

Pakistan Journal of Marine Sciences, Vol. 22(1&2), 43-59, 2013.

COMPOSITION OF MAJOR ZOOPLANKTONIC GROUPS IN SHAHBUNDER CREEK SYSTEM - INDUS DELTAIC AREA

Qadeer Mohammad Ali and Quratulan Ahmed

The Marine Reference Collection and Resource Centre, University of Karachi, Karachi - 75270, Pakistan

email: taxonomist@hotmail.com, marine.taxonomist@gmail.com

ABSTRACT: A study was conducted in Shahbunder creek system, Indus deltaic area to observe the composition of major zooplanktonic groups during October – December, 1997 (post monsoon period). Total fourteen (14) major groups of zooplankton were recorded from two stations. Three groups copepod, chaetognatha and zoea constituted the major component of zooplankton at both the stations. Copepod was the most dominant group, constituting 50.50% at station # 1 and 46.12 at station # 2. Highest mean (15182.0±1402.14), (9343.66±4246.11) were measured in copepods at station# 1 and station# 2 respectively. This is the first attempt on ecological and zooplanktonic studies in Shahbunder creek system. Hence, this study will enhance our knowledge on the creek ecosystem of Indus delta.

KEYWORDS: Shahbunder creek system, Indus delta, zooplankton, composition.

INTRODUCTION

Zooplanktons are referred to aquatic organisms floating and drifting with limited or no power of locomotion. Zooplankton forms an important link in the marine food chain as secondary producers by playing a vital role in the conservation of energy from primary to secondary level. They are often overlooked but critical to maintaining aquatic food web foundations by being the second trophic level in most aquatic environments and given that some aquatic insects, larval fish and some adult fish feed on zooplankton, they play a very important role in transferring energy across the food web (Sladeczek, 1958). The high proportion of copepods and crab larvae were observed in the guts of fishes which entered into marshes at high tide and left at low tide (Elizabeth *et al.*, 1994). This is a clear evidence of zooplanktonic niche in an aquatic food web, providing vital link between primary producers and the higher trophic level. Tropical aquatic ecosystems are the most productive areas with rich zooplankton population (Robertson and Blabber, 1992; Saravanakumar *et al.*, 2007b). The environmental conditions such as topography, water movement and stratification, salinity, oxygen, temperature and nutrients characterizing particular water mass also determine the composition of zooplankton biota (Karande, 1991).

Creeks are productive coastal environments used as feeding and nursery grounds (Lawal-Are *et al.*, 2010). In order to manage water quality, we need a broad understanding about zooplankton and their interaction with the environment (Suthers and Rissik, 2009). Zooplankton species distribution shows wide spatio temporal variations due to the different hydrographical factors on individual species. They also serve as good indicators of water quality as per the previous studies on zooplankton of Indian coastal

environment (Perumal *et al.*, 1999; Rajasegar *et al.*, 2000; Tiwari and Nair, 1993; Saraswathi, 1983). Many workers have studied the composition and structure of zooplankton in coastal waters of Pakistan which includes those of Ahmed (1951), Ali and Arshad (1966) and then Haq (1968). Glolobov and Grobov (1970), Fazal-ur Rehman (1973, b), Haq and Fazal-ur-Rehman (1973), Khan (1976) and Khan and Kamran (1975). Khan (1974) also worked on seasonal abundance of zooplankton.

Shahbander is located in the eastern part of the Indus deltaic creek system, climatically falls under semi arid zone. Indus delta is the 6th largest delta on the globe with an area of 29,524 sq kms. The Indus River is the 22nd largest river in the world, has developed this fan shaped delta which is one of the largest sediment bodies in the modern ocean basins. The present delta encompasses 17 major creeks which are characterized by mangrove forests, mud flats, salt marshes and sand dunes. 97% of the total mangrove cover in Pakistan is represented by the Indus delta comprising of approximately 95 % of almost mono-typic dominating species *Avicennia marina*.

The aim of this study was to conduct studies in Shahbander creek system of Indus delta and to collect data on the composition and abundance of major zooplankton groups along with physico-chemical parameters from two permanent stations.

MATERIALS & METHODS

Zooplankton samples were collected during post monsoon season (October – December, 1997) from two permanent stations in Shahbander creek system; Station # 1 Patora creek (24°0'28.77"N, 67°57'15.76"E), Station #2 Ghoray waro creek (24°4'36.29"N, 67°52'36.95"E) (Figure 1). Physico-chemical parameters including air temperature (°C), water temperature (°C), salinity (‰), Dissolved oxygen (mg/L), pH and visibility (cm) were recorded on monthly basis. Temperature was measured using mercury in glass thermometer, for air temperature (°C), copper sleeved thermometer was allowed to stabilize in open air for 10 seconds whereas for water temperature (°C) a plastic bottle was used. Salinity (‰) was measured with the help of a temperature compensated hand-held Refractometer (S/Mill- E, Atago Co. Ltd., Tokyo, Japan). Dissolved oxygen (mg/L) was measured with the help of portable DO meter (Orion Model 820). pH recorded with the help of a pocket pH meter (HACH pH tester, USA) by dipping into the water until the screen showed a fixed/stable reading as described by the manufacturer. Zooplankton sampling was done with the help of Hydrobios Ring trawl net of 500 µ mesh size through horizontal towing of 10 minutes haul at constant speed of 0.5 m/s in the surface waters during high tide. Hydrobios digital flow meter was used to record the volume of water passed through the net. Samples were immediately preserved in 5% buffered formalin in the field and kept in plastic containers.

In the laboratory, samples were split into aliquots (sub samples) which were sorted out into different major taxonomic groups, identified and counted in counting tray under a stereomicroscope (Nikon SMZ 10). The keys and identification references used were obtained from practical guide of (Newell and Newell, 1977).

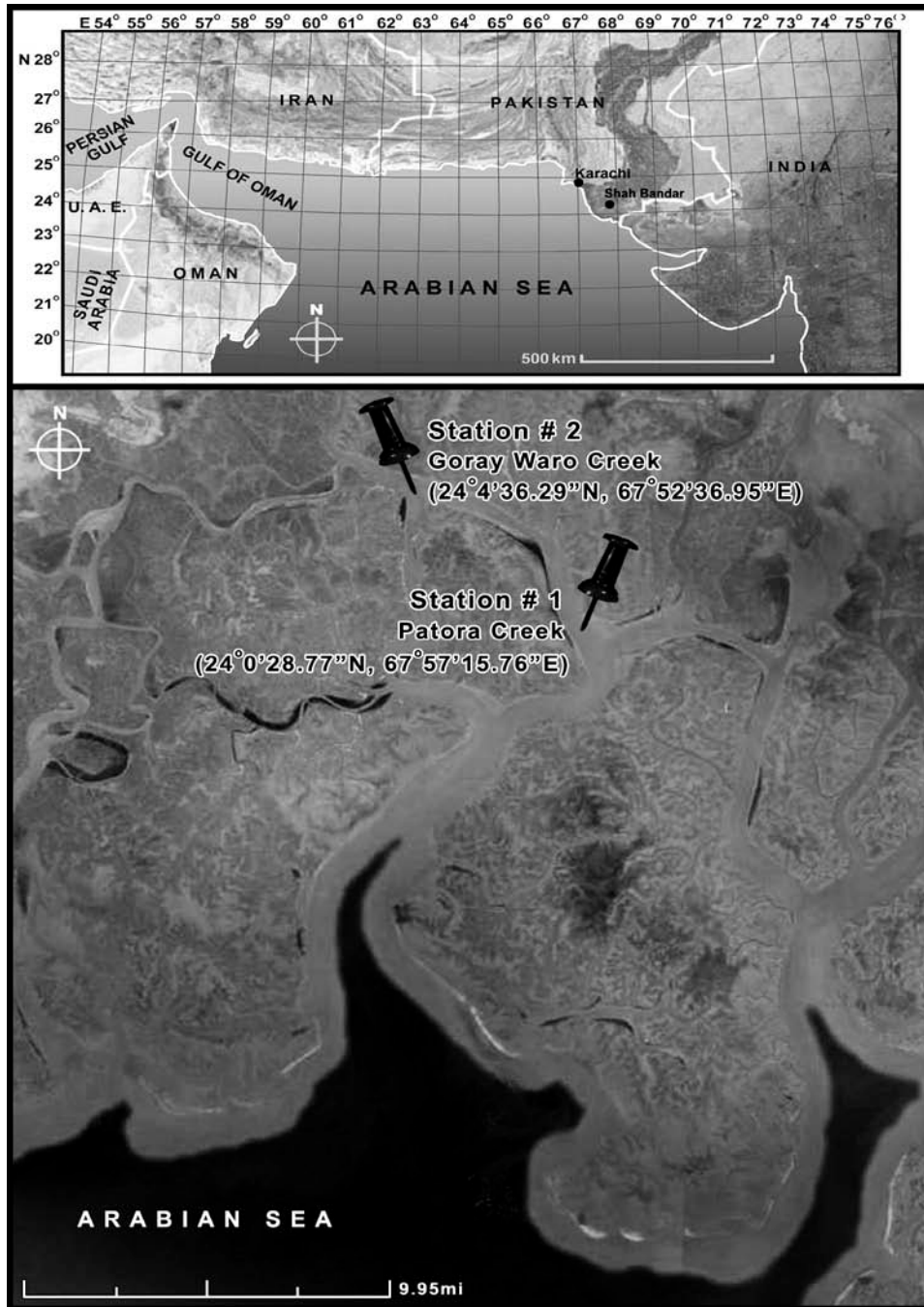


Fig. 1. Map showing the study area with 2 sampling sites station # 1 ((Patora creek) and station # 2 (Ghoray waro creek) alongwith geographic coordinates in Shahbunder creek system, Indus deltaic area.

RESULTS & DISCUSSION

A total (14) group of zooplankton were recorded from two permanent stations Station # 1 (Patora creek) and Station #2 (Goray waro creek) during October to December 1997. Highest air temperature (31°C), water temperature (29°C), salinity (39 ‰), DO (9.3 mg/L), pH (8) and visibility (20 cm) were recorded in October to December from station 1 and 2. Month of December shows lowest level of air and water temperature (Table 1). Table 2, shows highest mean of air temperature (25.33±4.93), water temperature (25.16±5.39), salinity (36.33±3.05), DO (8.83±0.64) and visibility (12.66±6.42) (Figure 2). Comparison of physico-chemical parameters (air temperature, water temperature, salinity, DO, pH and visibility between two stations were presented in (Figure 3 a, b, c, d, e, f, g). The physical and chemical properties of water immensely influence the uses of a water body for the distribution and richness of biota (Unanam and Akpan, 2006) and also influence both vertical and horizontal migration of aquatic organisms. It affects their distribution, diversity and feeding (Imam and Balarabe, 2012). Temperature is an important factor which regulates the biogeochemical activities in the aquatic environment. Water temperature influences aquatic weeds, algal blooms and surrounding air temperature (Perumal *et al.*, 1999 and Rajasegar *et al.*, 2000). The metabolic and physiological activities and life process such as feeding, reproduction, movements and distribution of aquatic organisms are greatly influenced by water temperature.

Table 1. Data on physico-chemical parameters collected from station # 1 (Patora creek) and station # 2 (Ghoray waro creek) during October to December 1997.

Locality	Air Temperature (°C)	Water Temperature (°C)	Salinity (‰)	Dissolved oxygen (mg/L)	pH	Visibility (cm)
Station=1 (Patora creek)						
October	30	27.5	33	7.8	8	11
November	23	29	37	9.0	8	10
December	22	19	39	9.2	8	10
Station=2 (Ghoray waro creek)						
October	31	27	29	8.1	8	8
November	23	20.5	35	9.1	8	20
December	22	19	38	9.3	8	10

Table 2. Mean and standard deviation (mean \pm SD, min-max) of different physico-chemical parameters from station # 1(Patora creek) and station # 2 (Goray waro creek) during October to December 1997.

Station	Air Temperature ($^{\circ}$C) Mean \pm SD (Min-Max)	Water Temperature ($^{\circ}$C) Mean \pm SD (Min-Max)	Salinity ($^{\circ}$/oo) Mean \pm SD (Min-Max)	DO mg/L Mean \pm SD (Min-Max)	pH Mean \pm SD (Min-Max)	Visibility (cm) Mean \pm SD (Min-Max)
Station=1 (Patora creek)	25.00 \pm 4.00 (22.00-30.00)	25.16 \pm 5.39 (19.00-29.00)	36.33 \pm 3.05 (33.00-39.00)	8.66 \pm 0.75 (7.80-9.20)	8.00 \pm 0.00 (8.00)	10.33 \pm 0.57 (10.00-11.00)
Station=2 (Goray waro creek)	25.33 \pm 4.93 (22.00-31.00)	22.16 \pm 4.25 (19.00-27.00)	34.00 \pm 4.58 (29.00-38.00)	8.83 \pm 0.64 (8.10-9.30)	8.00 \pm 0.00 (8.00)	12.66 \pm 6.42 (8.00-20.00)

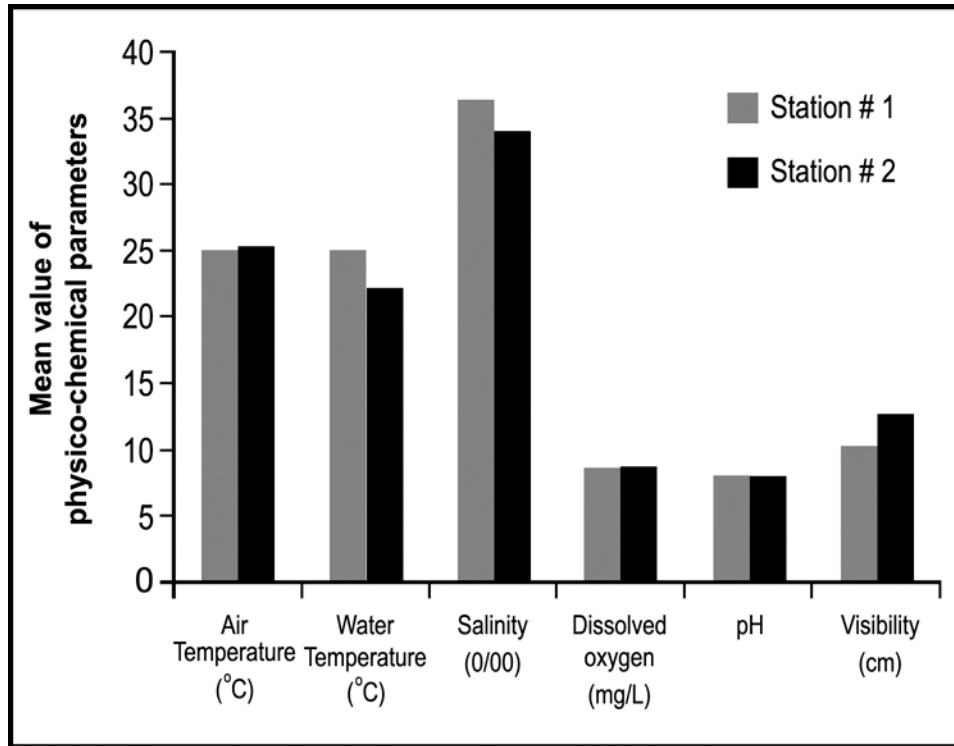


Fig. 2. Mean of physico-chemical parameters recorded from station # 1(Patora creek) and station # 2 (Ghoray waro creek) during October to December 1997.

A total of 14 taxa (hydromedusae, copepoda, mysids, amphipoda, acetes, lucifer, chaetognath, penaeid, caridean, zoea, megalopa, squilla larvae, fish larvae and fish eggs) were recorded during the studies. Total ($n=83478$ no/100m³) number of zooplankton were collected from station 1 and ($n=68774$ no/100m³) from station 2 (Table 3). The abundance of zooplankton occurred at station# 1 as October ($n=57840$ no/100m³), November ($n=10215$ no/100m³), December ($n=15423$ no/100m³) and station #2 as October ($n=40311$ no/100m³), November ($n=9325$ no/100m³) and December ($n=19138$ no/100m³) (Table 3 and 4).

At station # 1 the total number of hydromedusae ($n=379$ no/100m³), copepoda, ($n=45546$ no/100m³), mysids ($n=535$ no/100m³), amphipoda ($n=230$ no/100m³), acetes ($n=968$ no/100m³), lucifer ($n=480$ no/100m³), chaetognath ($n=23120$ no/100m³), penaeid ($n=44$ no/100m³), caridean ($n=596$ no/100m³), zoea ($n=9813$ no/100m³), megalopa ($n=77$ no/100m³), squilla larvae ($n=9$ no/100m³), fish larvae ($n=1230$ no/100m³), fish eggs($n=442$ no/100m³) and others ($n=9$ no/100m³) were recorded. The total number of individual were at station# 2 hydromedusae ($n=197$ no/100m³), copepoda, ($n=28031$ no/100m³), mysids ($n=105$ no/100m³), amphipoda ($n=166$ no/100m³), acetes ($n=580$ no/100m³), lucifer ($n=110$ no/100m³), chaetognath ($n=13190$ no/100m³), penaeid ($n=38$ no/100m³), caridean ($n=133$ no/100m³), zoea ($n=24467$ no/100m³), megalopa ($n=1255$ no/100m³),

squilla larvae (n=12 no/100m³), fish larvae (n=357 no/100m³), fish eggs(n=45 no/100m³) and others (n=44 no/100m³) (Table 3 and 4, Figure 4).

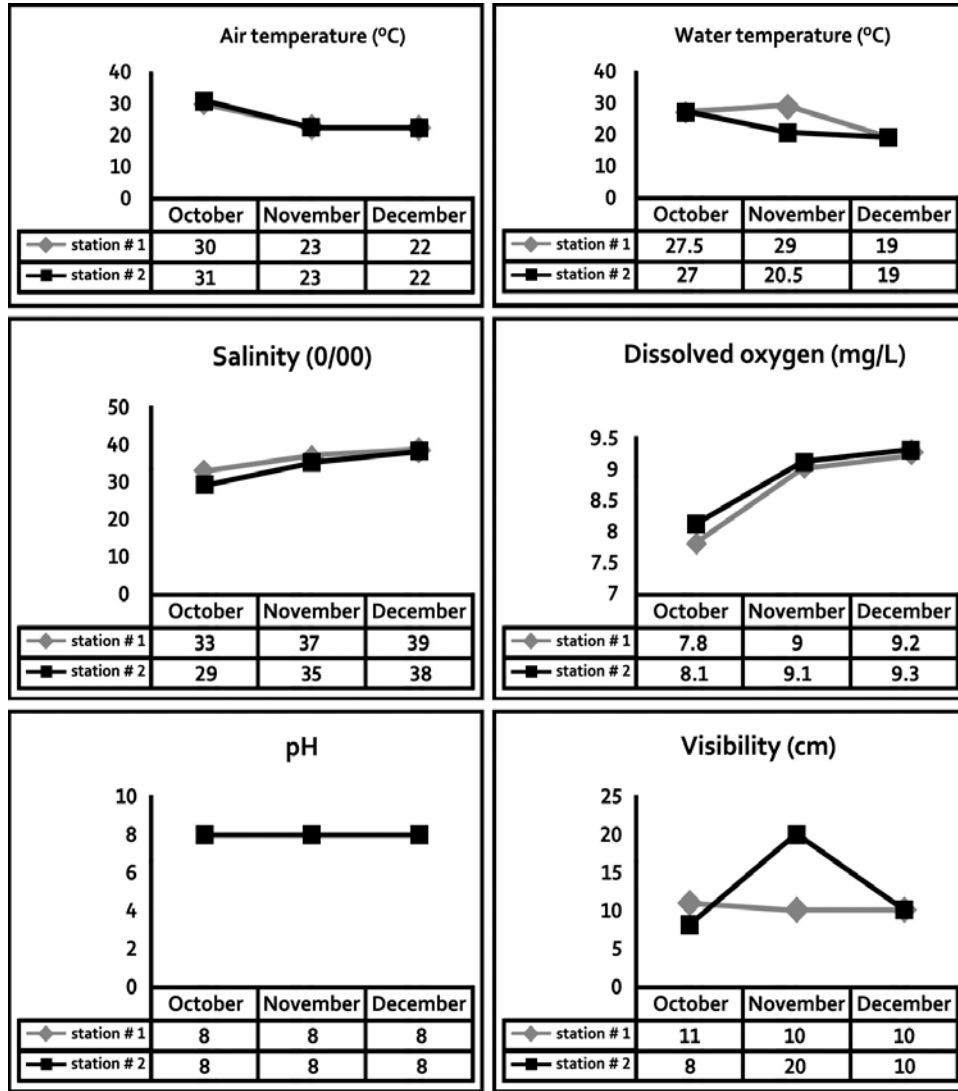


Fig. 3. Monthly variation in physico-chemical parameters between station # 1(Patora creek) and station # 2 (Ghoray waro creek) during October to December 1997.

Table 5 and 6 shows the percentage (%) composition of different zooplankton groups were highest in number at both stations as hydromedusae (0.76%), copepod (50.50%), mysids (0.91%), amphipoda (0.27%), acetes (0.99%), lucifer (0.46%), chaetognath (26.18%), penaeid (0.18%), caridean (0.48%), zoea (17.90%), megalopa (0.09%), squilla

Table 3. Numerical data of Zooplankton per 100m³ collected from station# 1 (Patora creek) during October to December 1997.

	October	November	December
MAJOR TAXA			
Total Zooplankton no/100m ³	57840	10215	15423
HOLOPLANKTON			
Hydromedusae	142	157	80
Copepoda	32898	4105	8543
Mysids	161	14	360
Amphipoda	161	31	38
Acetes	741	73	154
Lucifer	456	-	24
Chaetognath	16653	2355	4112
MEROPLANKTON			
Penaeid PL	9	35	-
Caridean PL	541	52	3
Zoea	4417	3356	2040
Megalopa	57	10	10
Squilla larvae	9	-	-
Fish larvae	1206	10	14
Fish eggs	380	17	45
Others	9	-	-

Table 4. Numerical data of Zooplankton per 100m³ collected from station # 2 (Ghoray Waro creek) during October to December 1997.

	October	November	December
MAJOR TAXA			
Total Zooplankton no/100m³	40311	9325	19138
HOLOPLANKTON			
Hydromedusae	99	21	77
Copepoda	11844	4441	11746
Mysids	81	3	21
Amphipoda	135	10	21
Acetes	153	-	427
Lucifer	90	3	17
Chaetognath	6219	3069	3902
MEROPLANKTON			
Penaeid PL	-	10	28
Caridean PL	126	7	-
Zoea	21132	1725	1610
Megalopa	27	3	1225
Squilla larvae	9	-	3
Fish larvae	351	3	3
Fish eggs	18	10	17
Others	-	3	41

Table 5. Percentage (%) composition of zooplankton per 100m³ collected from station # 1 (Patora creek) during October to December 1997 (all values are in %).

	October	November	December	Mean (%)
MAJOR TAXA				
Total Zooplankton no/100m³	57840	10215	15423	
HOLOPLANKTON				
Hydromedusae	0.24	1.53	0.51	0.76
Copepoda	56.87	40.18	55.39	50.50
Mysids	0.28	0.13	2.33	0.91
Amphipoda	0.28	0.30	0.24	0.27
Acetes	1.28	0.71	0.99	0.99
Lucifer	0.79	-	0.15	0.46
Chaetognath	28.79	23.05	26.70	26.18
MEROPLANKTON				
Penaeid PL	0.02	0.34	-	0.18
Caridean PL	0.94	0.50	0.02	0.48
Zoea	7.63	32.85	13.24	17.90
Megalopa	0.10	0.10	0.06	0.09
Squilla larvae	0.02	-	-	0.02
Fish larvae	2.08	0.10	0.09	0.75
Fish eggs	0.65	0.17	0.29	0.36
Others	0.02	-	-	0.02

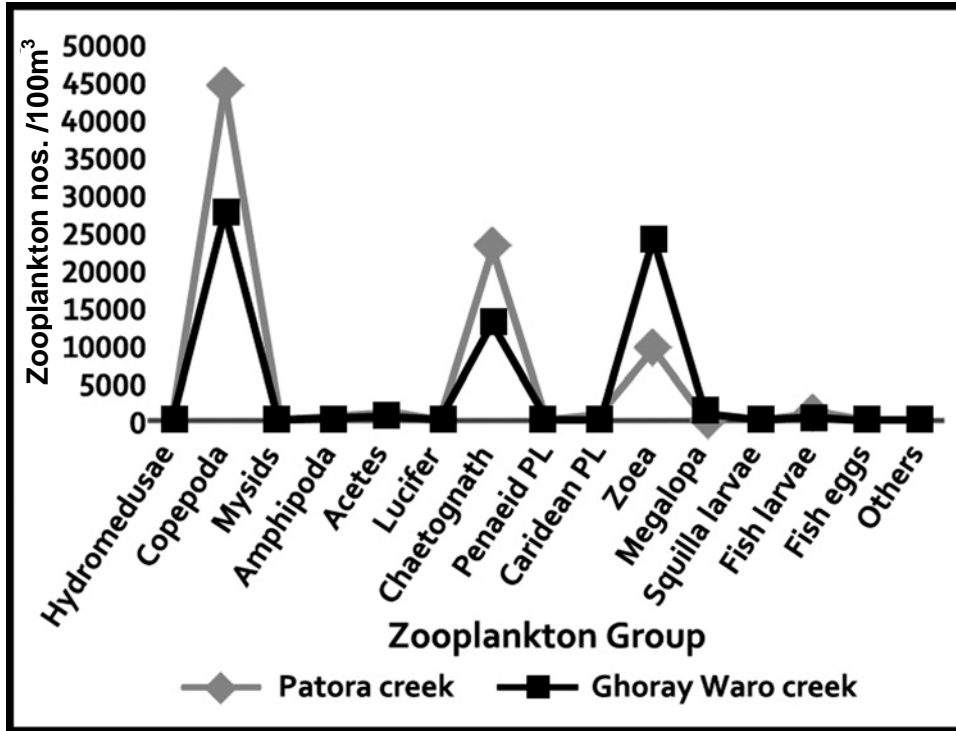


Fig. 4. Total number of zooplankton collected from station# 1 (Patora creek) and station# 2 (Ghoray Waro creek) during October to December 1997.

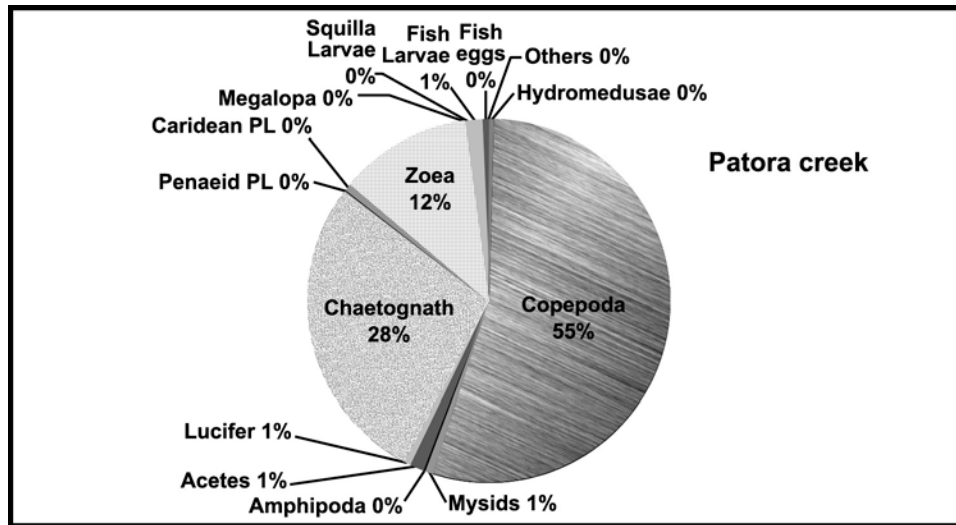


Fig. 5. Percentage (%) composition of zooplankton groups per 100m³ collected from station# 1 (Patora creek) during October to December 1997.

Table 6. Percentage (%) composition of zooplankton per 100m³ collected from station # 2 (Ghoray Waro creek) during October to December 1997 (all values are in %).

	October	November	December	Mean (%)
MAJOR TAXA				
Total Zooplankton no/100m ³	40311	9325	19138	
HOLOPLANKTON				
Hydromedusae	0.24	0.22	0.42	0.29
Copepoda	29.38	47.63	61.37	46.12
Mysids	0.20	0.03	0.10	0.11
Amphipoda	0.33	0.10	0.10	0.17
Acetes	0.37	-	2.23	1.3
Lucifer	0.22	0.03	0.08	0.11
Chaetognath	15.42	32.90	20.38	22.9
MEROPLANKTON				
Penaeid PL	-	0.10	0.14	0.12
Caridean PL	0.31	0.07		0.19
Zoea	52.42	18.50	8.41	26.44
Megalopa	0.06	0.03	6.40	2.16
Squilla larvae	0.02	-	0.01	0.015
Fish larvae	0.87	0.03	0.01	0.3
Fish eggs	0.04	0.10	0.08	0.07
Others	-	0.03	0.21	0.12

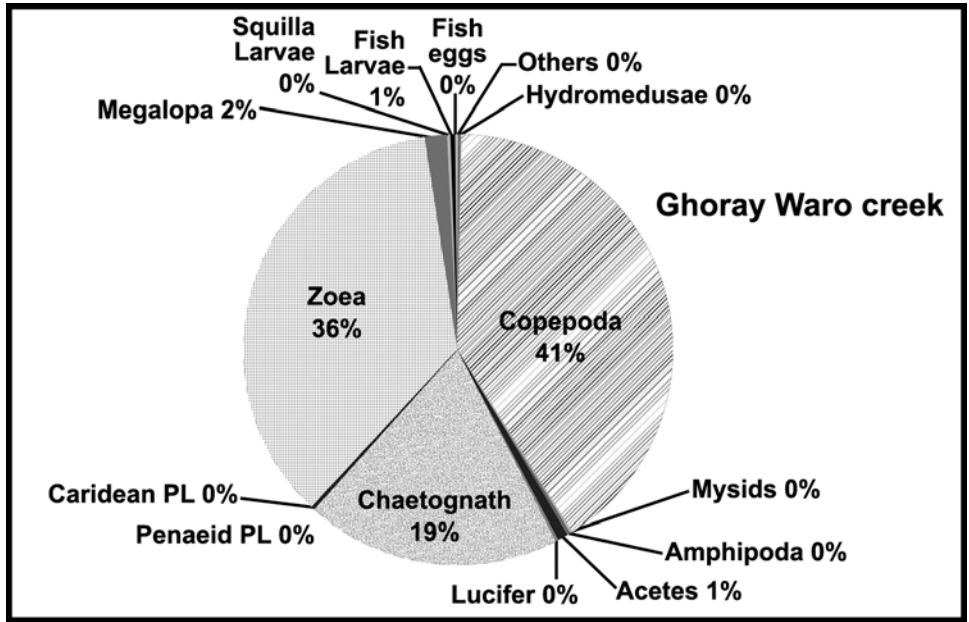


Fig. 6. Percentage (%) composition of zooplankton groups per 100m³ collected from station # 2 (Ghoray Waro creek) during October to December 1997.

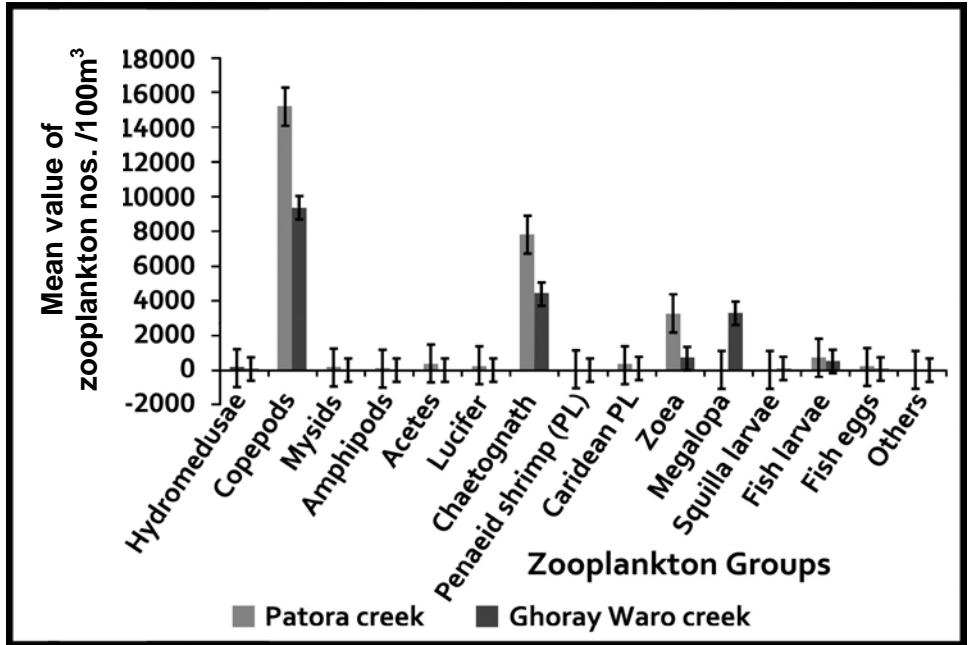


Fig. 7. Mean value of total number of zooplankton groups from station # 1 (Patora creek) and station # 2 (Ghoray Waro creek) during October to December 1997.

Table 7. Analysis of variance (ANOVA) performed between zooplankton and months.

		Sum of Squares	df	Mean Square	F	Sig.
Zooplanktons * Locality	Between Groups	36034602.67	1	36034602.67	0.077	0.795
	Within Groups	1866396291	4	466599072.7		
	Total	1902430893	5			
Zooplanktons * Months	Between Groups	1741501310	2	870750655.2	16.232	0.025
	Within Groups	160929583	3	53643194.33		
	Total	1902430893	5			
Locality * Months	Between Groups	0.000	2	0.000	0.000	1.000
	Within Groups	1.500	3	.500		
	Total	1.500	5			

*significant at the 0.05 level.

larvae (0.02%), fish larvae (0.75%) and fish eggs (0.36%) others (0.02%) were measured from station 1 (Table 5, Figure 5). Table 6 shows the percentage (%) composition of hydromedusae (0.29%), copepod (46.12%), mysids (0.11%), amphipoda (0.17%), acetes (1.3%), lucifer (0.11%), chaetognath (22.9%), penaeid (0.12%), caridean (0.19%), zoea (26.44%), megalopa (2.16%), squilla larvae (0.015%), fish larvae (0.3%) and fish eggs (0.07%) others (0.12%) from station 2 (Table 6, Figure 6).

From station # 1 highest mean (15182.0 ± 1402.14) was observed in copepods, and lowest mean (5.19 ± 3.00) were recorded in squilla larvae (Figure 7). Copepod shows highest mean value (9343.66 ± 4246.11) at station# 2 (Figure 7). During whole study period the composition of copepods was highest than other group because copepod are the major members of zooplankton in biomass and abundance in marine pelagic ecosystem (de Puelles *et al.*, 2003; Leandro *et al.*, 2007). The copepods could represent an important trophic link between the larger predators (Porter *et al.*, 1979). Among all metazooplankton, copepods are the most abundant taxa (55% to 95%) in most sea areas (Beers *et al.*, 1980; Webber *et al.*, 1995). Huda and Ahmed in (1988) reported seasonal variation in zooplankton groups in the Korangi Creek channel, which revealed that copepods were the most dominant group than decapods larvae and chaetognath.

Table 7 shows analysis of variance (ANOVA) between zooplankton, month and locality. No significant correlation was observed between zooplankton with locality and locality with months. However the significant correlation ($P > 0.05$, 0.025) ($F = 16.232$) was observed in zooplankton with months.

CONCLUSION

The present studies reveal that Shahbunder creek system supports a diverse zooplanktonic community and is an interesting area for further research studies. The zooplankton groups found during the study period suggests that they tolerate wide salinity fluctuations. This baseline information on the zooplankton composition is useful for assessment of aquatic biodiversity, especially fisheries resources in the creek system. And a potential base line data on zooplankton for future ecological investigation and monitoring of the Shahbunder creek system. This is the first attempt on ecological and zooplanktonic studies in Shahbunder creek system.

REFERENCES

- Ahmed, M., (1951). Plankton of Karachi Coast and Their Bearing on Fishes, *Agric. Pakistan*. 2:22-31.
- Ali, M., M. Arshad, (1966). Preliminary Observations on the Composition of Zooplanktons along Karachi Coast, *Agric. Pakistan*. 17:227-237.
- Beers JR, M.S. Reid and G.L. Stewart, 1980. Microplankton population structure in southern California nearshore waters, *Mar. Biol.* 60:209-226.
- de Puelles, M. L. F., D. Grás and S. Hernández-León, 2003. Annual cycle of zooplankton biomass, abundance and species composition in the neritic area of the Balearic Sea, western Mediterranean. *Marine Ecology* 24: 123–139.
- Fazal-ur-Rehman, (1973a). A new Calanoid Copepod, *Pontella Karachiensis* from W. Pakistan. *Crustaceana*. 24:152-156.

- Fazal-ur-Rehman, (1973b). Observations on the variations in planktonic copepod *Tortanusforipatus*(Giesbrecht, 1889) from the inshore waters of the Karachi coast, Pakistan. *Crustaceana*. 25:113-118.
- Globov, JA. and A.G. Grobov, (1970). Summary Account on the Scientific Research Works of the Expedition in the Waters Adjacent to the Islamic Republic of Pakistan (January to December 1969), Azor-Black Sea Research Institute of Marine Fishery and Oceanography, Ministry of Fisheries of the USSR, p. 166.
- Haq, SM., (1968). Observations on the variations in planktonic copepod *Undinula vulgaris* (Dana 1849) from the north Arabian Sea. *University studies*, 5:86-92.
- Haq, SM., Fazal-ur-Rehman, (1973). A new Calanoid Copepode, *Centropages Karachiensis* from the Inshore Waters of the Karachi Coast, West Pakistan, *Zool., Med.* 46:183-188.
- Huda, A.I. and J. Ahmad, (1988). Zooplankton Production Trends in the Inshore Waters of a Mangrove Ecosystem along the Karachi Coast. *Marine Science of the Arabian Sea*. 407-415 pp.
- Imam T.S., M.L. Balarabe, 2012. Impact of Physicochemical factors on zooplankton species richness and abundance in Bompai-Jakara catchment basin, Kano state Nigeria. *Bayero Journal of Pure and Applied Sciences* 5(2), 34-40.
- Karande, A.A., (1991). Use of epifaunal communities in pollution monitoring. *J. Environ. Biol.*, pp: 191-200.
- Khan, M.A., (1974). Seashore Distribution of bio-mass and Number of Zooplankton in Manora Channel During 1975-77, *Biologia*. 25: 182-203.
- Khan, M.A. and W.M. Kamran, (1975). *Cymbasoma tirmizii* sp. nov. (Copepoda) from Manora Channel (Northern Arabian Sea). *J. Sci., Univ. Karachi*. 3: 55-59.
- Khan, M.A., (1976). *Cymbasoma williamsoni* sp. nov. (Copepoda Monstrilloida-Monstrillidae) from Manora Channel (Northern Arabian Sea). *J. Sci., Univ. Karachi*. 4(1 and 2).
- Leandro, S.M., F. Morgado, F. Pereira and H. Queiroga, 2007. Temporal changes of abundance, biomass and production of copepod community in a shallow temperate estuary (Ria de Aveiro, Portugal). *Estuarine, Coastal and Shelf Science* 74: 215–222.
- Newell, G.E. and R.C. Newell, (1977). *Marine Plankton a Practical guide*. 5th Ed. Hutchinson & Co. (Publishers) Ltd 244 p.
- Perumal, P., P. Sampathkumar, P.K. Karuppasamy, (1999). Studies on the bloom forming species of phytoplankton in the Vellar estuary, southeast coast of India. *Ind. J. Mar. Sci.*, 28: 400-403.
- Porter K.G., M.L. Pace and J.F. Battey, 1979. Ciliate protozoas as links in freshwater planktonic food chains. *Nature*. 277:563-565.
- Rajasegar, M., M. Srinivasan and R. Rajaram, (2000). Phytoplankton diversity associated with the shrimp farm development in Vellar estuary, south India. *Seaweed Res. Utiln.*, 22: 125-131.
- Robertson, A.I. and S.J.M. Blabber, (1992). Plankton, epibenthos and fishcommunities. In: *Tropical mangrove ecosystems* (Eds.: A. I.Robertson and D.M. Alongi). *Coastal Estuar. Stud.* 41:173-224.

- Saraswathi, R., (1983). Hydrobiology of two estuarine systems (Arasalar and Kaveri) of the southeast coast of India with special reference to plankton. Ph.D. Thesis, Annamalai University, India.
- Sladeczek, V., (1958). A Note on the Phytoplankton-Zooplankton Relationship, Ecology, Ecological Society of America, 39:3:547-549.
- Saravanakumar, A., M. Rajkumar, J. Sesh Serebiah and G.A. Thivakaran, (2007b). Abundance and seasonal variations of zooplankton in the arid zone mangroves of Gulf of Kachchh-Gujarat, Westcoast of India. *Pak. J. Biol. Sci.*, 10, 3525-3532.
- Tiwari, L.R. and V.R. Nair, (1993). Zooplankton composition in Dharamtar creek adjoining Bombay harbour. *Indian J. Mar. Sci.*, 22: 63-69.
- Unanam, A.E. and A.W. Akpan, 2006. Analysis of physicochemical characteristics of some freshwater bodies in Essien Udim Local Government area of Akwa Ibom State, Nigeria. In: Proceeding of the 21st Annual Conference of the Fisheries Society of Nigeria (FI50N) Calabar, 13th -17th November, 2006.
- Webber M.K. and J.C. Roff, 1995. Annual structure of the copepod community and its associated pelagic environment off Discovery Bay Jamaica, *Mar. Biol.*, 123:467-479.