognath species, though the influence of each process varied greatly. The maximum secondary production was associated with the cool, high saline nutrient rich upwelling region. The higher abundance of epiplanktonic chaetognath in the upwelling zones further signifies their efficiency in the energy transfer towards higher trophic level. The cold core cyclonic eddy region was found to be more productive than the oligotrophic warm gyre region, but less productive than the upwelling region. Similar pattern was observed in chaetognath abundance also. Only a few species of chaetognaths contributed towards the higher abundance in the upwelling zone and cyclonic eddy region, indicating their better competency in these food-rich environments. Though BoB is generally considered as a low productive region compared to AS, abundance of chaetognath in MLD was higher in BoB than AS during SM. These basin scale and meso-scale physical processes (upwelling and cyclonic eddy) might have been responsible for the increased abundance of chaetognath during this period. Among the dominant species observed in the epipelagic layer, S*. enflata* showed a clear affinity towards cool waters whereas *S. neglecta* dominated in a relatively warm environment. Similar to physico-chemical parameters, chaetognath abundance also exhibited marked changes towards greater depth. Abundance was highest in MLD and below TC layer the abundance declined sharply in the oxygen deficient deeper layers. The thick ODW had strong impact on the chaetognath community and this is evident from the low abundance in BT – 300 m layer when compared to that in TC layer above and 300 – 500 m layer below. *S. decipiens* was observed as the most suitable species inhabiting this oxygen deficient environment.

During the FIM also, physical processes had a strong influence in the secondary production in AS. The Lakshadweep Low (LL) in the south eastern part of AS, covering a width of 1° longitude and a length of 3° latitude played a crucial role in the enhanced secondary production observed during this period. Among mesozooplankton, the observed higher abundance of copepod (96.7%) might have helped in the sustenance of abundant chaetognath community during this period. Compared to other seasons, the average chaetognath abundance in MLD was relatively high during FIM period. Relatively less surface temperature than SM (28.5 ± 0.3 and 30.6 ± 0.4 at SM and FIM respectively) and the food-rich environment might have favored their higher abundance. During this period, the percentage contribution of the matured individual was relatively higher in deeper layers when compared to WM. The absence of ODW in the mid-depth waters might have resulted in the higher migration tendency of matured species towards deeper layers.

In BoB, a low saline and warm environment prevailed in the epipelagic layer during FIM. Though the overall mesozooplankton biomass and abundance did not show much seasonal variation, in MLD, chaetognath abundance during this season was relatively less than SM period, but the number of species present in the 1000 m water column was higher than SM and WM. The equator ward movement of East India Coastal Current was observed to influence higher biological production in the coastal region from north towards south.

In the AS, the thickness of OMZ and ODW was high during WM when compared with other seasons. This thick OMZ and ODW layer had immense impact on the distribution pattern of zooplankton biomass and abundance. The vertical distribution of chaetognath community was also significantly affected by the intense oxygen deficient water mass. In the mid-depth waters, the thickness of these oxygen deficient layers progressively increased towards north and this might have been responsible for the congregation of chaetognaths mainly in the epipelagic layers of this region. Less number of species observed in mid-depth water (10 and 9 at BT – 300 m and 300 – 500 m) might have resulted by the enhanced surface migration. The occurrence of only immature individuals of the three deep water *Eukrohnia* species indicated the strong reluctance of the mature individuals to inhabit the oxygen deficient waters.

In BoB, relatively higher zooplankton biomass and abundance was observed in the MLD of the southern region during WM. Chaetognath abundance was also relatively higher in the southern part which was in contrast with the observation during SM and FIM. The differential impact of the environmental factors and physical forces might have been responsible for this. Though river runoff is lower during WM compared to SM, the surface layer stratification induced by the fresh water is a common phenomenon in the northern BoB (Shetye, 1996). This salinity stratification acts as a strong barrier in the efficient mixing of water column. In contrast, the occurrence of the cold gyre in the southern BoB might have influenced the development of nutrient rich environment thus resulting in higher secondary production. This food rich environment might have triggered the higher chaetognath abundance in the southern part.

A total of 28 species of chaetognath was observed during the study and 27 species were observed in both AS and BoB of which 26 species were common to both ocean basins. A few individual of *S. sibogae* was encountered at a single station along 8° N, in AS, during SM. *S. gazellae* was observed at a single oceanic station in 500 – 1000 m depth along 13° N in BoB during FIM. *S. enflata* was the dominant species in the upper two depth zones in both AS and BoB. This cosmopolitan epiplanktonic species showed preference for relatively cool and oxygenated environment. The short term and long term changes associated with the environmental variables might have strong influence on its distribution pattern. During IIOE observation also, it formed the dominant species in the upper 200 m water column and the abundance was relatively higher than the present observation. The climatic changes with relatively higher SST and also the expanding OMZ in mid-depth layer might have resulted in lowering the abundance observed during the present study. The short term changes associated with different mesoscale physical processes also showed a similar result with relatively higher abundance in the cold core eddy region and low abundance in the warm gyre region in BoB during SM. Thus, the increasing SST associated with climate changes give an indication towards its less dominancy in the epipelagic layers. An opposite trend was observed in the distribution pattern of *S. neglecta,* an abundant species observed in tropical and equatorial region (Nair, 1975). This epiplanktonic species showed higher abundance in the present study than IIOE period and formed the dominant species in the warm gyre region. This indicates the higher adaptability of this species to increasing SST in the context of climatic changes. In both AS and BoB, mesoplanktonic *S. decipiens* dominated in BT – 300 m and 300 – 500 m layers at most of the stations. In both the ocean basins these two depth layers were the most affected by the prevalence of ODW layer. Hence *S. decipiens* can be considered as a suitable indicator species for the oxygen deficient mid-depth layers in the tropical Ocean. The bioluminescent *E. fowleri* was the dominant species in the 500 – 1000 m depth layer of both the ocean basins. Their bioluminescent nature might be very much advantageous for them to find their prey in the aphotic deeper waters. Another *Eukrohnia* species, *E. minuta* was mostly observed in AS and was abundant below TC layer. This Indian Ocean species which was first described by Silas and Srinivasan (1969) was abundant in relatively shallower depths compared to other meso and bathyplanktonic *Eukrohnia* species. Though the observed chaetognath abundance was always higher in the MLD at most of the stations, the species diversity index (H′) was higher in the TC layer. The mixing of epiplanktonic and mesoplanktonic species might have been responsible for the high species diversity observed in the TC layer. The presence of thick oxygen deficient waters in mid-depth might have also resulted in the upward migration of the mesoplanktonic species towards the surface layers resulting in higher diversity in the subsurface TC layer. The existence of this oxygen deficient water mass might be a possible reason for the sudden decline in the abundance of chaetognaths below TC layer at most of the stations as majority of the species were reluctant to inhabit the unfavorable environment.

Compared to the IIOE observation, relatively higher number of species observed during the present observation in the upper 200 m was mostly contributed by a group of mesoplanktonic species. In tropical region, the spreading of OMZ in the mid-depth water (Stramma et al., 2008, 2010) can be one of the prominent factors resulting in the upliftment of the upper boundary of the habitat of the mesoplanktonic species. Another important observation of the present study is the relative higher abundance of chaetognaths in the northern region compared to its southern counterpart. The pole ward movement of the planktonic groups has been observed along various regions of global ocean as a consequence of the warming of the sea surface temperature (Hays et al., 2005; Batten and Walne, 2011). Due to the unique geographical setting of the Indian Ocean with its northern boundary being landlocked, the poleward movement of chaetognath species might have been restricted, thus resulting in the accumulation in the northern part leading to relatively higher abundance.

Though some of the chaetognath species were widely distributed in both coastal and oceanic stations, some species showed higher preference for either coastal or oceanic waters. The tropical species *S. bedoti* was abundant mostly in the coastal stations. This species has been previously recorded as a dominant species in low saline estuarine region (Nair, 1971). The higher abundance of this species in the coastal waters observed in the present study might have been due to the prevalence of favourable low saline habitat. *S. bipunctata* and *S. ferox* also had higher abundance in the coastal region. On the contrary, *K. pacifica*, *S. hexaptera* and *S. bedfordii* showed higher preference for oceanic water. In MLD, the abundant species such as *S. enflata*, *S. neglecta*, *S. regularis* and *S. pacifica* did not show any specific trend.

The vertical distribution of chaetognath species displayed differential attitude towards the physicochemical environment at different growth stages. The matured individuals of the epiplanktonic species were more reluctant to migrate into oxygen deficient mid-depth water than the immature stages. Likewise, the mature bathyplanktonic species when compared to the immature ones, exhibited reluctance to migrate into mid-depth waters from deeper layers. The higher oxygen demand of mature organism for egg and sperm production (Wishner et al., 2000), might be a possible reason for this restricted migration.

In both AS and BoB, the chaetognath population did not show any significant diel vertical migration. The existence of the thick OMZ played a crucial role in the restricted vertical migration tendency of chaetognath population. The occurrence of abundant copepod community in the surface layers, which are their main prey, might have also resulted in the restricted migration as these organisms showed less preference for food deficient deeper layers.

Prior to this study, only very little information was available on the ecology and distribution pattern chaetognaths in both the Arabian sea and the Bay of Bengal in relation to various mesoscale processes and physicochemical variables. This study, emphasizing the short term and long term influences of different meso-scale and basin scale physical events on the ecology of this important plankton group provides the baseline data for extensive ecological research on any major mesozooplankton group in this tropical low latitude region.

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Impact of oxygen-depleted water on the vertical distribution of chaetognaths in the northeastern Arabian Sea

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ABSTRACT

The influence of a thick layer of oxygen-depleted water (<0.2 ml l^{-1}) on the abundance and distribution of chaetognaths was investigated in the northeastern Arabian Sea (NEAS), a natural oxygen-deficient system in the global ocean. The species and maturity stage-wise distribution of this group were studied at five discrete depths down to 1000 m. A total of 22 species belonging to four genera were observed, and the genus *Sagitta* dominated, representing 60% (500–1000 m) to 89% (Mixed layer depth) of the total chaetognath population. Based on their vertical distribution limits, four groups were recognised, as follows: I: species abundant in surface water with a maximum distribution limit up to 300 m; II: species confined mainly to deeper waters (>500 m); III: species present throughout the water column (0–1000 m); and IV: species present in most layers, but with a preference for a specific depth stratum. A positive correlation ($P<0.01$) was observed in the abundance of chaetognaths and their main prey copepods, emphasising the strong trophic relationship between these groups. It was found that the intensely oxygen-deficient waters of the NEAS play a crucial role in the vertical distribution and abundance of chaetognath species of all four genera. This report presents information on the maturity stages and ontogenetic migration of this important planktonic group in relation to the oxygen-depleted water in the study region for the first time. The results obtained are also important for understanding the biological processes associated with a major oxygen minimum zone (OMZ) in the global ocean.

1. Introduction

Chaetognaths have drawn significant research interest as a major marine zooplankton taxon. Their abundance has been estimated to represent up to 30% of the wet weight biomass of copepods in the global ocean (Ryther, 1969; Reeve, 1970; Bone et al., 1991). The trophodynamics of this group in the pelagic realm are known to play an important role in global ocean ecology (Froneman and Pakhomov, 1998).

Vertical gradients in physico-chemical characteristics of the marine system play a key role in controlling the abundance, distribution limits and diversity of zooplankton (Banse, 1964; Röpke, 1993; Gallager et al., 2004). Like all other zooplankton groups, chaetognaths respond to different physical characteristics of the marine system through the process of dispersion (Nagai et al., 2008). Vertical migration, as a means of dispersion, helps chaetognaths to locate prey, escape predators (Stuart and Verheye, 1991; Batistić et al., 2003) and avoid stressed environments (Hardy, 1935; Besiktepe and Unsal, 2000).

The northeastern Arabian Sea (NEAS) in the northern Indian Ocean is a natural oxygen-deficient system (Naqvi et al., 2006, 2009) bounded by the western Indian continental shelf in the east and the Eurasian continent in the north. The oxygen minimum zone (OMZ, <0.5 ml l^{-1}) in the northern Arabian Sea is the thickest (~ 1 km) of the global oceans (Naqvi et al., 2009) and has persisted for thousands of years (Reichart et al., 1998). The existence of a thick oxygen-depleted water (ODW, <0.2 ml l^{-1}) layer (Helly and Levin, 2004) is a natural phenomenon of this area and shows a tendency for north south variation (Naqvi, 2008; Naqvi et al., 2009). The ecological sequelae of the OMZ and ODW persisting in this area are very intense, and only a few species can tolerate this extreme oxygen deficiency, thereby constraining the vertical habitat of most marine organisms (Prince and Goodyear, 2006; Bertrand et al., 2010). The relationship between oxygen deficiency and organisms that inhabit the pelagic realm has become a subject of great interest at the global level as it influences the distribution (Judkins, 1980; Fenchel et al., 1990; Saltzman and Wishner, 1997) and subsequently leads to physiological changes in these organisms (Lutz et al., 1994; Childress and Seibel, 1998). In the Indian Ocean, there have been few detailed studies on this important topic (Herring et al., 1998; Wishner et al., 1998; Levin, 2002; Madhu et al., 2003). In spite of the strong prevalence of the OMZ in the Arabian Sea, most earlier investigations have focused mainly on its effect on copepods (Gowing and Wishner, 1998; Wishner et al., 2000). Studies on chaetognaths in the Arabian Sea

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are limited and have generally focused on their distribution based on samples collected during the International Indian Ocean Expedition (IIOE, 1960–1965) more than four decades ago (Nair, 1972, 1978). A recent report on chaetognaths from the Andaman Sea also deals with their general diversity in a restricted region (Nair and Gireesh, 2010). The role of physical characteristics of the water column in this group of plankton is largely unknown in this area. The impact of a thick oxygen-deficient layer on the chaetognath distribution and its effect on different life and maturity stages are also not well understood in other parts of the global ocean (Giesecke and González, 2004).

The present study was designed to determine how the oxygen-deficient water column in the NEAS affects the vertical distribution of chaetognaths and whether their main prey copepods have any major influence on their abundance and distribution. Our hypothesis was that heterogeneity in the thickness of the ODW layer will have a direct impact on the vertical distribution of chaetognaths. To test this hypothesis, the following parameters were considered: (1) species-level identification of chaetognaths to understand the species-specific vertical distribution profile; (2) categorisation of chaetognaths into different life stages based on sexual maturity to determine whether the ODW has a different impact on different life stages; (3) vertical characteristics of the water column based on determining temperature, salinity, density and dissolved oxygen; and (4) trophic relationships to understand active biotic interactions in the system.

2. Methods

2.1. Sampling

Sampling was carried out in the NEAS between 29th November and 20th December 2006 (early winter monsoon) onboard the FORV *Sagar Sampada* (Cruise #251) as part of the Marine Research on Living Resources (MR-LR) programme. Stations were distributed along four zonal transects from 15°N to 21°N (Fig. 1). The transects were fixed at a 2° latitude interval, and in each transect, five stations were sampled at intervals of 1° longitude, extending from the coast to offshore. Diurnal observations were performed at one coastal station and one oceanic station along each transect (Fig. 1) at 6 h intervals for 24 h. The sampling times for all other stations were noted, to obtain a better understanding of temporal variations (Fig. 1).

At all stations, a CTD (SBE Seabird 911 plus) was used to obtain the temperature and salinity profiles of the water column. This instrument was operated close to the bottom at coastal stations and down to a depth of 1000 m at oceanic stations. The potential density (σt) was computed from the pressure, temperature and salinity obtained from the CTD. To estimate dissolved oxygen (DO), water samples were collected using a Rosette sampler from standard depths to 1000 m (surface, 10, 20, 30, 50, 75, 100, 150, 200, 300, 500, 750 and 1000 m) and analysed using Winkler's method (Grasshoff, 1983). Mesozooplankton sampling was performed using a multiple plankton net (Hydrobios, Germany) with a mouth area of 0.25 m^2 and a mesh size of 200 μm. Samples were collected from five discrete depth zones, including the mixed layer depth (MLD), the thermocline (TC), the base of the thermocline (BT) to 300, 300–500 and 500–1000 m, based on the temperature and density characteristics of the water column. The MLD was determined as the depth up to which a temperature decrease of 0.5 °C occurred from the sea surface temperature. The thermocline was defined as the depth where the temperature reached 15 °C. The net was towed vertically at a speed of 1 m s^{-1} and was operated at prefixed depth zones by shipboard control with electronic sensors. Samples were passed through a 200-μm mesh; excess water was removed with absorbent paper; and the displacement volume was measured (Harris et al., 2000). Copepods and chaetognaths were sorted from the whole sample or from an aliquot (50%) using a Folsom splitter and counted under a stereomicroscope. Their abundance was calculated based on the volume of water filtered through the net and expressed as

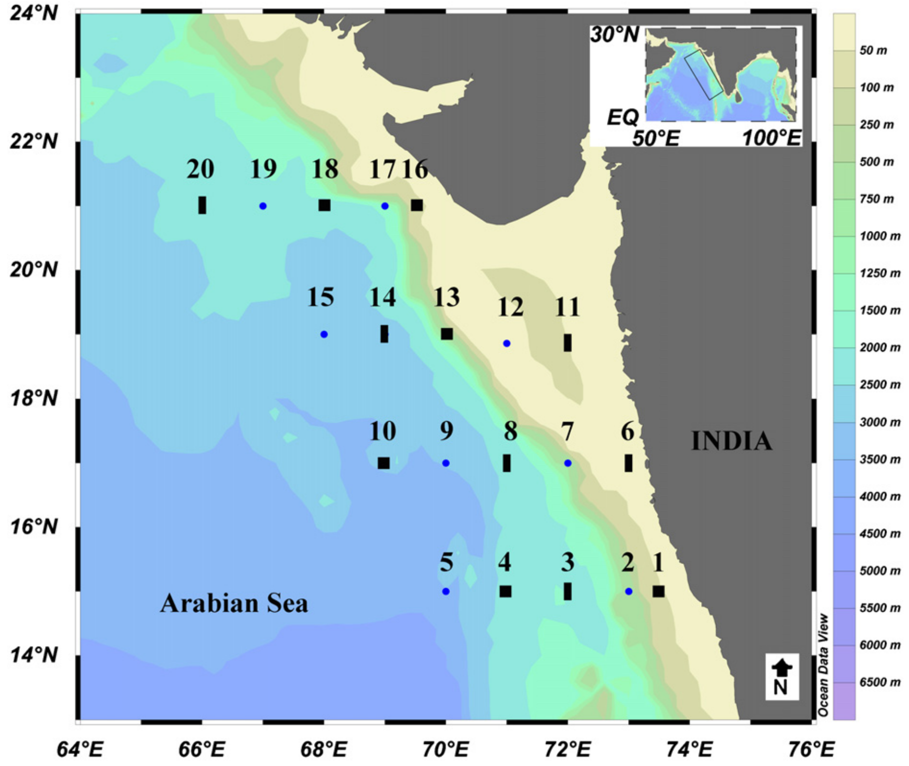

Fig. 1. Sampling locations in the northeast Arabian Sea. The circles denote diurnal stations. Filled squares denote day sampling and filled rectangle denote night sampling in regular stations.

[ind. (1000 m)$^{-3}$]. Based on ovarian development, the chaetognaths were grouped into 3 maturity stages, including Stage I, or immature (specimens with no visible ovaries); Stage II, or maturing (those with developing ova); and Stage III, or matured (individuals with one or more mature ova) (McLaren, 1969; Zo, 1973). All spent individuals were considered under stage III.

2.2. Statistical analysis

Principal component analysis (PCA) was carried out using the statistical programme PAST version 2.02 (Hammer et al., 2001), to understand the relationships between the biotic and abiotic variables. The mean values of the abiotic parameters for each depth stratum at all stations were considered for the analysis. As potential density is a derived parameter, it was not used in the analysis. Non-metric multidimensional scaling analysis (MDS) was performed for five depth strata based on the distribution of temperature, salinity, dissolved oxygen and chaetognath abundance at different stations and calculated using the Bray- Curtis similarity index with standardised $\log_{10}(x+1)$ data using PRIMER version 5.2.8 (Clarke and Warwick, 1994). Community indices, such as species diversity (H'), species richness (d) and species evenness (J'), were analysed for the chaetognaths to detect differences in their vertical assemblages. Species richness (d) was calculated only up to the TC layer, as the density below TC layer was <1 ind. (1000 m)$^{-3}$. To establish whether copepod abundance determines the vertical distribution of chaetognaths, the ratio of chaetognaths and copepods was calculated for each depth zone. The Pearson correlation coefficient (r) was calculated between the abundances of copepods and chaetognaths to detect their trophic relationship, followed by linear regression analysis with a 99% confidence band to estimate the magnitude of the relationship using Graph Pad Prism (version 5.01). A Wilcoxon matched pair test was carried out between the day and night abundances of chaetognaths and copepods at different depths at the diurnal stations, to determine whether the diel vertical migrations of these groups affect their abundance. This was done as a nonparametric test, not assuming Gaussian distributions, with two-tailed P-values and a 95% confidence interval. Analysis of variance (ANOVA) was performed on chaetognath abundance to have a better understanding of spatial variability.

3. Results

3.1. Physico-chemical environment

Sea surface temperature (SST) showed a gradual decrease from south to north (Fig. 2a). Along 15°N, it was ~29 °C and at 17°N, it ranged between 28.2 and 28.8 °C. A relatively low SST (~27.5 °C) was recorded along 19°N, and the lowest value was recorded along 21°N (25.7 °C). The upper 200 m layer was intensely stratified, with a strong vertical thermal gradient of 11–14 °C in the southern and 8–9 °C in the northern NEAS (Fig. 2a). MLD ranged from 21 m (station 10) to 63 m (station 18), with an average value of 45 ± 12 m. There was a difference in MLD between the northern (49 ± 12 m) and southern (40 ± 12 m) regions. The bottom of the thermocline layer varied widely between stations, ranging from 194 (station 2) to 314 m (station 19). The TC layer progressively deepened from south to north (217 ± 29, 220 ± 48, 261 ± 55 and 297 ± 12 m along 15°, 17°, 19° and 21°N, respectively; Fig. 2a)

Spatial variation in sea surface salinity (SSS) was marginal (34.6–36.6), and the gradients decreased towards the north (Fig. 2b). The vertical distribution of potential density (σt) showed higher gradients in the upper 200 m of the water column (Fig. 2c). Dissolved oxygen in surface layers (4.2–4.8 ml l^{-1}) did not show considerable variation, but a marked gradient was observed in the vertical profile along all transects, with a pronounced OMZ layer (<0.5 ml l^{-1}) being detected below subsurface waters. In the southern region along 15°N, the OMZ occurred between 120–1000 m (Fig. 2d). An acute OMZ (ODW <0.2 ml l^{-1}) was observed between 280–400 m at coastal stations and from 150–400 m at the oceanic stations. Along 17°N, the OMZ prevailed from 150 to 1000 m, and the ODW was detected between 200–775 m (Fig. 2d). In the northern region along 19°N, the ODW was found to extend between 200–820 m, while along 21°N, it was found between 180–800 m. Thus, an increasing trend in the thickness of the ODW layer was observed from south to north of NEAS.

3.2. Copepod abundance

At MLD, copepod abundance was relatively high in the northern region of the NEAS (Fig. 3a) and ranged between 114,814 and 1,062,295 ind. (1000 m)$^{-3}$. A marked difference in abundance was observed at BT–300 m between the northern [$67{,}743 \pm 17334$ ind. (1000 m)$^{-3}$] and southern sectors [8057 ± 6644 ind. (1000 m)$^{-3}$]. In depth zones below 300 m, the abundance was relatively higher in the southern region (Fig. 3a). The Wilcoxon matched pair test did not show any significant variation ($P>0.05$) in diel abundance, but the single factor ANOVA revealed significant variation in abundance between different depth zones ($P<0.05$) (Fig. 3).

3.3. Chaetognath abundance

Chaetognaths were abundant at MLD (71% of total chaetognaths in the water column from 0–1000 m) and ranged between 2274 and 44,444 ind. (1000 m)$^{-3}$. In upper three depth zones, their abundance was relatively higher in the northern region (Fig. 3b). At depths of 300–500 m, highest abundance was observed at station 19 [129 ind. (1000 m)$^{-3}$], while at depths of 500–1000 m, the southern region exhibited relatively higher abundance. Although no significant variation was found in diurnal abundance ($P>0.05$), a significant decrease in abundance with depth was noted ($P<0.05$). The ratio of the abundance of chaetognaths and copepods showed a decreasing trend from upper to deeper layers (0.04, 0.039, 0.032, 0.007 and 0.003 at MLD, TC and BT–300 m, 300–500 m and 500–1000 m, respectively).

3.4. Chaetognath composition

Twenty-two species belonging to 4 genera were recorded during the present study (Table 1). *Sagitta* represented the dominant genus (16 species), with a relative abundance of 60 (500–1000 m) to 89% (MLD). At MLD, 17 species were observed, among which two belonged to genus *Krohnitta* (9.9%) and one to genus *Pterosagitta* (1.1%). The TC layer was represented by 17 species and the BT–300 m layer by 10 species. Bathyplanktonic species of genus *Eukrohnia* (3 species) were sparse and occurred mostly in 500–1000 m in the water column (Table 1). The maturity stage composition showed dominance of Stage I ($>60\%$; Fig. 4). In the deeper layer, the less abundant species were represented by a higher immature population percentage (84% in 500–1000 m). The maximum mature (Stage III) population percentage occurred at MLD (20%) and gradually decreased in deeper layers (9%, 7%, 4% and 3% at TC, BT–300 m, 300–500 m and 500–1000 m, respectively; Fig. 4).

3.5. Vertical distribution and ontogenetic migration of different species of chaetognaths

Based on their vertical distribution limits, the observed chaetognath species were grouped into four categories.

(I) Species abundant in surface layers with a maximum distribution limit up to 300 m, such as *Sagitta neglecta*,

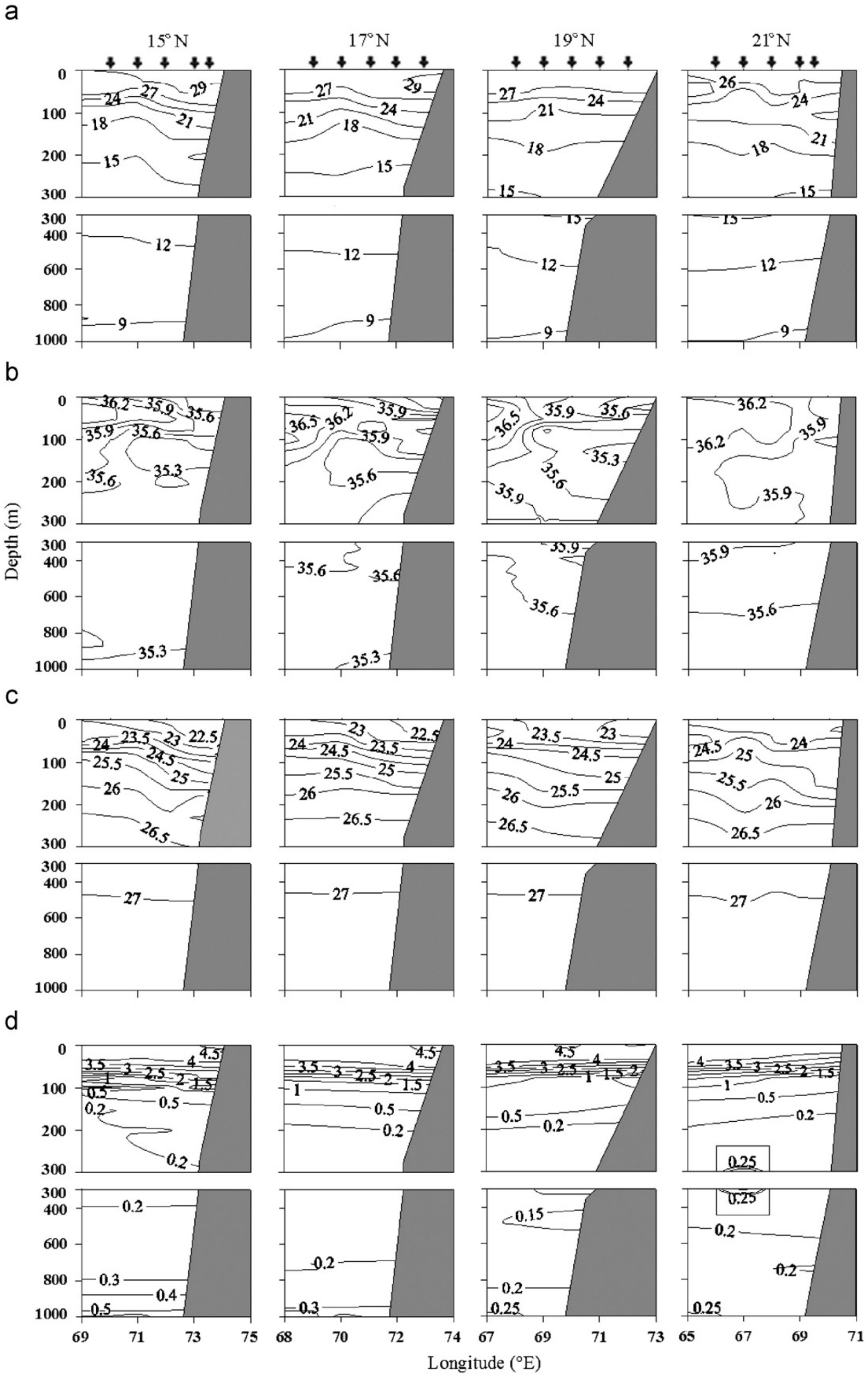

Fig. 2. Distribution of (a) temperature (°C), (b) salinity, (c) potential density (σt) and (d) dissolved oxygen (ml l^{-1}) in the upper 1000 m of the northeastern Arabian Sea. Station locations are indicated by the arrows.

Sagitta bedfordii, *Sagitta minima*, *Sagitta pulchra*, *Sagitta bipunctata*, *Sagitta planktonis* and *Pterosagitta draco*. *S. neglecta* was one of the major components in upper layers, representing 13%, 11% and 10.5% of the chaetognath population in the MLD, TC and BT–300 m zones, respectively (Fig. 5). The immature population dominated (>80%) the upper two strata, whereas

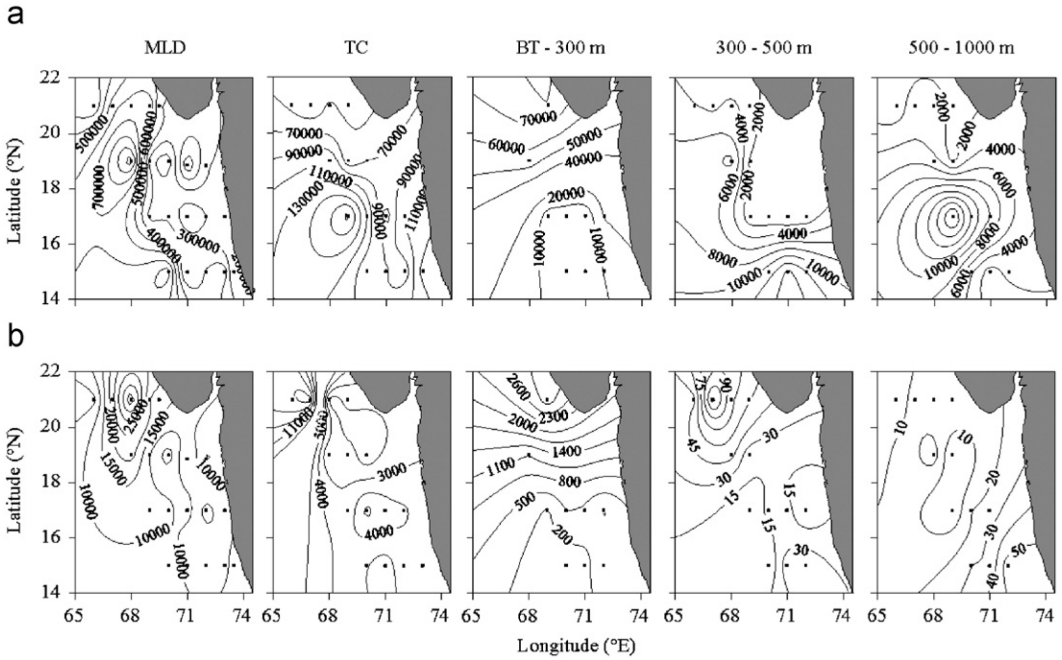

Fig. 3. Abundance [ind. (1000 m)$^{-3}$] of (a) copepods and (b) chaetognaths along different depth at northeastern Arabian Sea (MLD—Mixed layer depth, TC—Thermocline and BT—Base of thermocline).

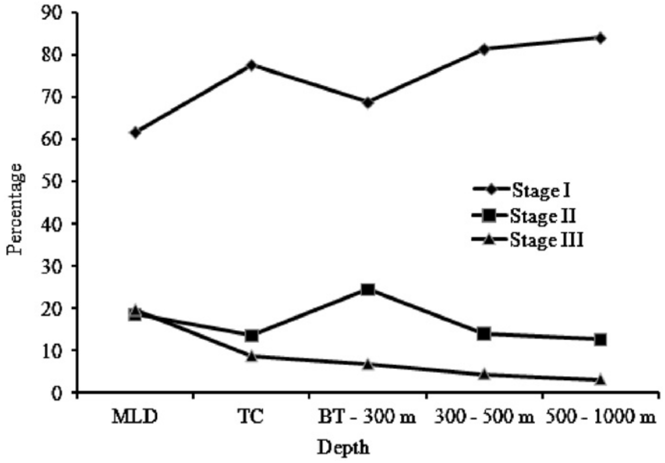

Fig. 4. Depth wise percentage composition of different maturity stages of chaetognaths (MLD—Mixed layer depth, TC—Thermocline and BT—Base of thermocline).

mature specimens formed the major part of the population (47.3%) in the BT–300 m layer (Fig. 6). *S. bedfordii* comprised 3–8% of the population, with maximum abundance at MLD [av. 402 ind. (1000 m)$^{-3}$]. Fig. 7 depicts the ontogenetic vertical migration of different species, considering the total abundance (including day and night) of a particular stage of a species as 100%. Among the species in this group, mature specimens of *P. draco* were abundant in the TC layer and immature specimens at MLD, whereas immature specimens of *S. pulchra* were more abundant in the TC layer, and the maturing (stage II) population was mostly collected from MLD. Regardless of maturity stages, the abundance of most of the other species (except *S. planktonis*) was high at MLD (Fig. 5).

(II) Species such as *Sagitta maxima*, *Eukrohnia bathypelagica*, *Eukrohnia minuta* and *Eukrohnia fowleri* were mostly confined to deeper waters (> 500 m). The bathyplanktonic species *S. maxima* was only observed in the southern region at depths of 500–1000 m, contributing 15% of the total chaetognath population of this layer (Fig. 5). Most of the species of *Eukrohnia* were restricted to depths below 500 m. They were mainly observed in the southern region (Fig. 8), and only immature stages were encountered during the study (Figs. 6 and 7).

(III) Species distributed throughout the water column (0–1000 m) included *Sagitta enflata*, *Sagitta decipiens*, *Sagitta robusta*, *Krohnitta pacifica* and *Krohnitta subtilis. S. enflata* represented the dominant species up to a depth of 500 m (Table 1). It contributed 5% (500–1000 m) to 48.4% (BT–300 m) of the total chaetognath population (Fig. 5). In the upper 300 m, its abundance was relatively high in the northern region (Fig. 8), and all three maturity stages were abundant at MLD (Fig. 7), among which stage III constituted 26.1% of the population (Fig. 6). Although stage I of *S. robusta*, *K. subtilis* and the mesopelagic species *S. decipiens* were distributed throughout the water column, their mature stages were restricted mainly to the upper layers (Fig. 7) in the northern region (Fig. 8).

(IV) *Sagitta hexaptera*, *Sagitta ferox*, *Sagitta pacifica*, *Sagitta regularis*, *Sagitta zetesios* and *Sagitta tasmanica* were the species present in most of the layers, but with a preference for a specific depth stratum. The cosmopolitan species, *S. hexaptera* was abundant in all layers except the BT–300 m zone. In the upper layers, its abundance was relatively high in the northern region while below a depth of 300 m, it was abundant in the southern region (Fig. 8). The immature stage of this species exhibited more active migration than the mature stage and migrated to deeper layers (> 300 m) only during night time (Fig. 7). *S. ferox* showed a similar trend, with a relatively higher migration tendency shown by immature individuals (Fig. 8).

3.6. PCA, multidimensional scaling and diversity indices

PCA indicated a positive relationship of chaetognath abundance with both dissolved oxygen and temperature. The groups between the depth strata found in the multidimensional scaling

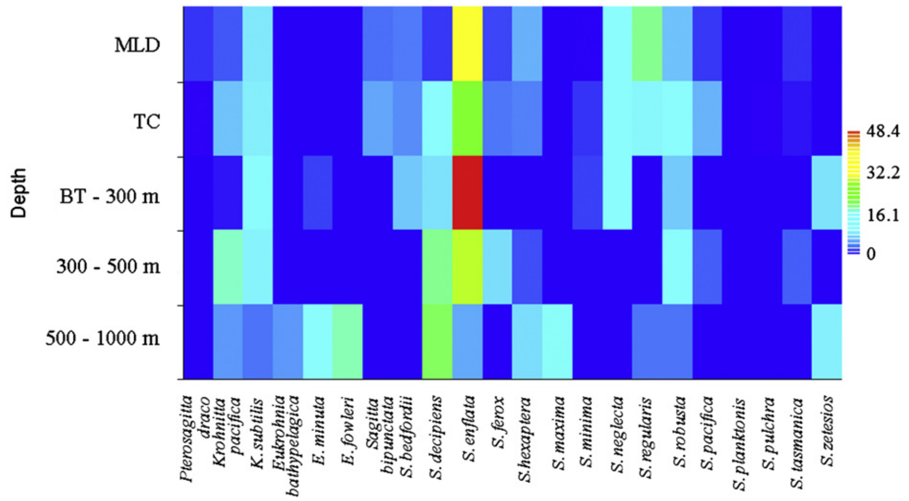

Fig. 5. Relative abundance (%) of each chaetognath species to total chaetognaths in each depth layer sampled (MLD—Mixed layer depth, TC—Thermocline and BT—Base of thermocline).

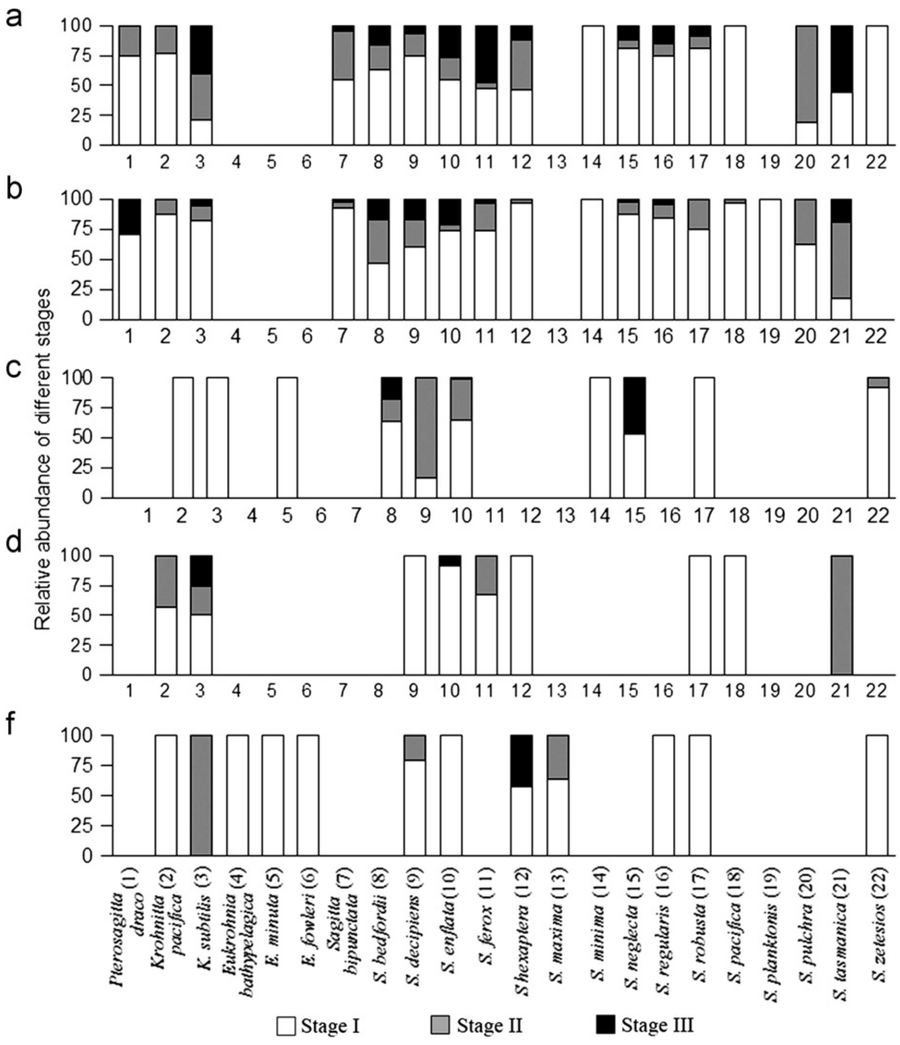

Fig. 6. Maturity stage-wise percentage composition of different chaetognath species at (a) mixed layer depth, (b) thermocline, (c) base of thermocline–300 m, (d) 300–500 m and (e) 500–1000 m.

analysis based on the distribution of temperature, salinity, dissolved oxygen and chaetognath abundance, showed a high degree of similarity between the last two plots (Fig. 9). Species diversity (H'), species evenness (J') and species richness (d) were high in the TC layer (2 ± 0.3, 0.9 ± 0.02 and 7.1 ± 2.6, respectively; Fig. 10a–c).

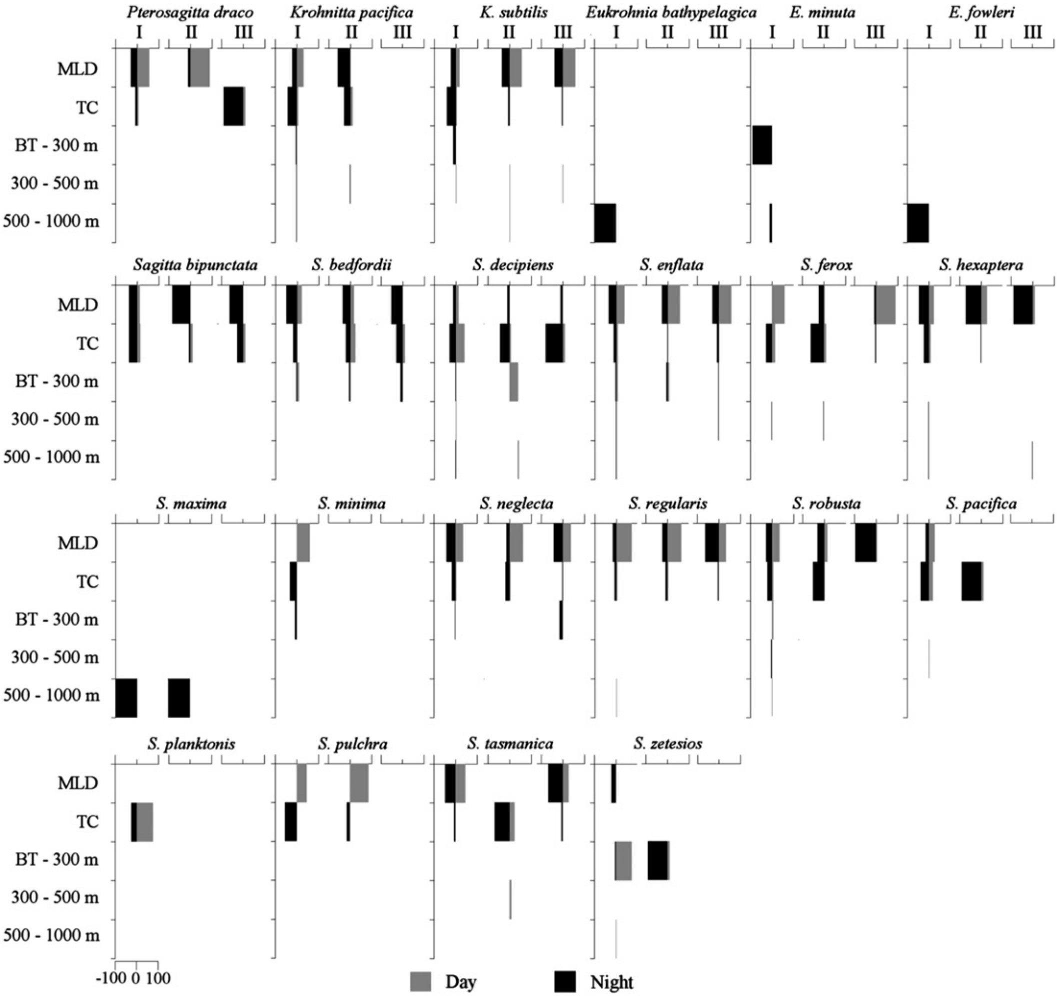

Fig. 7. Vertical distribution of different maturity stages of chaetognath species at different depth layers during day (grey) and night (black) (MLD—Mixed layer depth, TC—Thermocline and BT—Base of thermocline).

3.7. Relationship of chaetognaths with copepods

The Pearson correlation coefficient (r) calculated based on the abundance of chaetognaths and copepods at different stations and depth zones, revealed a significant positive correlation ($P < 0.01$, $r = 0.79$) between the two groups (Fig. 11).

4. Discussion

The results of the present study indicated a strong impact of ODW on the vertical distribution limit of chaetognath species. The profound OMZ (< 0.5 ml l^{-1}) and ODW (< 0.2 ml l^{-1}) in a major part of the water column below the subsurface layer indicate the existence of a pronounced oxygen-deficient water mass in the NEAS. The observed north–south difference in the thickness of the ODW layer ($15 < 17 < 19 < 21$°N) supports the earlier hypothesis that a more pronounced north–south gradation prevails in oceanographic parameters compared to along an east–west axis (Wyrtki, 1971; Naqvi, 2008). A similar trend of north–south gradation in the temperature profile resulted in deepening of thermocline layer (217 ± 29 and 297 ± 12 m at 15° and 21°N, respectively) from south to north. Thus, the system experiences different physical characteristics in the northern and southern parts of the NEAS. In the northern region, the thick ODW extending between depths of 200–800 m might be responsible for the zooplankton groups congregating mainly in the upper layers. The relatively higher abundance of copepods and chaetognaths in the upper layers (< 300 m) of the northern NEAS indicates their preference for oxygenated water (Fig. 3a and b). The higher abundance of chaetognaths [16,217 ind. (1000 m)$^{-3}$] observed at MLD in the northern region compared to the average abundance [< 4500 ind. (1000 m)$^{-3}$] recorded in the upper layer of the entire Indian Ocean (Fig. 2 in Nair, 1978) also supports this preference. Compared to the northern region, the relatively higher abundance of chaetognaths in deeper layers in the southern region might have resulted from the absence of the ODW in the majority of the deeper layers (> 400 and 775 m along 15°N and 17°N, respectively). In contrast to the characteristics observed in the northern NEAS, a relatively higher abundance of chaetognaths was observed at depths of 300–500 m at station 19, and this was mostly contributed by the immature stages of *K. pacifica*, *S. enflata* and *S. robusta*. Additionally, at this station, the chaetognath abundance in the TC layer was not only high but also was mainly contributed by the immature population. The higher abundance in the 300–500 m layer might have resulted from the downward migration of a portion of the population to avoid competition. The pocket-like zone (marked in Fig. 2d) around station 19 at depths of 200–500 m, exhibiting a relatively higher DO value (> 0.25 ml l^{-1}) than the surrounding region (< 0.2 ml l^{-1}), might also have been playing a crucial role in sustaining high chaetognath abundance at depths of 300–500 m at this station. A similar

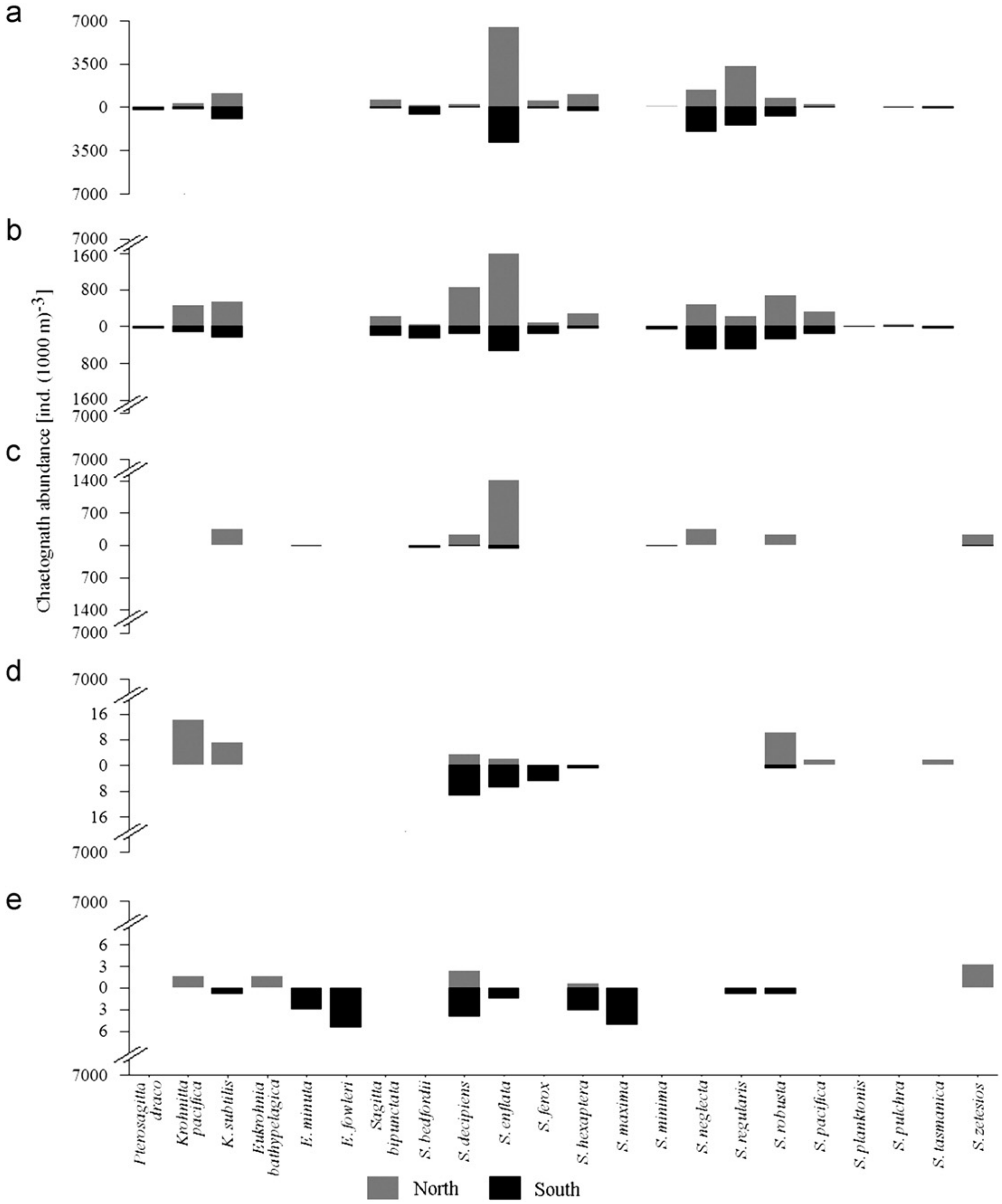

Fig. 8. Abundance of different chaetognath species at northern and southern part of the northeastern Arabian Sea along (a) mixed layer depth, (b) thermocline, (c) base of thermocline–300 m, (d) 300–500 m and (e) 500–1000 m.

observation of higher zooplankton abundance at the lower interface of the OMZ in conjunction with an increased DO concentration (0.05–0.1 ml l^{-1}) in the eastern tropical Pacific Ocean (Wishner et al., 1995) also corroborates our view.

The significant correlation observed between copepod and chaetognath abundance ($P<0.01$) provides support for the role of copepods in sustaining the population of this important carnivorous planktonic group, as observed in both OMZ and non-OMZ regions of different parts of the world oceans (Øresland, 2000; Kehayias, 2003; Giesecke and González, 2004). Although the gut content of chaetognaths was not analysed in the present study to establish the prey–predator relationship, the magnitude of the regression equation and the least squares line (Fig. 11) indicates the trophic relationship that exists between these two major prey and predator groups. The higher abundance of chaetognaths together with copepods in the upper three layers of the northern NEAS provides further evidence of the role of this trophic relationship. Compared to deeper waters, the relatively high percentage composition of mature chaetognaths (mainly epiplanktonic) in upper layers suggests that mature stages of some species are more sensitive to the ODW layer than the immature stages. However, this observation contrasts with the earlier observations made by Zo (1973), who found higher abundance of immature *S. elegans* in upper layers of relatively shallow oxygenated basin areas, and made by Johnson and Terazaki (2004), who reported a higher incidence of immature individuals of deeper water species, such as *Sagitta gazellae*, *Sagitta marri* and *Eukrohnia hamata*, in a relatively oxygenated (>3 ml l^{-1}) Australian sector of the Antarctic Ocean. Wishner et al. (2000) indicated that the oxygen demands of mature organisms are higher than those of immature individuals due to egg and sperm production and, thus, might lead to avoidance of oxygen-depleted water. The higher abundance of mature populations of the epiplanktonic species *K. subtilis*, *S. ferox* and *S. regularis* at MLD found in the present study (Fig. 7) also provides support for the view described above. We observed the presence of a thick ODW below the subsurface layer, and immature individuals showed a relatively stronger and more active migration tendency than mature individuals (Fig. 7). However this observation contradicts the findings of Russell (1931), who observed a greater migration tendency in adults of *S. elegans* in a relatively oxygenated Plymouth area. It appears that because matured individuals are more sensitive, they are reluctant to migrate into oxygen-deficient waters of deeper layers. The occurrence of only immature stages of epiplanktonic species, such as *S. regularis*, *S. robusta* and *K. pacifica*, at depths of 500–1000 m also corroborates this view.

The existence of the ODW appears to have a strong impact on the distributional limit of the four groups of chaetognaths recognised based on their vertical distribution pattern in the study region. Among the species abundant in surface layers, *S. bedfordii*, *S. neglecta* and *S. pulchra* have generally been reported in the upper 200 m of the water column (Nair, 1978), which is in agreement with the present observations. However, species such as *P. draco, S. bipunctata* and *S. minima* that have previously been recorded up to depths of 500 m in the non-OMZ region of the southern Arabian Sea and other parts of the Indian Ocean (Nair, 1978) were found to be restricted to the upper 300 m of the water column in the present study, thus indicating the possibility of avoiding the oxygen-deficient waters below. Similarly, the mesopelagic species *S. planktonis*, which has previously been recorded as mesoplanktonic in the non-OMZ southern part of the Indian Ocean (Nair and Madhupratap, 1984) and off the coast of Chile (Ulloa et al., 2000), was found to be confined to the thermocline layer, thereby avoiding the oxygen-depleted mid-depth waters (Table 1).

Bathypelagic species, such as *S. maxima* and all three species of *Eukrohnia*, were restricted mainly to deeper waters (>500 m) and were dominated by immature stages, as observed by Duró and Gili (2001) for the Weddell Sea. A likely reason for such a scenario may be that matured individuals of these species are distributed in relatively highly oxygenated waters in deeper layers, below the present depth of sampling. Their abundance only in the southern NEAS (except *E. bathypelagica*) also provides support for their preference for oxygenated waters.

Considering the third group, the presence of *S. enflata* and *S. decipiens* throughout the water column might have resulted from the vertical migration of a part of their population. *S. enflata* is a cosmopolitan species and is considered epipelagic, although it has been found in deeper layers (Alvariño, 1965; Furnestin, 1979). Vertical migration of *S. enflata* has been reported in different parts of the world ocean, mostly within upper layers (Pearre, 1974; Pierrot-Bults, 1982), whereas the depth range found in the present study was relatively greater. The difference in the thickness of ODW appears to play a key role in influencing the variation in the abundance and vertical distribution of *S. enflata* in the northern and southern NEAS. In the southern region, where the ODW was thinner, this species was abundant throughout the water column, whereas in the northern region, where the thickness of the ODW was greater, its abundance was restricted to the upper layers. This is also consistent with the observations made by Giesecke and González (2004) in Mejillones Bay, where *S. enflata* was found to be the dominant species but was abundant only above the OMZ layer, where the dissolved oxygen concentration was >1 ml l^{-1}. The relatively similar patterns of abundance shown by most species in this group strongly indicate to the effect of ODW on their vertical distribution.

Among the fourth group, *S. tasmanica*, which has previously been recorded mostly at depths of 200–1000 m in the non-OMZ region of the central and southern Indian Ocean (Pierrot-Bults and Nair, 1991), showed higher abundance in the upper two layers in the present study (Fig. 7), suggesting that this species might be avoiding the oxygen-deficient waters at deeper layers. Similarly, *S. hexaptera*, which has been reported to occur mostly in the 200–500 m depth stratum in the non-OMZ region of the southern Arabian Sea (Nair, 1978), was found in greater abundance in the upper two layers in the NEAS in the present study (Fig. 7). Both of these examples suggest that these species have a tendency to avoid the ODW layer. The presence of mature individuals of the latter species both in upper (MLD) and deeper (500–1000 m) layers shows that it is an actively migrating species, but the low oxygen content in the middle layer might be hampering its

Table 1
Average abundance of chaetognath species [ind. $(1000\text{ m})^{-3}$] at different depth strata.

Species	MLD	TC	BT–300 m	300–500 m	500–1000 m
Pterosagitta draco	139	27	–	–	–
Krohnitta pacifica	257	270	6	6	1
Krohnitta subtilis	1047	369	86	3	1
Eukrohnia bathypelagica	–	–	–	–	1
Eukrohnia minuta	–	–	11	–	2
Eukrohnia fowleri	–	–	–	–	3
Sagitta bipunctata	357	215	–	–	–
Sagitta bedfordii	402	169	54	–	–
Sagitta decipiens	142	471	65	7	3
Sagitta enflata	4704	991	417	11	1
Sagitta ferox	190	132	–	3	–
Sagitta hexaptera	701	148	–	1	1
Sagitta maxima	–	–	–	–	3
Sagitta minima	48	45	11	–	–
Sagitta neglecta	1718	494	91	–	–
Sagitta regularis	2415	391	–	–	1
Sagitta robusta	788	458	55	5	1
Sagitta pacifica	148	238	–	1	–
Sagitta planktonis	–	9	–	–	–
Sagitta pulchra	35	22	–	–	–
Sagitta tasmanica	128	30	–	1	–
Sagitta zetesios	27	–	66	–	2

abundance at mid-depths. This is also supported by earlier reports on the restricted vertical migration of zooplankton groups between the upper and lower interface of the OMZ in the tropical Pacific Ocean (Wishner et al., 1995). The relatively higher abundance of *S. hexaptera*, *S. regularis* and *S. ferox* in upper layers of the northern NEAS and below a depth of 300 m in the southern NEAS (Fig. 8), provides further evidence that these species exhibit a tendency to avoid the thick ODW in the northern NEAS (Fig. 9).

The PCA biplot indicates a tendency for higher chaetognath abundance associated with high dissolved oxygen and water temperatures, whereas the MDS plot shows a close similarity of abundance only to dissolved oxygen, thus highlighting the role of oxygen in controlling chaetognath abundance (Fig. 9). The depth zones that were found in similar groups in both MDS plots were the upper three layers, where dissolved oxygen values were relatively high, thus supporting the congregated abundance in these layers. The group formed between the deeper two layers, where the ODW was more prominent, further supporting the influence of dissolved oxygen in controlling the vertical distribution of these species. The higher ratio of chaetognath and copepod abundance in the relatively oxygenated upper layers compared to the oxygen-deficient deeper layers provides additional evidences that the presence of dissolved oxygen rather than the abundance of copepods plays a more decisive role in controlling the vertical distribution of chaetognaths. The insignificant relationship ($P > 0.05$) observed between the day and night abundance of chaetognaths might have resulted from the restricted vertical migration of some species in the presence of the thick ODW layer. Similar observations have been made by Fernandes and Ramaiah (2008) with respect to the mesozooplankton biomass and density pattern in the OMZ of the Bay of Bengal (Fig. 10). The observed greater species richness and diversity in the thermocline layer suggest that this niche is suitable for many chaetognath species. Similar reports of maximum species diversity existing at 125–250 m water depths in the Indian Ocean (Nair, 1978) and maximum zooplankton biomass and density being found in the TC layer in the Pacific Ocean (Saltzman and Wishner, 1997) are also consistent with the present observations. As suggested by Pierrot-Bults and Nair (1991), the mixing of mesopelagic and epipelagic species in this layer might contribute to the high species richness and diversity in

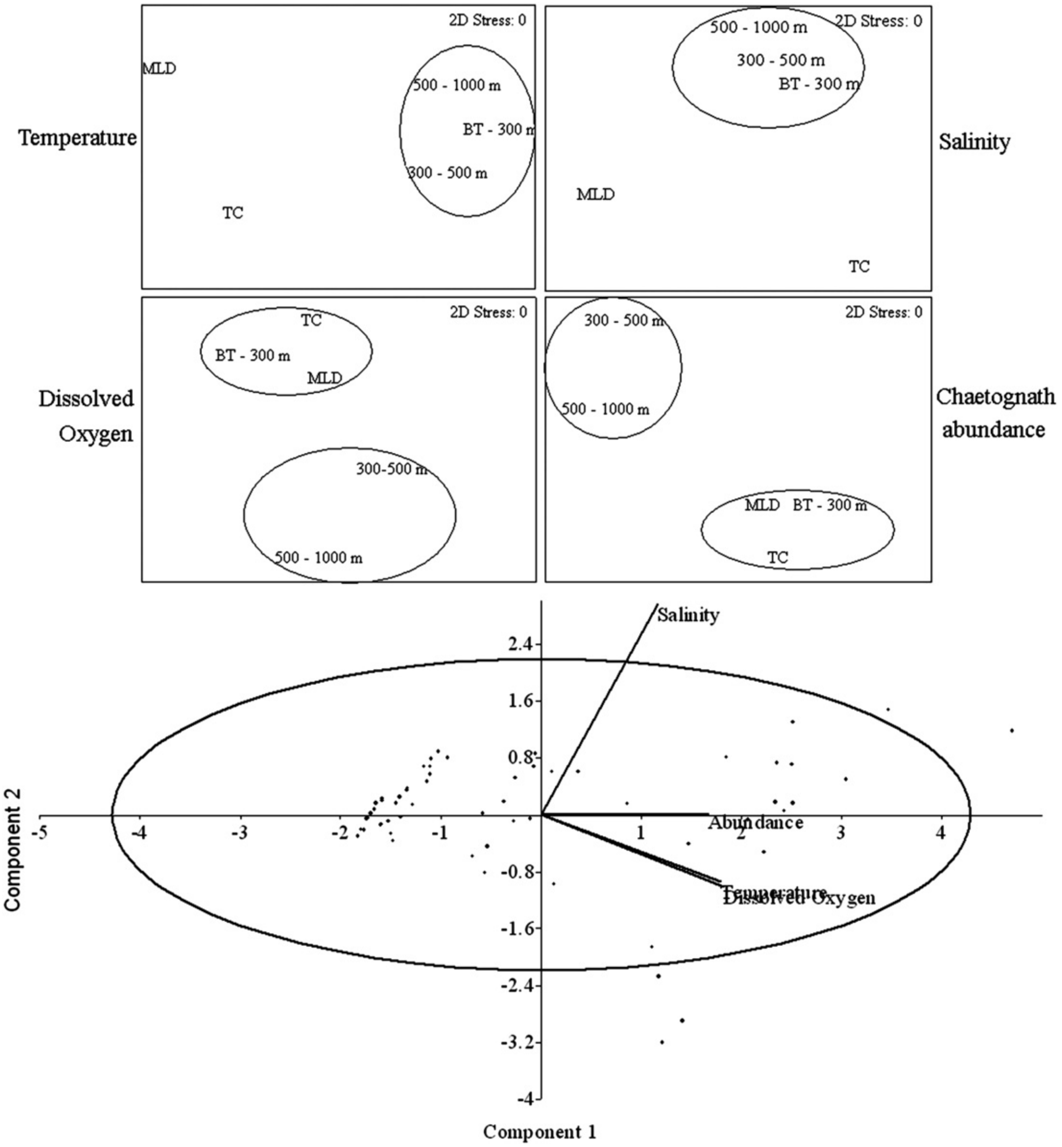

Fig. 9. MDS analyses showing similarity between different depth strata based on the biotic and abiotic parameters and PCA biplot showing the internal relationships of those parameters.

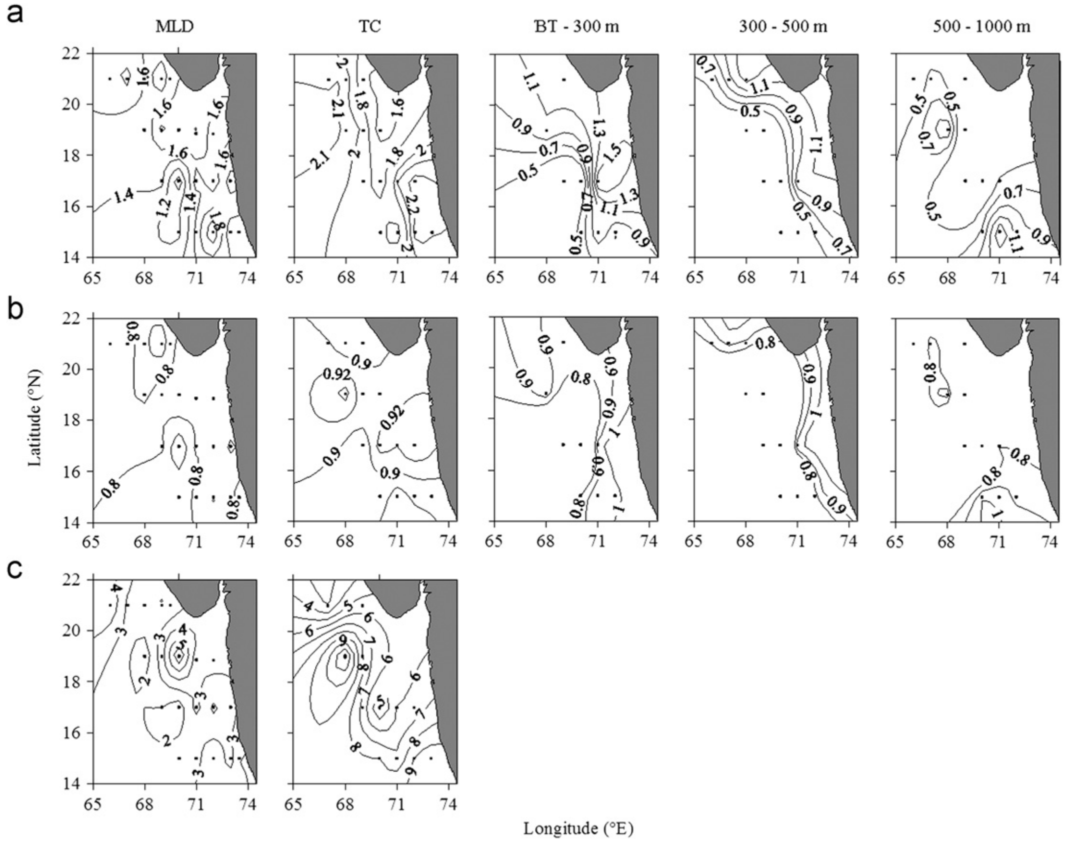

Fig. 10. Diversity indices (a) species diversity, (b) species evenness and (c) species richness along different depths at northeastern Arabian Sea.

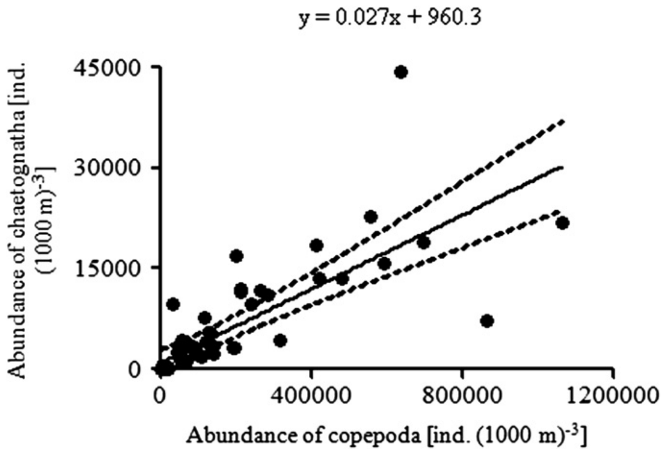

Fig. 11. Relationship between copepods and chaetognaths. The regression equation and the 99% confidence band are shown.

this region (Fig. 10). The existence of the intense ODW layer has also been playing a prominent role in this by controlling the vertical migration of the investigated species towards deeper layers. The high evenness in distribution (> 0.6) throughout the water column indicates that strong oxygen deficiency plays a key role in influencing the distribution of most of these species, as none of them dominated at any station (Fig. 11).

5. Conclusions

The present study indicates the impact of oxygen deficiency on the vertical distribution limits of chaetognath species in a natural oxygen-deficient system in the NEAS. Physical factors, such as salinity and temperature, are also responsible for the formation of two physically distinct characteristics in the northern and southern regions of the NEAS, although they had a negligible effect in influencing the distribution limits of chaetognath species. The major phenomenon that has a limiting effect on the vertical migration of chaetognaths in the NEAS can be concluded to be species-specific sensitivity to oxygen-depleted water. The difference in the ODW thickness in the northern and southern regions affected the distribution of copepods and chaetognaths, resulting in relatively higher abundance of both groups in the upper layers of the northern region. The significant relationship observed between copepods (major prey) and chaetognaths (predator) highlights the active trophic relationship existing in this oxygen-deficient system. The results of the present study, which emphasise the effect of ODW on chaetognaths, a major invertebrate predator group, will be useful in designing detailed research focusing on the effect of ODW on other important zooplankton groups.

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