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ORIGINAL RESEARCH

Mesozooplankton of the Omani shelf: taxonomy, seasonality, and spatial distribution

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Abstract The total zooplankton biomass was determined for 216 samples collected during seasonal surveys onboard a research vessel. Some of these samples were processed to the level of species. In 2007–2008, the Omani shelf was populated by a highly productive epipelagic plankton community. The chlorophyll-*a* concentration was high throughout the seasonal cycle and likewise the zooplankton biomass, where seasonal values varied from 543 to 723 mg m^{-3}. Spatial distribution of zooplankton biomass over shelf waters was highly heterogeneous, with maximal heterogeneity observed during the South-west Monsoon. The mean biomass and size structure of the zooplankton community did not exhibit statistically significant seasonal changes. On the species level, seasonal changes dealt with a massive appearance of the copepod *Calanoides carinatus s.f.* in shelf waters, to which organisms migrated from the deep, during the South-west Monsoon. The population represented mainly by c4 and c5 copepodite stages ascending to upper layers during its ontogenetic migration has occupied the entire Omani shelf area. However, this migration did not contribute markedly to seasonal variation of the total zooplankton biomass.

Keywords Zooplankton · Arabian Sea · Coastal upwelling · Ontogenetic migration

Introduction

The issue of spatial–temporal structure in the zooplankton community inhabiting the Omani shelf was basically skipped by basin-scaled International expeditions devoted to the Arabian Sea. For instance, a major part of JGOFS oceanographic stations of 1990s was oriented toward the pelagic processes in oceanic regions (Smith 2005). The earliest expedition that covered coastal Oman, was carried out by R/V "Fridtjof Nansen," from March to June 1976 and dealt with zooplankton studies (Anonymous 1975). From December 1989 to

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November 1990, a zooplankton survey of the Omani shelf was carried out by R/V "Rastrelliger," focusing on the assessment of spatial–temporal variations of total zooplankton biomass (Thangaraja et al. 2011). Later on in August 1995, the US R/V "Malcolm Baldrige" made a part of its sampling along the Omani shelf, with an accent on acoustical measurements of diel vertical migrations (Hitchcock et al. 2002). In 2002, the R/V "Charles Darwin" carried out a 28-day cruise along the Omani shelf, with the main objective of producing a bathymetry map and sampling the benthic community (Jacobs 2003). The survey was accompanied by CTD casts which were important for further insights into the thermo-haline structure of water masses.

A comprehensive study of zooplankton ecology is of great importance for analyzing the states of the northern Indian Ocean like Oman, because many commercial fish species are planktivorous; a challenge which points out the necessity of studying the details of their food resources. An academic interest in zooplankton research is associated in part with seasonal changes, in particular with the phenomenon entitled the "paradox" of the Arabian Sea zooplankton, stating that biomass is invariant despite seasonally changing primary production (Baars 1999; Madhupratap et al. 1996). Magnitudes of seasonal changes in zooplankton biomass are valuable characteristics in understanding the limitation of algal bloom magnitudes by zooplankton grazing (Smith 2001). It is believed that about 40 % of primary production could be ingested by mesozooplankton, which is an indicative of the importance of this group in trophic relationships in epipelagic plankton communities (Roman et al. 2000).

The Omani shelf is the region notorious for its intensive seasonal upwelling, which is footprinted in ontogenetic vertical migrations of abundant zooplankton species. The copepod *Calanoides carinatus s.f.* is one of these. It has been shown that the population migrates to the upper layers rich in diatoms which it grazes on. However, the data establishing this concept came from a single local sampling site (Smith et al. 1998). In fact, the Oman shelf area was largely missed in all the JGOFS sampling. Schemes of standard transect of the JGOFS cruises point out only one station out of eight, located on the shelf (Lane et al. 1998). In order to estimate the spatial scale of the ontogenetic migration phenomenon, a field survey of the whole shelf is inevitable.

Here we present results of five seasonal surveys carried out over the Omani shelf overlooking the western Arabian Sea. Data come from the expedition sponsored by the Oman Ministry of Fisheries and implemented in 2007–2008 by New Zealand Consultant Bruce Shallard and Associates who subcontracted the New Zealand Institute of Water and Atmospheric Research, Deliotte New Zealand, Independent Fisheries New Zealand, and Al Riyami Group (McKoy et al. 2009). We discuss spatial distribution and seasonal changes in the abundance of species, as well as the total zooplankton biomass.

Data and methods

Data on the wind speed were retrieved from the NCAR/NCEP reanalysis database (Kistler et al. 2001), in which the daily averages were extracted for the western Arabian Sea region incorporating the Omani shelf (15–23°N; 57–60°E). Maps for sea surface height anomalies were acquired from the CCAR Global Near Real-Time SSH Anomaly/Ocean Color Data Viewer (http://eddy.colorado.edu/ccar/data_viewer/index).

Satellite-derived MODIS Aqua weekly Level-3 products for the chlorophyll-*a* concentration (with a 4-km spatial resolution) were obtained from the National Aeronautics and Space Administration (NASA) database (http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_8day). Monthly time series were acquired using the GES-DISC Interactive Online Visualization and Analysis Infrastructure software, as part of the NASA's Goddard Earth Sciences Data and Information Services Center.

Zooplankton sampling was a part of seasonal surveys consisting of five voyages of the R/V "Mustaqila1" carried out along the shelf in the 20–250 m depth range, from the Ras al Hadd region to the southernmost part of the Omani shelf (to the Yemen border). Sampling was accompanied by the RBD CTD probe casts (with conductivity, temperature, density, and dissolved oxygen concentration measurements), echo-soundings, and fish trawls (Table 1).

Zooplankton were collected around the clock at 216 stations along the offshore transects (Fig. 1). A net with an opening of 60 cm equipped with 500 µm mesh net was used for oblique vertical hauls. Samples were preserved in 4 % buffered formaldehyde. The wet weight (mass) of 216 samples was estimated in the lab by using an electronic balance, after blotting, and expressed in mg m^{-3}. Subsamples from 20 samples collected

Table 1 General characteristics of the "Mustaqila1" voyages

Voyage code	Time range	Demersal stations/trawls	CTD stations	Zooplankton samples (stations)
OMA0701	Sep–Oct 2007	101	386	0
OMA0702	Nov–Dec 2007	104	459	0
OMA0801	Jan–Mar 2008	120	644	55
OMA0802	Apr–Jun 2008	123	603	79
OMA0803	Aug–Sep 2008	129	520	82

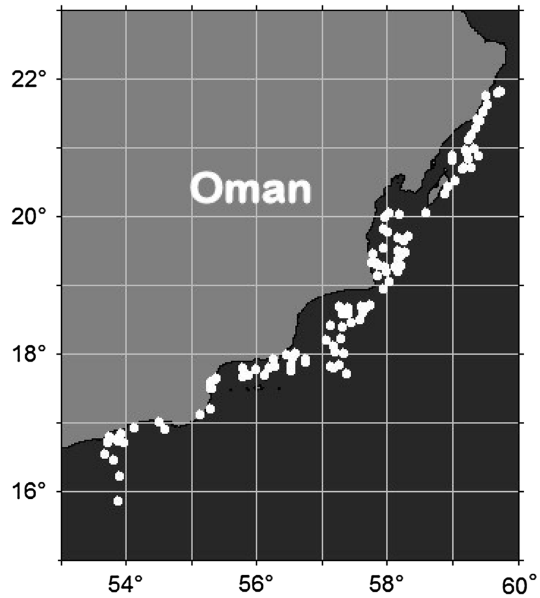

Fig. 1 Zooplankton sampling sites along the Omani shelf from September 2007 to September 2008

during winter, spring, and summer seasons were subjected to taxonomic analysis to the species level and size measurements.

A Simrad EK60 acoustic instrument with 38, 120, and 200 kHz transducers was used for routine acoustic surveys. Transects across the shelf began at a 200 m depth and extended out to 8 km offshore. When deep-scattering layers were identified on the sounder, pelagic trawls were used to catch the organisms. Later on, catches were sorted by species (McKoy et al. 2009). The P55 midwater trawl with a 10 mm liner in the cod end was used to sample mesopelagic organisms.

Results

In terms of time span, a major part of the zooplankton sampling was carried out from January to September 2008. We begin the analysis of seasonal changes from the Winter North-east Monsoon, through the Spring Inter-monsoon and finally, to the Summer South-west Monsoon period. During winter and summer monsoons, the prevailing wind direction is parallel to the coast, but it has opposite directions (Böhm et al. 1999). This does not allow a coastal current (the East Arabian Current) to set up upwelling during winter, but maximizes the offshore Ekman transport and thus the upwelling intensity during the summer.

The year 2008 was notorious for its unusually calm winter monsoon, in which the wind speed in February was gradually decreasing, compared to the previous years, whereas the winds featured in the South-west

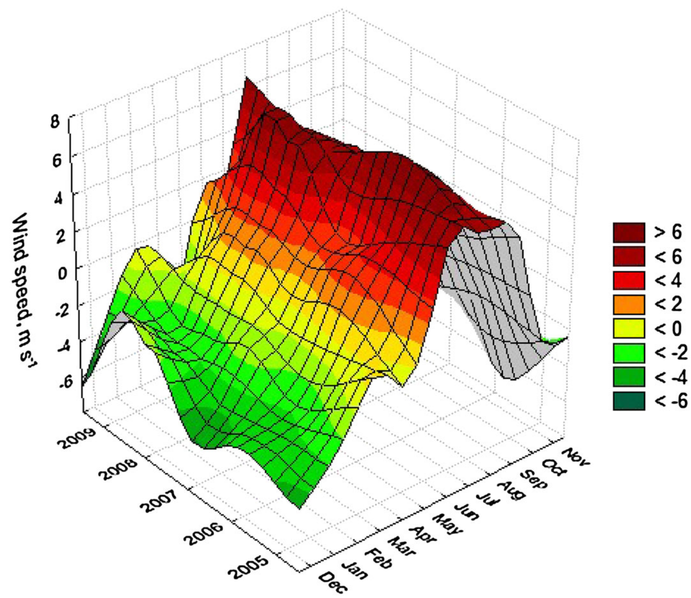

Fig. 2 Monthly changes of meridional component of the wind speed over the western Arabian Sea including the Omani shelf region (15–23°N; 57–60°E). Values are positive when the wind blows from west to east

Monsoon (in August) were gradually increasing (Fig. 2). Overall, summer winds possessed high meridional speeds compared to the winter monsoon winds.

The series of CTD casts carried out during zooplankton sampling have captured the seasonal variability of the thermo-haline structure over the Omani shelf (Fig. 3).

This variability is largely based on a reversing of the East Arabian Current, changing its direction from north-eastward during the South-west Monsoon to the opposite (south-westward) during the North-east Monsoon. Figure 3 exemplifies vertical structure corresponding with the monsoonal and inter-monsoonal seasons. Visible is a deepened mixed layer established by an evaporatively driven convective overturning characteristic for the North-east Monsoon. Salinity in the deeper portion of this layer was in the region of 36.55 ppm.

During the Spring Inter-monsoon, the mixed layer was much less pronounced. A relaxation and subsequent collapse of the East Arabian Current has favored the formation of layered structures, which, in the given case, was reflected by vertical distribution of salinity (Fig. 3). The South-west Monsoon is notorious for its wind-driven coastal upwelling, shallow mixed layer, and subsequent low temperatures in the seasonal thermocline entrained from beneath. For instance, temperature was 21 °C at a 50 m depth, versus 21.5 and 23.5 °C during the Spring Inter-monsoon and North-east Monsoon periods.

Mesoscale variability contributed to the vertical thermo-haline structure as well. Cyclonic and anticyclonic eddies were observed across the shelf throughout the year (Fig. 4). A 3-year weekly animation of the sea surface height anomalies (with a fragment exemplified by Fig. 4) has pointed out three major types of eddies observed in the western Arabian Sea.

Numerous eddies move from the Arabian Sea interior westward toward the Omani shelf, throughout the entire year. During the North-east Monsoon, eddies in the western Arabian Sea were poorly developed and the sea surface height anomalies associated with eddies were quite weak. These eddies were observed throughout the Spring Inter-monsoon season as well. During the South-west Monsoon, parts of eddies were generated by the East Arabian Current and its confluence with the current headed out from the Gulf of Oman. In terms of kinetic energy, these are the most powerful eddies in this region. Some of them moved southward when the confluence of currents collapsed, approaching the Fall Inter-monsoon season.

Footprints of monsoon and inter-monsoon periods were pronounced in the chlorophyll-*a* concentration remotely sensed by the MODIS scanner (Fig. 5). The seasonality of chlorophyll changes was pronounced over shelf waters, but most clearly it was observed over the open sea regions. During the South-west Monsoon, shelf concentrations exceeded the Spring Inter-monsoon period nearly fourfold.

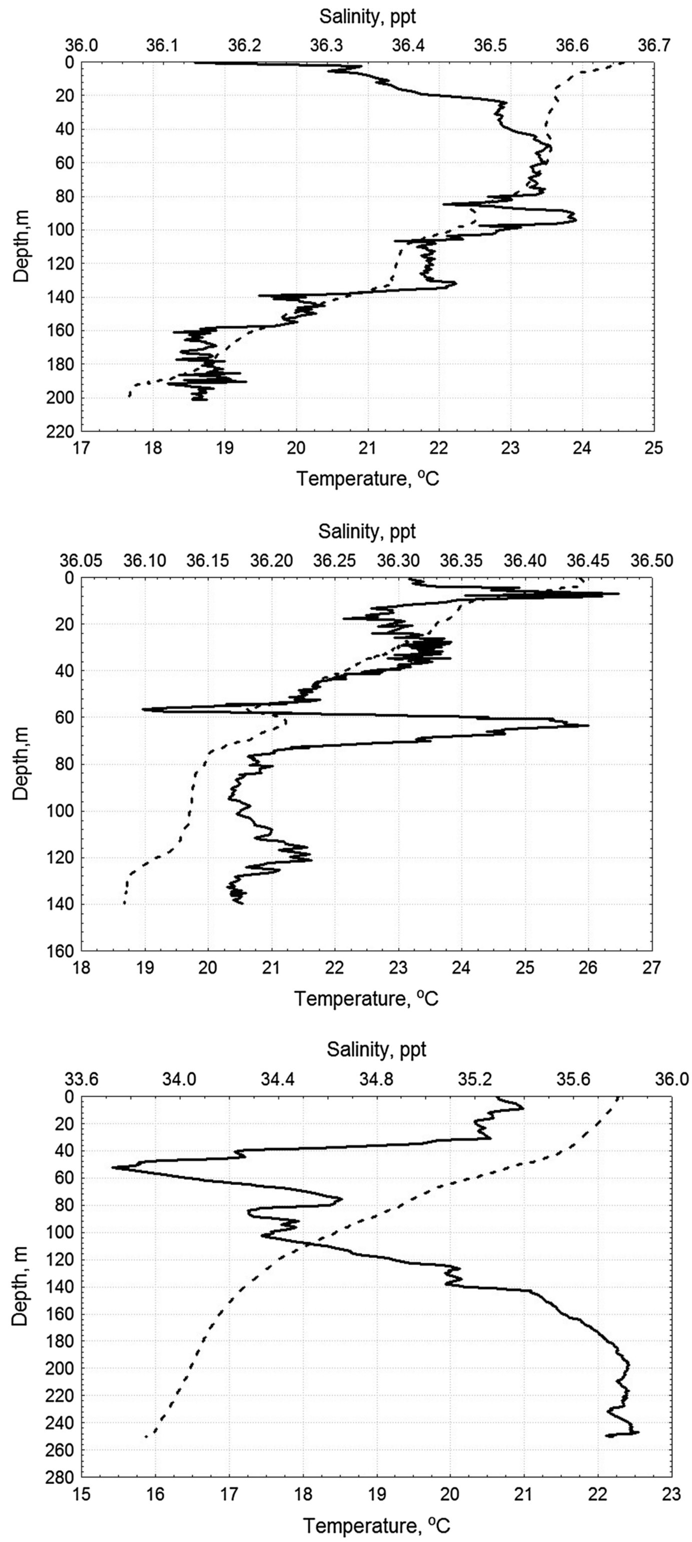

Fig. 3 Vertical distribution of temperature and salinity over the Omani shelf during North-east Monsoon, Spring Inter-monsoon, and South-west Monsoon. *Upper panel* St.316, 18 February, 2008; 10°01.73°N, 57°21.09°E. *Middle panel* St.210, 6 May, 2008; 19°11.92°N, 58°08.82°E, and *low panel* St.173, 18 August, 2008; 18°19.78°N, 57°33.43°E

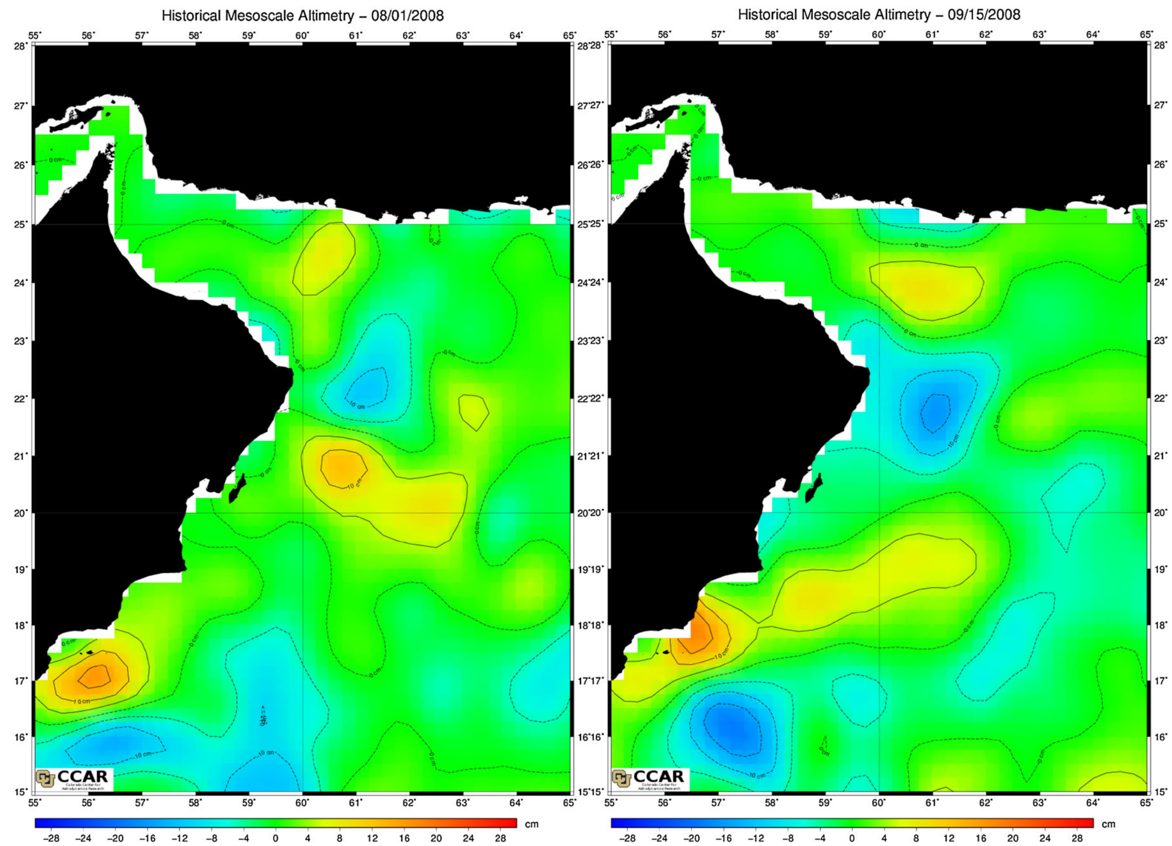

Fig. 4 Maps of sea surface height anomalies (in cm) featuring the South-west Monsoon season. *Left* to *right* 1 August, 2008, and 15 September, 2008

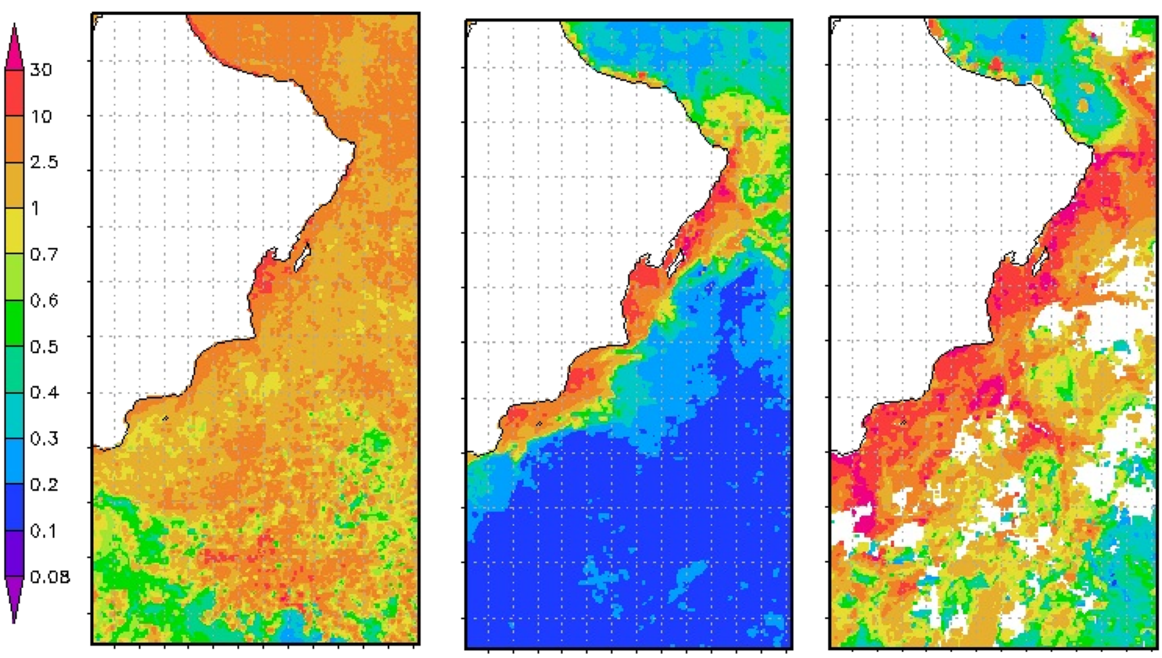

Fig. 5 Seasonal changes of the chlorophyll-*a* concentration in the western Arabian Sea (including the Omani shelf). The vertical color bar stands for the chlorophyll-*a* concentration (mg m^{-3}). From *left* to *right* North-east Monsoon (January–February, 2008), Spring Inter-monsoon (April–May, 2008), and South-west Monsoon (August–September, 2008). White zones in the right figure stand for a cloud mask

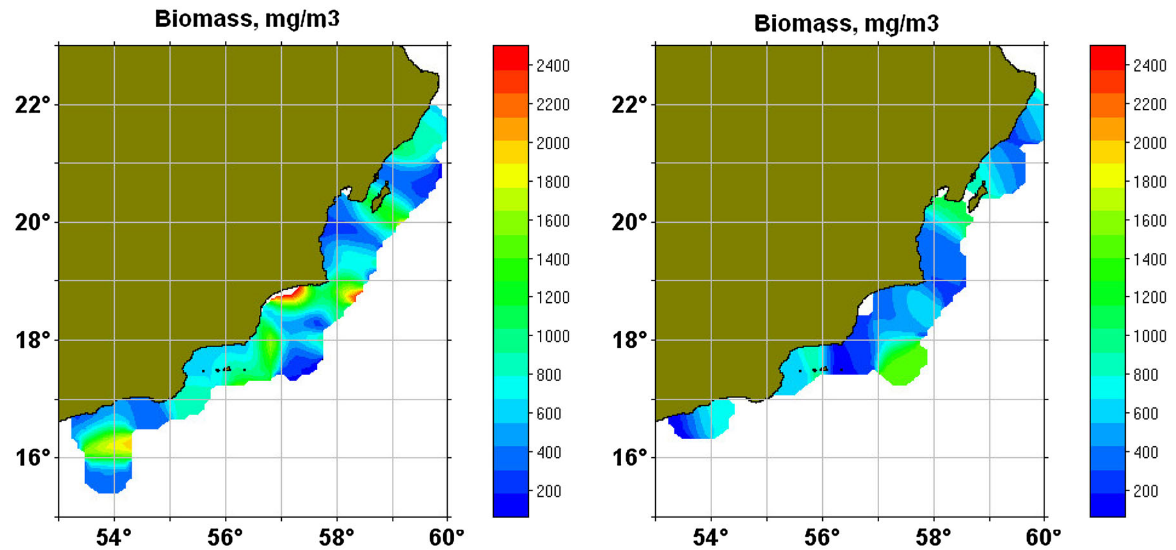

Fig. 6 Spatial distribution of zooplankton biomass during Spring Inter-monsoon (*left figure*) and South-west Monsoon periods

Table 2 Some basic characteristics of the Omani shelf (2008)

Seasons	NEM	SIM	SWM	FIM
Euphotic depth (m)	39 ± 6	66 ± 5	22 ± 8	No data
Dissolved oxygen (mg L^{-1}) (1–10 m)	4.6 ± 0.7	4.5 ± 0.2	4.3 ± 0.9	No data
Temperature (°C) (1–10 m)	24.2 ± 0.9	26.8 ± 1.3	24.5 ± 3.9	No data
Salinity (ppt) (1–10 m)	36.4 ± 0.1	36.4 ± 0.2	36.2 ± 0.2	No data
Chlorophyll-*a* concentration (mg m^{-3}) (surface)	2.0 ± 1.8	2.4 ± 5.2	8.8 ± 10.8	No data
Number of daily zooplankton stations	25	53	42	3
Zooplankton biomass (mg m^{-3})	689 ± 672	723 ± 690	543 ± 705	619
Variance/mean ratio of zooplankton biomass (mg m^{-3})	656	659	915	No data
Mean prosome length of copepods (mm)	1.9 ± 0.8	2.0 ± 1.0	1.8 ± 0.9	No data
Myctophids (biomass) (t km^{-2})	No data	155	1,200,000	No data

NEM North-east Monsoon, *SIM* Spring Inter-monsoon, *SWM* South-west Monsoon, *FIM* Fall Inter-monsoon

In analyzing spatial and seasonal distribution of zooplankton, we excluded samples collected at night, in order to eliminate the impact of diel vertical migrations, which could cause from a two- to a fivefold increase of zooplankton abundance and biomass (Goswami and Shrivastava 1996; Luo et al. 2000; Smith et al. 1998). Only samples collected during day time (from 6 am to 6 pm) were used to construct the maps. This procedure has limited our subsequent assessments of spatial distribution, making them statistically reliable for the Spring Inter-monsoon and the South-west Monsoon periods only (Fig. 6).

Maps revealed the biomass distributed mosaically over the shelf area during both seasons. Local maxima with values of approximately 1400–2000 mg m^{-3} were observed across the shelf and near the shelf edge during both monsoon periods. No seasonal changes were pronounced, regarding the total zooplankton biomass. The mean seasonal values were 689, 723, 543, and 619 mg m^{-3} for the North-east Monsoon, Spring Inter-monsoon, South-west Monsoon, and Fall Inter-monsoon periods (Table 2). No statistical differences among mean biomass values were observed since the variation was large, which is reflected by the standard deviations.

In spatial distribution, the variance-to-mean ratio has been used as the spatial heterogeneity index (Okubo 1980; Piontkovski and Melnik 2006). In the present study, the ratio was treated as a simple way to assess spatial heterogeneity of zooplankton biomass distribution. As far as the Omani shelf waters are concerned, patchiness in biomass distribution was maximal during the South-west Monsoon (Table 2).

An absent seasonality on the level of total zooplankton biomass was accompanied by a relatively stable species composition of the dominant (by abundance) groups—copepods; 40 species were found during the North-east Monsoon, 38 species during the Spring Inter-monsoon, and 34 species were present in the South-west Monsoon. Of those, 11 species (about 30 %) were present throughout the year (Table 3).

As for the groups of dominant zooplankton species (including copepods), the composition changed throughout the seasons. In the North-east Monsoon, the top five dominant groups were represented by families *Oikopleuridae*, *Sagitta*, and copepod species *Cosmocalanus darwinii*, *Nannocalanus minor*, and *Euchaeta sp.*, which comprised 15, 10, 10, 5, and 10 % of the total zooplankton abundance, respectively.

In the Spring Inter-monsoon season, fish eggs, decapod larvae, and females of the copepod *Centropages tenuiremis* dominated the total abundance of zooplankton, and contributed 8 % to total numbers. In the South-west Monsoon, the zooplankton community was dominated by c4 and c5 developmental stages of the copepod *Calanoides carinatus s.f.*, followed by *Centropages tenuiremis* and *Oikopleuridae. C. carinatus s.f.* comprising 51 % of the total zooplankton abundance. The other relatively abundant copepod species was *Rhincalanus nasutus*—with a maximal total prosome length of about 3.5 mm (Table 4).

The dominant group exhibited its presence all across the shelf, although the abundance of c4 and c5 copepodite stages of *Calanoides carinatus s.f.*, varied markedly, from 19 to ~6800 ind. m^{-3} (Fig. 7). In comparison to the North-east Monsoon and Spring Inter-monsoon seasons, the South-west Monsoon was notorious for the dominance of the late copepodite stages and adults of *Calanoides carinatus s.f., Centropages tenuiremis,* and *Rhincalanus nasutus* in samples.

In order to analyze seasonal changes in the size structure of the entire zooplankton community, organisms were distributed across 16 size classes with the resolution of 0.4 mm. The medians of these classes were used to approximate size distributions (Fig. 8). No prominent changes were observed over seasons. The group with the mean size of 1.8 mm was the dominant one throughout all three seasons. Overall, the community of the North-east Monsoon was characterized by a broad spectrum, whereas the spectrum of the South-west Monsoon community was narrow. The contribution of the dominant group increased, from 28 % during the North-east Monsoon to 59 % during the South-west Monsoon. The twofold increase was driven by the appearance of *Calanoides carinatus s.f.* No statistical differences were observed among seasons change in the organisms' mean size. Intra-seasonal variation in the mean size was large, which is reflected in the range of standard deviation (Table 2).

Discussion

Seasonal surveys of the zooplankton community across the Omani shelf have enabled us to characterize it as highly productive, with the mean mesozooplankton biomass varying from 543 to 723 mg m^{-3} throughout the seasonal cycle. These values exceeded the average biomass of the open Arabian Sea regions by three times, which was in a range of 100–200 mg m^{-3} according to the map of the International Indian Ocean Expedition (Bogorov et al. 1968; Prasad 1968).

Processing of samples has allowed us to identify three general spatial–temporal patterns: (1) the dominance of copepods in the total zooplankton abundance over the shelf waters, (2) the absence of seasonal changes in the level of total zooplankton biomass, and (3) the absence of seasonal changes in the size structure of the zooplankton community.

A leading contribution of copepods to the total abundance of zooplankton has been reported for various regions of the Arabian Sea (Padmavati et al. 1998; Smith and Madhupratap 2005) including Omani coastal waters (Piontkovski et al. 2013). This taxonomic group dominates the zooplankton abundance regardless of seasons.

As far as the seasonality of mesozooplankton biomass is concerned, published data are controversial. The "paradox" of zooplankton biomass reported for the western and eastern Arabian Sea in the early 1990's (Baars 1999; Madhupratap et al. 1992, 1996) was challenged by subsequent investigators stressing the presence of seasonality (Jyothibabu et al. 2010).

On the level of abundance, lack of seasonal changes of copepod abundance was reported for the central and eastern Arabian Sea (Madhupratap et al. 1996). Nonetheless, it was denoted that the North-east Monsoon season "is always characterized by an increase in the abundance of the cyclopoid copepods, particularly

Table 3 List of the copepod species found in samples collected during the North-east Monsoon (NEM), Spring Inter-monsoon (SIM), and the South-west Monsoon (SWM)

NEM	SIM	SWM
Acartia plumosa	*Acartia amboinensis*	*Acartia amboinensis*
Acrocalanus gracilis	*Acartia plumosa*	*Acartia plumosa*
Acrocalanus longicornis	*Acrocalanus longicornis*	*Acrocalanus longicornis*
Calanopia elliptica	*Calocalanus pavo*	*Bestiolina arabica*
Calanopia parathompsoni	*Candacia bradyi*	*Calanoides carinatus s.f.*
Candacia catula	*Candacia curta*	*Calocalanus plumulosus*
Candacia curta	*Canthocalanus pauper*	*Centropages orsini*
Candacia discaudata	*Centropages furcatus*	*Centropages tenuiremis*
Candacia truncata	*Centropages tenuiremis*	*Copilia mirabilis*
Canthocalanus pauper	*Copilia mirabilis*	*Corycaeus pacificus*
Centropages orsini	*Copilia quadrata*	*Eucalanus elongatus*
Centropages tenuiremis	*Corycaeus crassiusculus*	*Euterpina acutifrons*
Clausocalanus furcatus	*Corycaeus pacificus*	*Farranula gibbula*
Copilia mirabilis	*Corycaeus speciosus*	*Haloptilus mucronatus*
Corycaeus crassiusculus	*Cosmocalanus darwinii*	*Heterorhabdus papilliger*
Corycaeus pacificus	*Eucalanus elongatus*	*Mesocalanus tenuicornis*
Cosmocalanus darwinii	*Euchaeta indica*	*Nannocalanus minor*
Euchaeta indica	*Euchaeta rimana*	*Oithona brevicornis*
Euchaeta rimana	*Labidocera acuta*	*Oithona plumifera*
Labidocera acuta	*Lucicutia gaussae*	*Oithona setigera*
Nannocalanus minor	*Nannocalanus minor*	*Oncaea mediterranea*
Oithona plumifera	*Oncaea venusta*	*Oncaea venella*
Oncaea venusta	*Paracalanus aculeatus*	*Paracalanus aculeatus*
Paracalanus aculeatus	*Paracalanus tropicus*	*Paracalanus aculeatus minor*
Pareucalanus attenuatus s. l.	*Pontellina plumata*	*Paracalanus indicus*
Pontellina plumata	*Rhincalanus cf. nasutus*	*Pleuromamma indica*
Pontellopsis regalis	*Sapphirina metallina*	*Pseudodiaptomus serricaudatus*
Rhincalanus rostrifrons	*Sapphirina nigromaculata*	*Rhincalanus cf. nasutus*
Sapphirina nigromaculata	*Sapphirina opalina*	*Scolecitrichopsis ctenopus*
Sapphirina opalina	*Sapphirina scarlata*	*Subeucalanus crassus*
Sapphirina scarlata	*Subeucalanus crassus*	*Subeucalanus mucronatus*
Sapphirina stellata	*Subeucalanus mucronatus*	*Subeucalanus pileatus*
Scolecithrix danae	*Subeucalanus pileatus*	*Subeucalanus subtenuis*
Subeucalanus crassus	*Subeucalanus subcrassus*	*Temora turbinata*
Subeucalanus pileatus	*Subeucalanus subtenuis*	
Subeucalanus subcrassus	*Temora discaudata*	
Subeucalanus subtenuis	*Temora turbinata*	
Temora discaudata	*Undinula vulgaris*	
Temora turbinata		
Undinula vulgaris		

Oithona species, regardless of location in the Arabian Sea" (Smith and Madhupratap 2005). We have not observed this phenomenon, presumably because of the coarse mesh size used; the *Oithona* species were extremely rare in winter samples, in which females of *Oithona plumifera* were observed.

Thangaraja et al. (2011), who analyzed the total zooplankton biomass collected by a 200 µm net across the Omani shelf, have reported a 1.8-fold increase during the North-east Monsoon in comparison to the Fall Inter-monsoon period.

Table 4 List of the most abundant copepod species on the Omani shelf

	Ontogenetic stage	Body length (mm)
NEM		
Cosmocalanus darwinii	f	2.3–2.4
Nannocalanus minor	f	1.8–2.0
Subeucalanus subtenuis	f	3.3–3.6
Euchaeta indica	f	2.4–2.7
Euchaeta rimana	f	3.5
Euchaeta spp.	c5	1.0–3.0
Nannocalanus minor	f	1.8
Acrocalanus longicornis	f	1.2–1.4
Subeucalanus crassus	c5	2.5–2.7
Temora discaudata	f	1.8–2.0
SIM		
Centropages tenuiremis	f	1.6–2.0
Centropages tenuiremis	m	1.5–1.7
Subeucalanus subtenuis	f	3.0–3.2
Subeucalanus subtenuis	c4	2.0–2.2
Subeucalanus pileatus	f	2.0–2.3
Subeucalanus pileatus	c5	1.8–2.0
Subeucalanus pileatus	c4	1.6–1.7
Subeucalanus crassus	c2	1.4–1.5
Subeucalanus crassus	c3	1.9–2.0
Acartia amboinensis	f	1.5–1.6
Subeucalanus crassus	f	3.0–3.3
Subeucalanus crassus	c2	1.5–1.7
Subeucalanus pileatus	c3	1.4–1.5
Temora discaudata	c2	1.2–1.3
SWM		
Calanoides carinatus s.f.	f	2.3–2.7
Calanoides carinatus s.f.	c4	1.7–2.0
Calanoides carinatus s.f.	c5	2.3–2.5
Centropages tenuiremis	f	1.7–1.9
Centropages tenuiremis	m	1.5–1.7
Rhincalanus cf. nasutus	c5	3.5

NEM the North-east Monsoon, *SIM* Spring inter-monsoon, *SWM* the South-west Monsoon, *f* females, *m* males, *c2–c5* ontogenetic stages (copepodites)

In 1994–1996, the absolute maximum in zooplankton biomass was observed during the South-west Monsoon, in the area of coastal upwelling (Smith et al. 1998). The most abundant copepod species in the upwelling area in the upper 25 m layer were the small-bodied copepods *Paracalanus aculeatus*, *Paracalanus denudatus*, and *Parvocalanus dubia*. Four species (*P. denudatus, P. dubia, P. aculeatus* and *Acartia longicornis*) accounted for 36 % of the total abundance. With two other species added (*Subeucalanus crassus* and *Calanoides carinatus s.f.*), the group accounted for 37 % of total abundance (Smith and Madhupratap 2005). In our case, the group accounting for a major part of total abundance was notoriously different (Table 3). However, the mesh size used in our studies was larger (500 vs 150 µm), which shifted size characteristics and species composition within the community.

During the 1994–1995 cruises, high-frequency acoustical measurements carried out off the Omani shelf pointed out the lowest zooplankton biovolumes during the summer South-West Monsoon, intermediated during fall inter-monsoon, and the highest during the winter North-east Monsoon (Pieper et al. 2001).

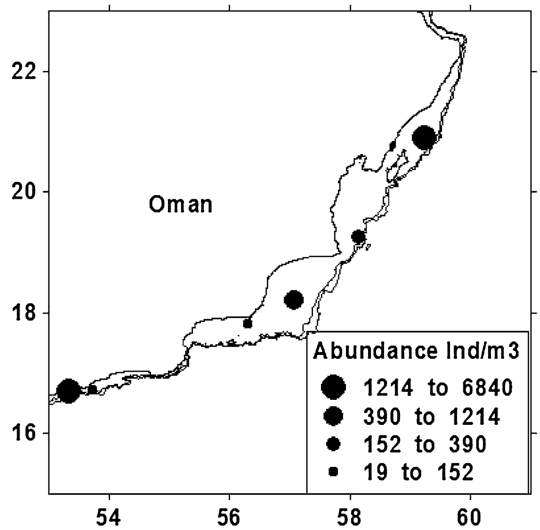

Fig. 7 Spatial distribution of the abundance of *Calanoides carinatus s.f.* during the South-west Monsoon

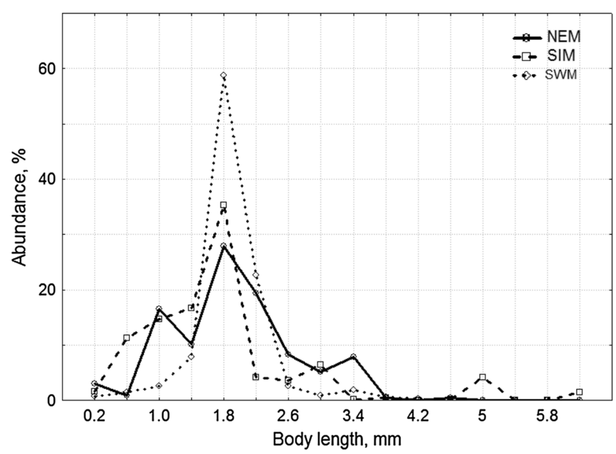

Fig. 8 Size structure of zooplankton community over seasons. The abundance of size groups is shown by % of the total zooplankton abundance. *NEM* North-east Monsoon, *SIM* spring inter-monsoon, and *SWM* South-west Monsoon

The UK "Arabesque" expedition sampled mesozooplankton during and after the 1994 South-west Monsoon (Stelfox et al. 1999), but almost all their "zooplankton stations" (1 out of 8) were outside the shelf area, in which the zooplankton biomass showed a decline from the North-east Monsoon to the fall inter-monsoon period.

One of the factors contributing to seasonal changes and heterogeneous distribution of zooplankton biomass should be a trophic pressure imposed by myctophids. These fishes actively ingest zooplankton, in particular at night when myctophids migrate to upper layers from the deep. Fish trawls and echo-soundings carried out during five seasonal cruises have implied dense layers of myctophids, 20–40 m thick, at about a 200–450 m depth, extending offshore from the shelf during the day and ascending to the upper layer at night, along the shelf edge. The myctophid biomass varied gradually over seasons and was composed mainly of *Benthosema pterotum*. For instance in the Ras al Hadd region, total myctophid catches accounted for 155 t km^{-2} during the Spring Inter-monsoon, with a subsequent increase of up to 1.2 M t km^{-2} by the end of the South-west Monsoon (Devine and Macaulay 2009). Interestingly, these huge changes did not induce an immediate reduction of zooplankton biomass in summer, although the mean value was minimal during the subsequent Fall Inter-monsoon season (Table 2).

On the species level, the most striking feature about seasonal changes in the zooplankton community was the massive appearance of *Calanoides carinatus s.f.* in the upper mixed layer, to which the population migrated in September, ascending from the depth of about 400 m. This species ingests predominantly diatoms in upwelling areas of the western Indian Ocean (Smith 2001). Interestingly, the appearance of *Calanoides carinatus s.f.* does not induce prominent seasonal changes in the total zooplankton biomass (Table 2).

We do not have the phytoplankton samples collected at the same place and time as the zooplankton sampling, so remotely sensed chlorophyll-*a* concentration was the only source used to estimate the magnitude of phytoplankton biomass change over seasons. The chlorophyll maps implied a fairly high biomass in all seasons. A peculiarity of 2008, which was unusual in many aspects including the distortion of a common well-developed seasonal cycle of chlorophyll-*a*, was the appearance of a massive harmful algal bloom of *Cochlodinium polykrikoides* during the Fall inter-monsoon, which lasted until spring-2009 (Richlen et al. 2010; Al-Azri et al. 2014).

In terms of spatial distribution, our data point out that the population of *Calanoides carinatus s.f.* occupies the whole shelf area—from Salalah to Ras al Hadd, although the spatial pattern has exhibited a prominent heterogeneity of biomass distribution—the feature reported by the previous survey carried out in August-1995, when the threefold variance of the dry weight of the biomass was reported along the southern part of the Omani shelf (Hitchcock et al. 2002).

Once the population of *Calanoides carinatus s.f.* occupies shelf waters, the question is how it gets there (over the continental slope, to depths less than 200 m), if the core of the population is located seaward, in oceanic waters, at the depth of 400 m? At least two aspects of the on-shelf advection could be proposed; the first one is transport by the East Arabian Current from the south. The second one is transport by cyclonic and anticyclonic eddies induced by Rossby waves propagating westward toward the Omani coast (Chelton et al. 2007). In the western Arabian Sea, spatial heterogeneity of zooplankton distribution could be largely explained as being caused by eddies and the mesoscale frontal zones between them (Hitchcock et al. 2002; Piontkovski and Melnik 2006).

On the scale of the Arabian Sea, a statistical relationship between the available potential energy of an eddy field and spatial heterogeneity of zooplankton biomass was reported (Piontkovski et al. 1995). The Omani shelf is a small part, but there, mesoscale eddies are common elements of a regional circulation (Flagg and Kim 1998; Piontkovski and Al-Jufaili 2013; Smith et al. 1991). Eddies entering Omani shelf waters from the central Arabian Sea have been the subject of a specialized expedition aimed at studying the role of eddies in the structure and functioning of the pelagic ecosystem of the western Arabian Sea (Piontkovski and Banse 2006). Zooplankton were collected in the upper 100 m layer at 109 stations in February–April 1990. Biomass maxima usually occurred at the edges of eddies and in frontal zones. The difference between biomass in these maxima was in a region of two- to fourfold.

The variance-to-mean ratio pointed out that zooplankton biomass possessed the most heterogeneous distribution throughout the shelf during the South-west Monsoon period (Table 2). This is the season when eddies are most common over a seasonal cycle of their occurrence in the western Arabian Sea (Piontkovski and Al-Jufaili 2013).

Conclusion

In 2007–2008, the Omani shelf was populated by a highly productive epipelagic plankton community. The chlorophyll-*a* concentration was high throughout a seasonal cycle and so was the mesozooplankton biomass, values of which nearly threefold exceeded the average biomass of the open Arabian Sea regions. Spatial distribution of zooplankton biomass over shelf waters was highly heterogeneous. The biomass and size structure of the zooplankton community did not exhibit prominent seasonal changes. However, spatial distribution of the zooplankton biomass throughout the shelf was most heterogeneous during the South-west monsoon season.

On the species level, the most striking feature in seasonal changes of the zooplankton community was the massive appearance of the copepod *Calanoides carinatus s.f.* in shelf waters, to which the population migrated in September. The population, ascending to upper layers during its ontogenetic migration, has occupied the entire Omani shelf area from Salalah to Ras al Hadd.

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References

Al-Azri AR, Piontkovski SA, Al-Hashmi KA, Goes JI, Gomes HR, Glibert P (2014) Mesoscale and nutrient conditions associated with the massive 2008 *Cochlodinium polykrikoides* bloom in the Sea of Oman/Arabian Gulf. Estuar Coast 37:325–338

Anonymous (1975) Reports on cruises Nos. 1 and 2 of R.V. "Dr. Fridtjof Nansen". Indian Ocean Fishery and Development Programme. Pelagic Fish Assessment Survey, North Arabian Sea. FAO, Rome

Baars MA (1999) On the paradox of high mesozooplankton biomass, throughout the year in the western Arabian Sea: re-analysis of IIOE data and comparison with newer data. Ind J Mar Sci 28:125–137

Bogorov VG, Vinogradov ME, Voronina NM, Kanaeva IP, Syetova IA (1968) The distribution of zooplankton biomass in the upper layer of the world's ocean. Rep USSR Acad Sci (Dokladyi Academii Nayk SSSR) 182:232–245 **(in Russian)**

Böhm E, Morrison J, Manghnani V, Kim HS, Flagg C (1999) The Ras al Hadd Jet: remotely sensed and acoustic Doppler current profiler observations in 1994-1995. Deep-Sea Res II 46:1531–1549

Chelton DB, Schlax MG, Samelson RM, Szoeke RA (2007) Global observations of large oceanic eddies. Geophys Res Let 34:L15606. doi:10.1029/207GL030812

Devine J, Macaulay G (2009) Fish resources assessment survey of the Arabian Sea Coast of Oman: Habitat. Technical Report 4. Mesopelagic Fisheriy Resources of the Arabian Sea Coast of Oman. Bruce Shallard and Associates, Muscat

Flagg CN, Kim HS (1998) Upper ocean currents in the northern Arabian Sea from shipboard ADCP measurements collected during the 1994-1996 JGOFS and ONR programs. Deep-Sea Res II 45:1917–1959

Goswami SC, Shrivastava Y (1996) Zooplankton standing stock, community structure and diversity in the northern Arabian Sea. In: Proceedings of the Second Workshop-Scientific Results. FORV Sagar Sampada, pp. 127–137

Hitchcock GL, Lane P, Smith S, Luo J, Ortner PB (2002) Zooplankton spatial distributions in coastal waters of the northern Arabian Sea, August 1995. Deep Sea Res II 49:2403–2423

Jacobs CL (2003) RRS Charles Darwin Cruise 143. Sheherezade II: Geological and biological surveys of the Arabian Sea and the continental slope of Oman. Southhampton Oceanography Centre Cruise Report, No. 42

Jyothibabu R, Madhu NV, Habeebrehman H, Jayalakshmy KV, Nair KKC, Achuthankutty CT (2010) Re-evaluation of "paradox" in the eastern Arabian Sea based on ship and satellite observations. J Mar Syst 81:235–251

Kistler RE, Kalnay W, Collins S, Saha G, White J, Woollen M, Chelliah W, Ebisuzaki M, Kanamitsu V, Kousky H, van den Dool RJ, Fiorino M (2001) The NCEP-NCAR 50-year reanalysis: monthly means CD-ROM and documentation. Bull Am Met Soc 82:247–268

Lane P, Smith S, Zavagoza J, Prusova I, Roman M (1998) U.S. JGOFS Technical Report: Copepod taxonomy, abundance and biomass in the upper 300 meters of the Arabian Sea during the Southwest Monsoon of 1995. RSMAS Technical Report 98-007. University of Miami, Miami, p 409

Luo J, Ortner PB, Forcucci D, Cummings SR (2000) Diel vertical migration of zooplankton and mesopelagic fish in the Arabian Sea. Deep Sea Res II 47:1451–1473

Madhupratap M, Haridas P, Ramaiah N, Achuthankutty CT (1992) Zooplankton of southwest coast of India: abundance, composition, temporal and spatial variability in 1987. In: Desai BN (ed) Oceanography of Indian Ocean. Oxford & IBH, New Delhi, pp 99–112

Madhupratap M, Gopalakrishnan TC, Haridas P, Nair KKC, Aravindakshan PN, Padmavati G, Paul S (1996) Lack of seasonal and geographic variation in mesozooplankton biomass in the Arabian Sea and its structure in the mixed layer. Cur Sci 71:863–868

McKoy J, Bagley N, Gauthier S, Devine J (2009) Fish Resources of the Arabian Sea coast of Oman: Project summary. In Technical Report 1. Bruce Shallard and Associates, Muscat

Okubo A (1980) Diffusion and ecological problems: mathematical models. Biomathematics, vol 10. Springer, New York

Padmavati G, Harids P, Nair KK, Gopalakrishnan TC, Shiney P, Madhupratap M (1998) Vertical distribution of mesozooplankton in the central and eastern Arabian Sea during the winter monsoon. J Plankton Res 20:343–354

Pieper RE, McGehee DE, Greenlaw CF, Holliday DV (2001) Acoustically measured seasonal patterns of zooplankton in the Arabian Sea. Deep-Sea Res II 48:1325–1343

Piontkovski SA, Al-Jufaili S (2013) Coastal upwellings and mesoscale eddies of the western Arabian Sea: some biological implications. Int J Ocean Oceanogr 7:93–115

Piontkovski SA, Banse K (2006) Overview of results. In: Banse K, Piontkovski SA (eds) The mesoscale structure of the epipelagic ecosystem of the open northern Arabian Sea. Universities Press, Hyderabad

Piontkovski SA, Melnik TA (2006) Mesozooplankton of the north-west Arabian Sea. In: Banse K, Piontkovski SA (eds) The mesoscale structure of the epipelagic ecosystem of the open northern Arabian Sea. Universities Press, Hyderabad

Piontkovski SA, Williams R, Peterson W, Kosnirev VK (1995) Relationship between oceanic zooplankton and energy of eddy fields. Mar Ecol Progr Ser 128:35–41

Piontkovski SA, Al-Maawali A, Al-Mantheri W, Al-Hashmi K, Popova E (2013) Zooplankton of Oman coastal waters. Agr Mar Sci 18:37–50

Prasad RR (1968) Maps on total zooplankton biomass in the Arabian Sea and the Bay of Bengal. International Indian Ocean Expedition Plankton Atlas, vol. 1, Fasc. 1. Indian Biological Centre, National Institute of Oceanography, CSIR, New Delhi

Richlen ML, Morton SL, Jamali EA, Rajan A, Anderson DM (2010) The catastrophic 2008-2009 red tide in the Arabian Gulf region, with observations on the identification and phylogeny of the fish-killing dinoflagellate *Cochlodinium polykrikoides*. Harmful Algae 9:163–172

Roman M, Smith S, Wishner K, Zhang X, Gowing M (2000) Mesozooplankton production and grazing in the Arabian Sea. Deep-Sea Res II 47:1423–1450

Smith S (2001) Understanding of the Arabian Sea: reflections on the 1994-1996 Arabian Sea expedition. Deep-Sea Res II 48:1385–1402

Smith S (2005) The Arabian Sea of the 1990s: new biogeochemical understanding. Progr Oceanogr 65:113–115

Smith SL, Madhupratap M (2005) Mesozooplankton of the Arabian Sea: patterns influenced by seasons, upwelling, and oxygen concentrations. Progr Oceanogr 65:214–239

Smith SL, Banse K, Cochran JK, Codispoti LA, Ducklow HW, Luther ME, Olson DB, Peterson WT, Prell WL, Surgi N, Swallow JC, Wishner K (1991) U.S.JGOFS: Arabian Sea Process Study. U.S. JGOFS Planning Report No. 13. Woods Hole Oceanographic Institution, Woods Hole

Smith S, Roman M, Prusova I, Wishner K, Gowing M, Codispoti L, Barber R, Marra J, Flagg C (1998) Seasonal response of zooplankton to monsoonal reversals in the Arabian Sea. Deep-Sea Res II 45:2369–2404

Stelfox CE, Burkill PH, Edwards ES, Harris RP, Sleigh MA (1999) The structure of zooplankton communities, in the 2 to 200 μm size range, in the Arabian Sea during and after the SW monsoon, 1994. Deep-Sea Res II 46:815–842

Thangaraja M, Al-Aisry A, Al-Kharusi L (2011) Ecology, abundance and spatial distribution of zooplankton biomass in the waters of Sultanate of Oman. South Ind Coast Mar Bull 3:5–13