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RESEARCH PAPER

Seasonal variations of surface mesozooplankton community structure in the Sea of Oman and the Arabian Sea

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التغيرات الموسمية في بنية مجتمع العوالق الحيوانية السطحية في بحر عمان وبحر العرب

سعود بن سالم البوسعيدي١، ميشيل رينيه كلايربودت٢

ABSTRACT. The different characteristics and atmospheric forces over the Sea of Oman and the Arabian Sea are assumed to influence zooplankton seasonality and community structure. This work aimed to characterize the abundances and seasonality of coastal and surface mesozooplankton communities in the Sea of Oman (Muscat) and the Arabian Sea (Salalah), and the effects of environmental factors on their distribution. Zooplankton samples two contrasting coastal regions; 22 in the Sea of Oman, and 20 in the Arabian Sea, were collected during 2013-2014 from the surface and analyzed. Total zooplankton abundance was divided by the number of samples to obtain the monthly average abundance per meter cube (ind·m^{-3}) of sea water. A total of 91 species were observed from all 42 samples of which 58 were copepods, among which 47 were calanoid copepods. Species composition varied significantly between the two locations. The similarity between the two communities was highest (samples were closest to each other) during the winter, and showed the largest differences in composition in the summer. The seasonal changes in community structures were most significant for copepods and calanoid copepods (p= 0.0002 and p= 0.0003 respectively) and less significant for non-copepods (p= 0.0057). Only few species (17 in the Sea of Oman and 20 in the Arabian Sea) represented more than 90% of the total zooplankton abundance. There was a distinct pattern of seasonal variation in the abundance of zooplankton in the Arabian Sea, especially copepods and meroplankton, but there was no such pattern in the Sea of Oman. Some successful species such as *Temora turbinata and Penilia avirostris* in the Sea of Oman, and *Oithona spp*. in the Arabian Sea seem able to exploit a wide range of prey from phytoplankton to small ciliates and thus feed through the microbial loop.

KEYWORDS: Mesozooplankton, Copepod, Abundance, Arabian Sea, Sea of Oman, Northeast monsoon, Southwest monsoon

الملخص: من المفترض أن تؤثر الخصائص والرياح الموسمية المختلفة على بحر عمان وبحر العرب على موسمية وبنية مجتمع العوالق الحيوانية. يهدف هذا العمل إلى وصف وفرة وموسمية مجتمعات العوالق الحيوانية الساحلية والسطحية في بحر عمان (مسقط) وبحر العرب (صلالة)، وتأثير العوامل البيئية على توزيعها. جُمعت وحُللت عينات من العوالق الحيوانية السطحية لمنطقتين ساحليتين ذواتي خصائص متناقضة؛ 22 من بحر عمان و20 من بحر العرب، خلال 2014-2013. قُسِّم إجمالي وفرة العوالق الحيوانية على عدد العينات للحصول على متوسط الوفرة الشهري لكل متر مكعب (عدد/م٣) من مياه البحر. صُنِّف ما مجموعه 91 نوعًا من العوالق الحيوانية من جميع العينات البالغ عددها 42 عينة، منها 58 نوعًا من مجدافيات الأرجل، من بينها 47 نوعًا تتبع كالانويد مجدافيات الأرجل. اختلفت تشكيلة الأنواع بشكل كبير بين الموقعين. كان التشابه بين المجتمعين أعلى في فصل الشتاء (كانت العينات الأقرب لبعضها البعض)، وظهر أكبر الاختلافات في تشكيلة الأنواع خلال الصيف. كانت التغيرات الموسمية في بنية مجتمع العوالق مختلفة جدا (أي ذات فروق معنوية كبيرة) بالنسبة لجميع مجدافيات الأرجل (p=0.0002) وكذلك مجموعة (calanoid copepods) كالانويد مجدافيات الأرجل (p=0.0003) وأقل أهمية بالنسبة لغير مجدافيات الأرجل (p=0.0057). عدد قليل من الأنواع (17 في بحر عمان و20 في بحر العرب) مثلت أكثر من 90٪ من إجمالي وفرة العوالق الحيوانية. كان هناك نمط مميز للتباين الموسمي في وفرة العوالق الحيوانية في بحر العرب، وخاصة مجدافيات الأرجل والعوالق الحيوانية المؤقتة (Meroplankton)، ولكن لم يكن هناك مثل هذا النمط في بحر عمان. بعض الأنواع الناجحة مثل *Temora turbinata* و *Penilia avirostris* في بحر عمان و *Oithona spp*. في بحر العرب يبدو أنها قادرة على استغلال مجموعة واسعة من الفرائس من العوالق النباتية إلى عوالق حيوانية صغيرة كالهدبيات وبالتالي تتغذى من خلال الحلقة الميكروبية.

الكلمات المفتاحية: العوالق الحيوانية، مجدافيات الأرجل، وفرة، بحر العرب، بحر عمان، الرياح الموسمية الشمالية الشرقية، الرياح الموسمية الجنوبية الغربية.

Introduction

Oman, in addition to the Arabian/Persian Gulf, is open to the Sea of Oman (formerly known as Gulf of Oman) and the Arabian Sea. Both the Sea of Oman and the Arabia sea received considerable attention in terms of oceanographic studies in general, and zooplankton in particular. Despite many scientific expeditions that explored the open water and oceanic northeastern Arabian Sea, the community structure of shallow water coastal mesozooplankton along the Omani shelf in a spatial-temporal context was not investigated. Most of these research cruises focused on the Arabian Sea and only rapidly passed through the Sea of Oman. This area should probably be considered as data deficient in terms of zooplankton. In addition, nearly all of these scientific expeditions targeted a particular season (i.e., pre- or post-monsoon) and rarely covered a whole calendar year.

Due to its characteristic location, Omani seas (Sea of Oman and Arabian Sea) are affected by monsoonal

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wind patterns. Oceanographic processes driven by the sea-land differential temperature over the Arabian Sea and the Indian Subcontinent (the southwest monsoon (SWM) and winter (the northeastern monsoon (NEM) are reflected in the characteristics of the Sea of Oman and the Arabian Sea.

The Sea of Oman is exposed to the northeasterly winds that peak in the winter (December to February) creating the northeastern monsoon (NEM), which is the prevailing atmospheric force along the Sea of Oman (Piontkovski et al., 2013). The sea surface temperature (SST) varies throughout the year. The highest SST is usually during June-July and cools down to the minimum in February during NEM. The dry and cool northeast winds over the Sea of Oman overturn the water column vertically (i.e., convective mixing) that pumps nutrients upward which enhances productivity (Madhupratap et al., 1996b) and supports zooplankton growth.

The Arabian Sea is subjected to annual reversal wind systems, the northeast and southwest monsoons. The energetic southwest monsoon (SWM) extends from June through September, during which, a coastal upwelling develops along the southern coasts of Oman (Morrison et al., 1998; Kidwai and Amjad, 2000; Uye et al., 2000; Sarma, 2002). This seasonal upwelling brings nutrient-rich water from the depth that enhances the phytoplankton growth and, eventually, the fishery as well (Qasim, 1982; Madhupratap et al., 1996b; Kazmi, 2004).

The southwest monsoon (SWM) has more impact on the ecosystem in general and zooplankton in particular. Zooplankton biomass in the Arabian Sea is higher during (SWM) and more pronounced inshore than offshore, further away from direct influence of the upwelling (Smith et al., 1998). Several copepod species such as *Temora turbinata, Centropages tenuiremis*, and a few genera belonging to Family Paracalanidae were linked to this upwelling areas (Madhupratap et al., 1990) in the Arabian sea.

Among the unique copepods, *Calanoides natalis*, which was identified previously as *Calanoides cf carinatus* (Smith et al., 2020). A recent genetic study (Bradford-Grieve et al., 2017) concluded that throughout its geographic range this species remains near the coasts, from the Bay of Biscay in the Atlantic all the way around Africa then northwards towards the Arabian Sea. This species is considered a bio-indicator of upwelling areas in Oman as well (Smith, 1982).

The contrasting characteristics of these two water masses are assumed to influence both zooplankton seasonality and community structure. This study aimed to

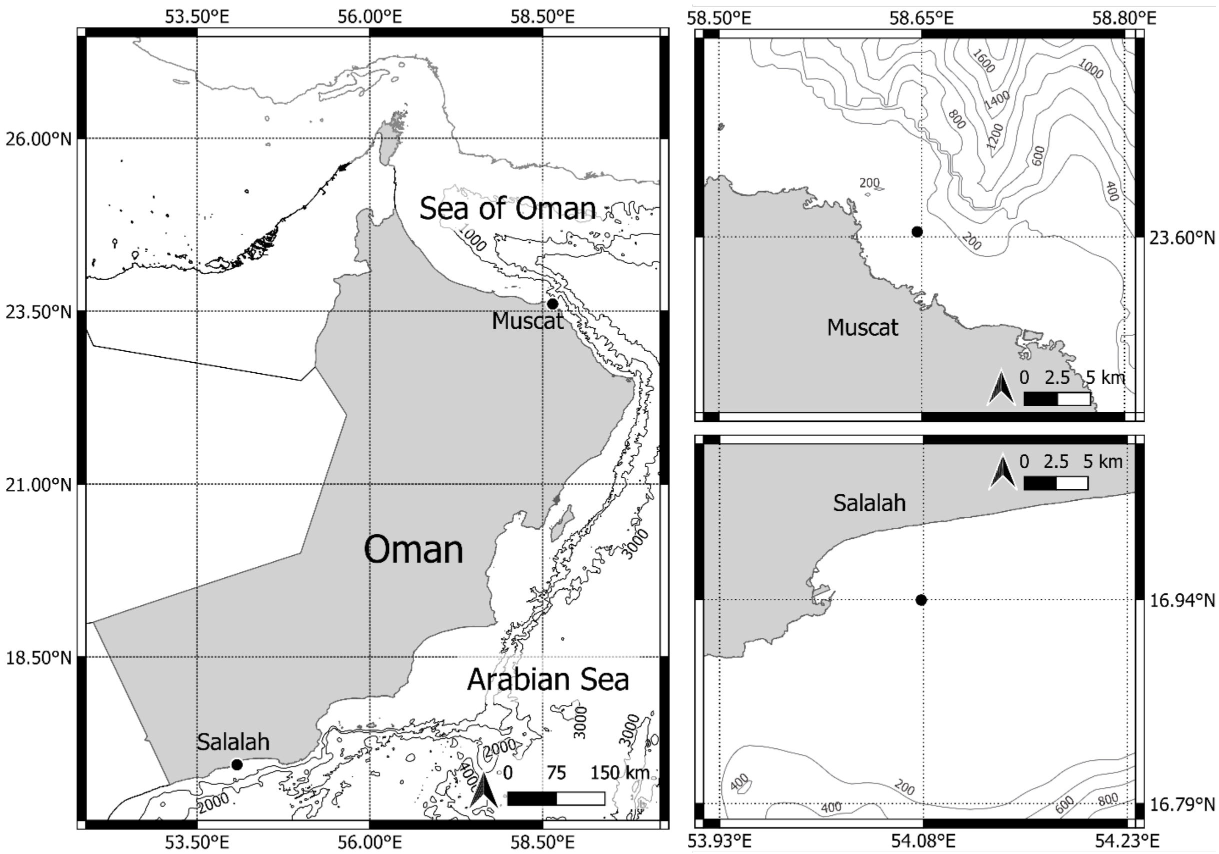

Figure 1. Map of Oman and the research locations (black dots) in the Sea of Oman (Muscat) and the Arabian Sea (Salalah).

characterize the abundances and seasonality of coastal and surface zooplankton communities (copepods and non-copepods) in the Sea of Oman (Muscat) and the Arabian Sea (Salalah), and the effects of environmental factors on their distribution.

Material and Methods

Samples of zooplankton were collected from two regions of the northern Indian Ocean contrasted by their oceanography; Muscat in the Sea of Oman, and Salalah in the Arabian Sea (Figure 1). These two stations were chosen due to the seasonal biological and physico-chemical changes that occur in these water masses as a result of the reversal of southwest monsoon (SWM) and northeast monsoon (NEM). The samples were collected monthly for two years from the beginning of 2013 until the end of 2014. A plankton net of 200 μm mesh size and 60 cm ring diameter was used to collect samples. The net was towed horizontally just below the surface behind a small boat at a constant speed of 2 knots for five minutes. The boat cruised in a circular motion and the angle between the boat and the towed net is about 45 degrees. Each sample was transferred to 500 ml plastic bottles and preserved with 1.5-2% formaldehyde (40-50 ml Formalin 40% solution/ L). Flowmeter (Hydro-Bios) readings before and after sampling were taken, which were then used to calculate the distance towed and the volume of filtered seawater.

All the samples of 500 ml were divided into aliquots of 250 ml using a Folsom plankton splitter. Then, using a Hensen-Stempel Pipette or a Hensen plunger, a subsample volume of 5 ml was drawn to be examined and counted under a stereomicroscope using a Bogorov chamber. The zooplankton species were identified to the lowest taxonomic level possible using the available guides (Al-Yamani et al. 2011a, 2011b; Al-Busaidi and Al-Aisri 2012; Prusova et al. 2012). The total copepod abundances reported here included adult and copepodite stages CI-CVI. For several taxa, difficult to identify to the species or even genus level, individuals were assigned to larger taxonomic groups (Eucalanidae, Paracalanidae, *Euchaeta sp*., *Oithona sp., Copilia sp., Macrosetella sp*., etc.). In addition, for some taxa, the immature specimens were also grouped into a single category such as (Calanoida, *Pseudodiaptomus sp., Acartia sp., Temora sp*., etc.). For non-copepods, the levels of identification varied from species (*Penilia avirostris*) to genus (e.g. *Lucifer, Evadne, Creseis,* etc.), families (Porcellanidae, Desmopteridae, etc.) up to Classes (Gastropoda, Stomatopoda, Ostracoda, etc.) or even Phyla (Echinodermata).

A total of 42 samples (22 from Muscat and 20 from Salalah) were analyzed. Using filtered volume, Zooplankton counts were transformed into population density (individual per cubic meter; ind m^{-3}) following (Thompson and Schweigert, 2007). The total copepod abundances included both adults and copepodite stages CI-CVI.

In addition to zooplankton samples, environmental variables, seawater temperature (°C), salinity (PSU), dissolved oxygen concentration (mg L^{-1}), pH, and chlorophyll-a level (mg L^{-1}), were measured at each station at the time of sampling using a Conductivity-Temperature-Depth (CTD) from Idronaut 316 plus™. Missing environmental data were compensated from satellite and Argo floats data. Missing sea surface temperature and chlorophyll-*a* concentration data were completed using Giovanni's monthly averaged data of 4 km resolution (MODIS-Aqua MODISA_L3m). Whereas Argo float's data were used to fill in the gaps of missing salinity data. Argo data were retrieved from ESSO Indian National Centre for Ocean Information Services (INCOIS), Government of India. The environmental parameters were linked to zooplankton data in order to find out which of the parameters has the greatest impact on zooplankton distribution and abundance throughout the seasons at both stations.

Statistical analysis

Statistical analysis tools, such as Principal Component Analysis (PCA) and non-metric MDS, were used to support and illustrate the results of the analysis. Several ecological indices, such as diversity (Shanon and Simpson indices), richness (Margalef and Menhinick indices), and evenness indices were also calculated and analyzed separately (Ismail and Zaidin, 2015). The statistical analyses of the ecological indices were calculated using PAST© software (ver. 3.25; (Hammer et al., 2001).

To evaluate changes in community structures between seasons and locations, a 2-way non-parametric Permutation Multiple Analysis of Variance (PERMANOVA) was applied to log-transformed abundance data (to reduce the effect of the few most abundant species) using the quantitative Bray-Curtis similarity (Legendre and Legendre, 2012). The same analysis was applied to four datasets: (i) all zooplankton, (ii) copepods, (iii) calanoid copepods, and (iv) non-copepods. Two factors were considered in the analysis: location (Sea of Oman vs Arabian Sea) and season (Spring, Summer, Fall and Winter) as well as their potential interaction. The differences in community structures were visualized using Non-Metric Multidimensional Scaling (NMDS).

Table 1. Monthly average abundance (ind m^{-3}) and percentage share (% of the copepod counts) of the three main orders of copepods in the Sea of Oman and the Arabian Sea. The number between brackets in copepod groups represents the total number of taxa.

Copepods (ind m^{-3})	Sea of Oman	Arabian Sea
Calanoida (47)	1102 (74.85%)	1820 (85.98%)
Cyclopoida (6)	363 (24.69%)	290 (13.69%)
Harpacticoida (5)	7 (0.46%)	7 (0.33%)

To quantify the importance of the different species as indicators of either the Sea of Oman or Arabian Sea Communities, the indicator value (IndVal) was calculated for each species based on the fidelity and specificity of this species in relation to the community (Dufrene and Legendre, 1997). The test of significance for this indicator was calculated using 1000 permutations using the IndVal function in the R-package labdsv (Roberts, 2019).

Results

Hydrographic parameters

Temperature: The highest sea surface temperatures in the Sea of Oman always coincide with the summer season during the southwest monsoon (SWM) where it can reach up to 32.3°C as was recorded in June 2014. Whereas, the lowest temperature was 22.8°C in February 2014 which was recorded during the northeast monsoon (NEM) in the winter. On the contrary, the highest temperature in the Arabian Sea was in May 2013 during the spring intermonsoon (SIM, 29.9°C) and the lowest was recorded during SWM in July 2014 (23.0°C) (Figure 2).

Chlorophyll-*a*: The peak values of chlorophyll-*a* in the Sea of Oman were recorded in February 2013 (7.25 mg L^{-1}) and March 2014 (11.56 mg L^{-1}) during NEM. Whereas in the Arabian Sea, the peak was in September for both years (12.50 and 4.71 mg L^{-1} respectively). The peak coincided with the end of SWM (Figure 2).

Salinity: The region being devoid of major rivers, the sea surface salinity values in the Sea of Oman vary little but were always higher than in the Arabian Sea during 2013-2014 (Figure 2). There was a seasonality in the surface salinity values in both areas but with opposite patterns. In the Sea of Oman, salinity tended to increase during the summer and decrease during the winter whereas in the Arabian Sea surface salinity tended to progressively decrease during the SW monsoon and increase during the winter (NE monsoon) (Figure 2).

Zooplankton community structure

During this survey, a total of 91 species were observed from all 42 samples of which 58 were copepods, among which 47 were calanoid copepods. From the 33 species of non-copepods, most species were crustaceans (cirripeds, cladocerans, decapods) but also appendicularians, chaetognaths, and doliolids.

Copepoda: The relative monthly abundances indicated that few species represented the vast majority of the mesozooplankton (Figure 3). In the Sea of Oman *Temora turbinata* were by far the most common organisms (588 ind m^{-3} on average) whereas in the Arabian Sea the most common taxa were *Pseudodiaptomus sp.* (466 ind m^{-3}). In the Sea of Oman, only 17 species represented 90% of the overall abundance, whereas in the Arabian Sea 20 species represented 90% of the overall abundance (Figure 3).

Some species appeared restricted to the Arabian Sea (e.g. *Calanoides natalis* and *Undinula vulgaris*) whereas others seem to be associated with the Sea of Oman (e.g. *Centropages typicus* and *Labidocera pavo*), suggesting differences in community structure between the two areas. Zooplankton taxa were first divided into copepods and non-copepods. Copepods were more abundant in both locations, representing 74.13% of the total zooplankton counts in the Sea of Oman and 76.48% in the Arabian Sea.

In the Subclass Copepoda, the order Calanoida was the most abundant and diverse group at both locations, whereas Harpacticoida was the least abundant and diverse (Table 1). In the Sea of Oman in particular, there were several months during which no harpacticoid copepods were observed (Figure 4).

The overall abundance of copepods varied irregularly and was characterized by peaks of abundances of a few species of calanoids. In the Sea of Oman, several peaks both in 2013 and 2014 were dominated by *Temora turbinata* (Figure 4). In November 2013, Paracalanidae (622 ind m^{-3}) and *Centropages orsinii* (600 ind m^{-3}) also contributed to about ⅓ of the total abundance each. In the Arabian Sea on the other hand, the main peak in Aug-Oct 2014 was due to a larger number of *Pseudodiaptomus* spp. that included *P. serricaudatus* (Aug 2014; 2079 ind m^{-3}), *P. arabicus*, and *Pseudodiaptomus* sp. (Sep-Oct 2014; (8744-1429 ind m^{-3} respectively). In addition, numerous copepodites of these species were also recorded at that time. The smaller peaks in the summer and fall of 2013 were dominated by *Acartia plumosa* (June; 1316 ind m^{-3} and September; 763 ind m^{-3}) and in 2014 by *Acartia amboinensis* (June; 780 ind m^{-3}). The fall peaks were in great part due to several species of Paracalanidae (Oct-Nov 2013; 515-671 ind m^{-3} respectively).

Calanoida copepods: A total of 37 calanoid species were identified in the Sea of Oman and 43 taxa in the Arabian Sea, of which 34 were common between the two locations. The monthly average abundance (± std. dev.) in the Sea of Oman was 1102 ± 1340 ind m^{-3}, whereas in the Arabian Sea it was 1820 ± 2306 ind m^{-3}.

Table 2. Monthly average abundance of cyclopoid copepods (ind m^{-3}). The number between parentheses represents the number of months for which each species was recorded out of 22 samples in the Sea of Oman and 20 in the Arabian Sea

	Cyclopoid copepods	Monthly average abundance (ind m^{-3})	
		Sea of Oman	Arabian Sea
1	*Oncaea sp.*	187.3 (22)	87.3 (19)
2	*Corycaeus sp.*	150.1 (22)	111.1 (20)
3	*Oithona sp.*	19.3 (17)	84.9 (20)
4	*Farannula sp.*	4.3 (11)	5.7 (13)
5	*Copilia sp.*	1.8 (11)	0.5 (5)
6	*Sapphirina sp.*	0.7 (6)	0.2 (3)

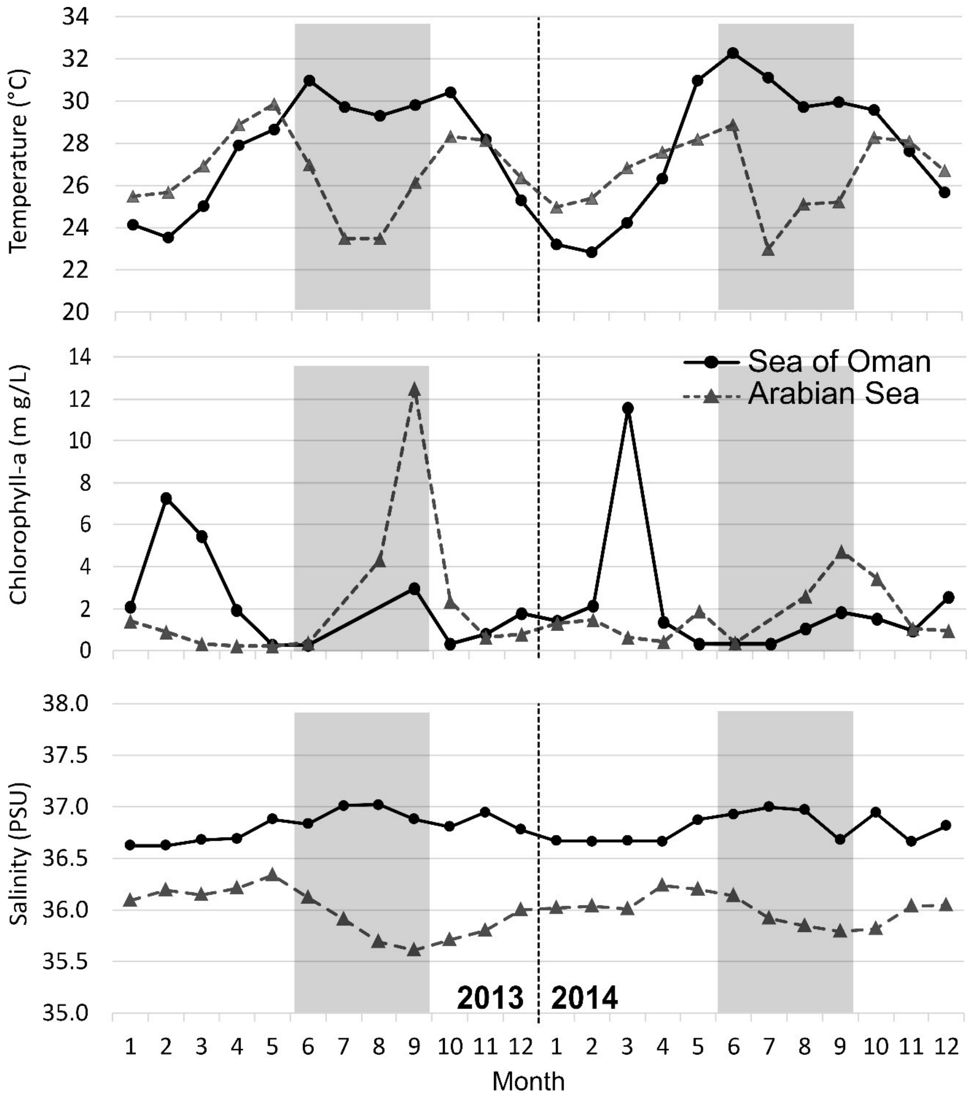

Figure 2. Seasonal variation of the surface temperature (°C), chlorophyll-a (mg L^{-1}), and salinity (PSU) in the Sea of Oman and the Arabian Sea in 2013-2014. The shaded area represents the southwest monsoon (SWM) period (June to September)

Some species were found throughout the year and observed in all or most samples whereas most species are found only in a few samples. Among copepods, only 5 species were found in more than 75% of the samples, both in the Arabian Sea and in the Sea of Oman. On the other hand, more than 20 species were only found in 25% of the samples.

Table 3. Average monthly abundance of Harpacticoid copepod (ind m^{-3}). The number between parentheses represents the number of months for which each species was recorded out of 22 samples in the Sea of Oman and 20 in the Arabian Sea

Harpacticoid copepods	Monthly average abundance (ind m^{-3})	
	Sea of Oman	Arabian Sea
1 *Clytemnestra sp.*	0.19 (2)	0.95 (2)
2 *Euterpina sp.*	0.25 (3)	5.09 (14)
3 *Macrosetella sp.*	0.43 (2)	0.68 (5)
4 *Microsetella sp.*	0.31 (3)	0.41 (3)
5 *Tigriopus sp.*	5.56 (3)	0.07 (1)

The 10 globally most abundant taxa made up more than 80% of the total calanoid abundance in both regions (Figure 6). Of these species, 5 were shared between the two locations: *Centropages orsinii, Clausocalanus sp., Canthocalnus pauper*, Eucalanidae, and members of the family Paracalanidae (including the following genera: *Acrocalanus, Bestiolina, Calocalanus, Paracalanus, and Parvocalanus*). Five other species appeared to be associated either with the Arabian Sea or with the Sea of Oman (Figure 5).

The three most abundant calanoid copepods in the Sea of Oman during 2013-2014 were *Temora turbinata* (53.40% of calanoid individuals), Paracalanidae (15.64%), and *Centropages orsinii* (5.45%); *Temora turbinata* and Paracalanidae constituted 69.04% of all Copep-

Table 4. Monthly average (ind m^{-3}) of non-copepod groups. Empty cells refer to taxa that were not observed. The samples were ordered by decreasing abundance in The Sea of Oman

Non-Copepods	Monthly average abundance (ind m^{-3})	
	Sea of Oman	Arabian Sea
Penilia avirostris	116.10	0.07
Appendicularia	97.02	176.36
Evadne sp.	82.60	13.04
Chaetognatha	51.89	39.39
Doliolida	50.99	147.98
Cirripedia	18.83	5.57
Luciferidae	16.48	101.25
Gastropoda	15.87	37.62
Ostracoda	13.46	32.94
Fish egg	9.45	11.27
Brachyura	8.40	3.80
Creseis sp.	6.57	5.03
Bivalvia	4.17	20.44
Amphipoda	3.58	2.24
Siphonophorae	3.09	7.40
Annelida	2.84	6.38
Echinodermata	2.28	2.85
Caridea	2.22	1.22
Cnidaria	2.13	11.14
Pleopsis sp.	0.93	
Ctenophora	0.86	0.27
Decapoda	0.86	1.49
Anomura	0.83	0.07
Fish larvae	0.56	0.20
Stomatopoda	0.56	0.07
Euphausiidae	0.43	14.26
Isopoda	0.19	0.41
Hemichordata	0.12	
Porcellanidae	0.12	0.27
Pteropoda	0.06	
Salpidae	0.06	
Desmopteridae		0.34
Membranipora		7.81

oda. Whereas, the three most abundant calanoids in the Arabian Sea were *Pseudodiaptomus* sp. (28.16%), Paracalanidae (18.70%), and *Pseudodiaptomus serricaudatus* (9.04%). In terms of occurrence in the Sea of Oman, Paracalanidae were found in all the 22 samples (i.e., 100% of the samples), *Temora turbinata* was encountered in nearly 96% of the samples, and *Centropages orsinii* in 68.18% of the samples. In the Arabian Sea, Paracalanidae were found in all the samples (100%), *Pseudodiaptomus serricaudatus* was encountered in 10 (50%) sample whereas *Pseudodiaptomus* sp. was observed in 9 (45%) of the 20 samples.

Some species were found only in one location. Three calanoid species were only observed in the Sea of Oman; *Labidocera kroyeri, Labidocera pavo*, and *Pontellopsis herdmani*, of which the most abundant was *Labidocera pavo*, which had a monthly average of 16 ind m^{-3}. On the other hand, nine species were only observed in the Arabian Sea: *Acartia negligens, Calanoides natalis*, identified as *Calanoides carinatus* (*Kroyer, 1848*) in many studies, *Candacia catula, Labidocera acutifrons, Nannocalanus minor, Pontellina plumata, Scolecithrix danae, Tortanus insularis*, and *Undinula vulgaris*. The monthly average of the two most abundant species *Acartia negligens* and *Calanoides natalis* were 20 and 18 ind m^{-3} respectively. The latter species, i.e., *Calanoides natalis*, is considered rather unique because of its ontogenetic vertical migration characteristic of upwelling areas (Smith et al., 2020). It was only found on 4 occasions, all during the SWM. In August 2013, 34 ind m^{-3} were observed, and in 2014 there was a slight increase in the number to 45 ind m^{-3}. In September, only one specimen was found in 2013, however, a much larger abundance was observed in 2014 with 268 ind m^{-3}.

Cyclopoida copepods: Cyclopoida represented the second most abundant order of copepods in both regions. It accounted for 24.69% of the copepod count in the Sea of Oman and 13.69% in the Arabian Sea. This order was represented by six genera: *Copilia, Corycaeus, Farranula, Oithona, Oncaea*, and *Sapphirina*. *Corycaeus, Oncaea*, and *Oithona* were the most abundant genera within the group in both regions, but Oithona was nearly 5 times more abundant in the Arabian Sea (Table 2), whereas both *Coryaceus*, and *Oncaea* were more abundant in the Sea of Oman. Oithona represented nearly 30% of the cyclopoid individuals in the Arabian Sea but only around 5% in the Sea of Oman. Despite no clear pattern in the Sea of Oman, Oithona in the Arabian sea showed a seasonal increase during SWM and the following fall intermonsoon (FIM) before declining (Figure 8). The last three genera (*Farranula, Copilia* and *Sapphirina*) together represent around 2% of the copepod species counts (Figure 7). The time series indicated large variations in the monthly abundances of all these species, without clear patterns.

Harpacticoida copepods: The third and least abundant group of copepods was the Order Harpacticoida. Its percentage share among all subclass Copepoda in the Sea of Oman and the Arabian Sea throughout the study was only 0.46% and 0.33% respectively. Five genera from this group were found in the samples; these were *Clytemnestra sp., Euterpina sp., Macrosetella sp., Microsetella sp.*, and *Tigriopus sp* (Table 3). In the Sea of Oman, *Tigriopus sp.* constituted more than 80% of all harpacticoids records with a monthly average of 5.56 indv m^{-3} although this value resulted from a single sample with 110 ind m^{-3}. *Euterpina* was only recorded twice in the Sea of Oman with a monthly average of <1 ind m^{-3} but was the most abundant species in the Arabian Sea, 70.76% (5.09 ind m^{-3}). This taxon was recorded in 14 samples (Table 3). In terms of temporal occurrence in the samples, Harpacticoida were found in 17 of the 20 samples in the Arabian Sea (mostly during the fall and winter), whereas in the Sea of Oman, it was only found in half the samples (10 out of 22) but without a clear temporal pattern.

Non-copepod zooplankton: The relative contribution of non-copepod zooplankton in the Sea of Oman and the Arabian Sea was 25.87% and 23.52% respectively. With the exception of *Penilia avirostris* observed only in

Table 5. Two-way PERMANOVA for 4 groups of zooplankton abundance (log-transformed) as a function of both Location and Season. The Bray-Curtiss similarity coefficient was used to measure similarities between samples. The groups were all zooplankton, copepods, calanoid copepods and non-copepods

All zooplankton					
Source	**Sum of sqrs**	**df**	**Mean square**	***F***	***p***
Location	0.66197	1	0.66197	6.5773	0.0001
Season	0.61505	3	0.20502	2.037	0.0001
Interaction	-0.016326	3	-0.005442	-0.054071	0.1631
Residual	3.4219	34	0.10065		
Total	4.6826	41			

Copepods					
Source	**Sum of sqrs**	**df**	**Mean square**	***F***	***p***
Location	0.69736	1	0.69736	7.3462	0.0001
Season	0.65685	3	0.21895	2.3065	0.0002
Interaction	-0.030127	3	-0.010042	-0.10579	0.2442
Residual	3.2276	34	0.094928		
Total	4.5516	41			

Calanoid copepods					
Source	**Sum of sqrs**	**df**	**Mean square**	***F***	***p***
Location	0.86199	1	0.86199	7.1972	0.0001
Season	0. 7475	3	0.24917	2.0804	0.0003
Interaction	-0.096249	3	-0.032083	-0.26788	0.4462
Residual	4.0721	34	0.11977		
Total	5.5853	41			

All zooplankton					
Source	**Sum of sqrs**	**df**	**Mean square**	***F***	***p***
Location	0.61519	1	0.61519	5.3434	0.0001
Season	0.59821	3	0.1994	1.732	0.0057
Interaction	0.0074417	3	0.0024806	0.021546	0.1313
Residual	3.9144	34	0.11513		
Total	5.1352	41			

the Sea of Oman, all other groups of non-copepod zooplankton were found in both locations but with different abundances. The five most abundant groups based on their monthly average (ind m^{-3}) that formed 80% of all non-copepod zooplankton abundance in the Sea of Oman were *Penilia avirostris*, Appendicularia, *Evadne sp*., Chaetognatha, and Doliolida. In the Arabian Sea, the composition was slightly different. The most abundant non-copepod zooplankton, comprising 80% of this diverse group were: Appendicularia, Doliolida, Luciferidae, Chaetognatha, and Gastropoda (Table 4). The occurrence of these groups in the Sea of Oman samples ranged between 68.18-100% of the samples and in the Arabian Sea, their occurrence ranged between 75-100% of the samples.

In terms of relative abundances of the different groups of non-copepod mesozooplankton, their relative abundances in the Arabian Sea was always slightly higher than their relative abundance in the Sea of Oman except for chaetognaths and cladocerans which were more abundant in the Sea of Oman.

The ratio meroplankton/holoplankton (Figure 9) appeared variable in the Sea of Oman without a clear temporal pattern. On the other hand, in the Arabian Sea, the ratio dropped during the southwest monsoon (SWM). In February 2014, Meroplankton constituted one-third of the whole zooplankton in the Sea of Oman and that was attributed to the high abundance of Cirripedes (337 ind m^{-3}). The highest peak of the Meroplankton ratio in the Arabian Sea in December 2013 was due to the high abundance of gastropods (166 ind m^{-3}) and bivalves (68 ind m^{-3}).

Community Analysis

Diversity index: A principal component ordination of the samples using 12 different diversity indices provides a mechanism to isolate the main components of the variability in biodiversity over time. The first axis (PC1) which was highly correlated with Shannon, Simpsons, and Brilloins indices (combining richness and evenness) represented 67% of the variability in diversity. The second principal component (PC2) was highly correlated

Table 6. Indicator values (IndVal analysis) of the zooplankton assemblages of the Sea of Oman and the Arabian Sea.

Species	Community	Indicator Value	p-Value
Temora turbinate	Sea of Oman	0.8103	0.001
Penilia avirostris	Sea of Oman	0.6717	0.001
Evadne sp.	Sea of Oman	0.6142	0.003
Labidocera pavo	Sea of Oman	0.5455	0.001
Anomura	Sea of Oman	0.2915	0.029
Centropages tenuiremis	Arabian Sea	0.6719	0.001
Oithona sp.	Arabian Sea	0.6511	0.003
Euterpina sp.	Arabian Sea	0.6329	0.001
Calanoida	Arabian Sea	0.5956	0.001
Acartia sp.	Arabian Sea	0.5596	0.009
Canthocalanus pauper	Arabian Sea	0.5516	0.048
Paracalanidae	Arabian Sea	0.5497	0.017
Appendicularia	Arabian Sea	0.5488	0.022
Euphausiidae	Arabian Sea	0.5459	0.001
Cnidaria	Arabian Sea	0.5183	0.049
Bivalvia	Arabian Sea	0.5138	0.035
Membranipora	Arabian Sea	0.5000	0.001
Ostracoda	Arabian Sea	0.4961	0.034
Centropages sp.	Arabian Sea	0.4705	0.005
Pseudodiaptomus serricaudatus	Arabian Sea	0.4543	0.004
Acartia plumosa	Arabian Sea	0.3741	0.004
Cosmocalanus darwinii	Arabian Sea	0.3109	0.026
Nannocalanus minor	Arabian Sea	0.3000	0.008
Acartia negligens	Arabian Sea	0.3000	0.009
Calanoides natalis	Arabian Sea	0.2500	0.019

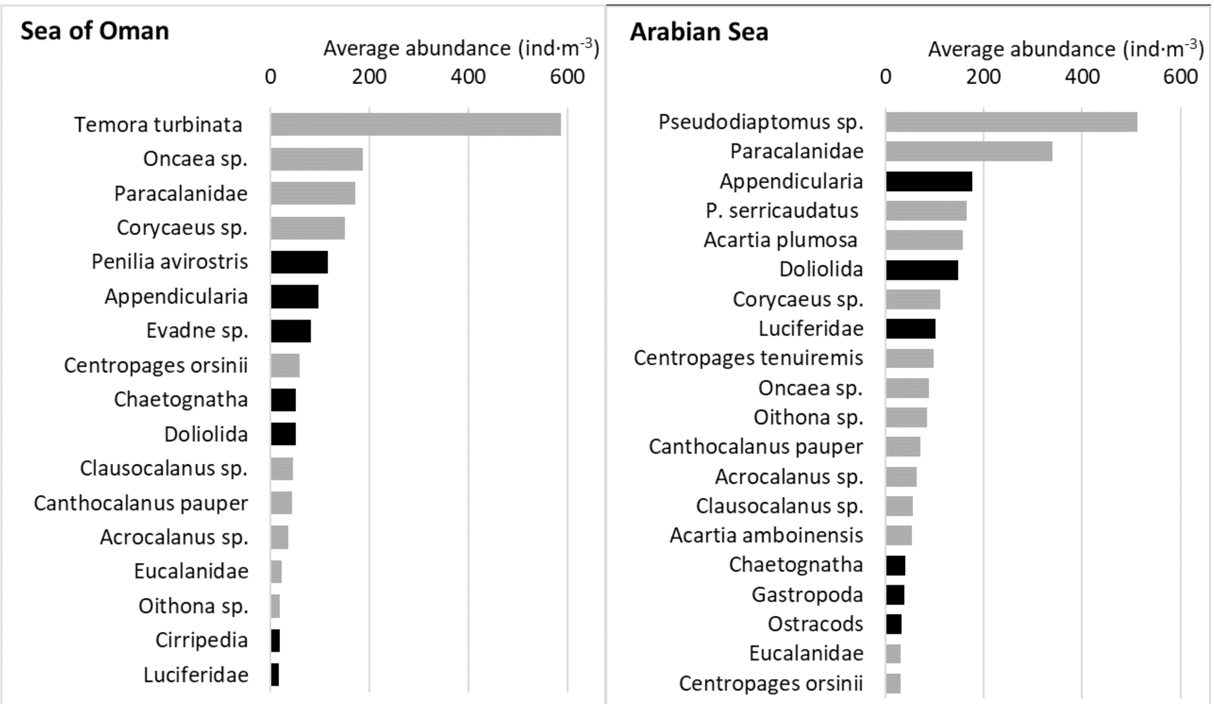

Figure 3. Zooplankton species that represented 90% of total abundance in both locations. Gray bars denote copepods and black bars represent non-copepod species.

to the number of Taxa (S) and Chao's index (both indicators of species richness) and represented 22% of the overall variability.

Over time, the first axis of the PCA had maximum values in the fall and winter and a large drop in diversity during the summer (summer monsoon) both in the Sea of Oman and in the Arabian Sea. The exact timing of the drop seemed to fluctuate from year to year. On the other hand,

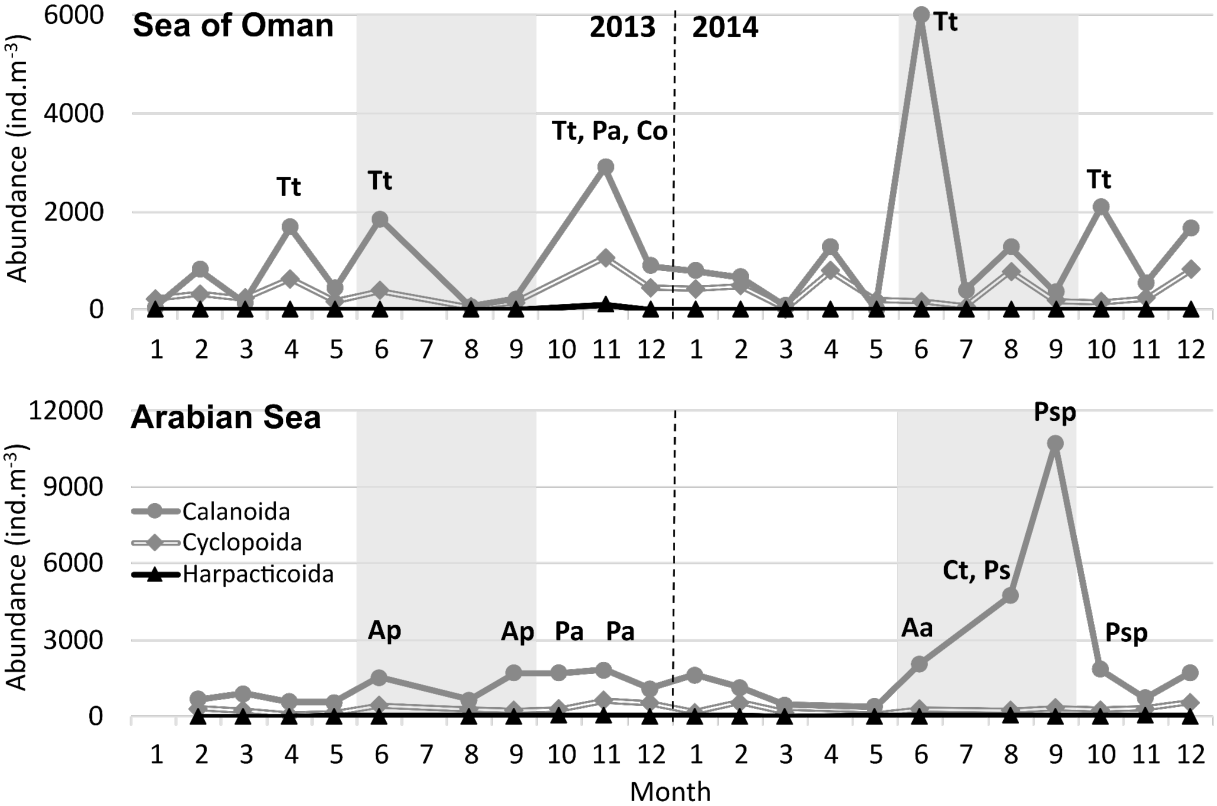

Figure 4. Abundance of copepod orders in the Sea of Oman (up) and the Arabian Sea (down). The following letters written on peak months document to most abundant calanoid species; Tt: *Temora turbinata*, Pa: Paracalanidae, Co: *Centropages orsinii*, Ap: *Acartia plumosa*, Aa: *Acartia amboinensis*, Ct: *Centropages tenuiremis*, Ps: Pseudodiaptomus serricaudatus, Psp: Pseudodiaptomus sp. The shaded areas indicate the southwest monsoon (SWM).

the second principal component (number of species) did not show any seasonality in its variability (Figure 10).

Geographical and Seasonal Variability: On the MDS based on Bray-Curtis similarity between samples of zooplankton (Stress = 0.20910), the samples from the Arabian Sea were very distinct from those of the Sea of Oman. There was also a pattern in the similarities (Bray-Curtis) between the different seasons. During the Northeast Monsoon (NEM) and the Fall Intermonsoon (FIM), the sample points were located near the center of the plot although distinct between the Arabian Sea and the Sea of Oman. During the Spring Intermonsoon (SIM) the samples from the Sea of Oman tended to show larger differences in composition (lower similarities) but the samples from the Arabian sea continued to form a small cluster near that of the NEM. During the summer Southwest Monsoon (SWM), in both areas, the similarities between samples decreased as the sample dots tended to spread away from each other, indicating large variations in composition (Figure 11A). When adding the correlation between the MDS axis with the 3 environmental variables measured at both sampling stations, salinity appears to be well correlated with the first horizontal axis (PC1), responsible for the distinction between the two locations.

Using a PERMANOVA on the Bray-Curtis similarity between samples, the effects of both location and season were very significant (p = 0.0001 and p = 0.0001 respectively) but the interaction between the factors, although significant (p = 0.1631) was much weaker. The significant interaction likely corresponds to the difference in patterns of the two regions during the SIM (Table 5).

When we limited the analysis to copepods only, the effects of both location and season remained very significant (p =0.0001 and p = 0.0002 respectively) but the interaction between the factors was not significant (p = 0.2442). The overall patterns, however, remained quite similar with winter (NEM) and fall (FIM) communities quite homogenous in both locations but spring (SIM) and summer (SWM) communities progressively developing large differences in compositions (Table 5). Salinity was still the variable that was best correlated with the axis that separated the two locations (Figure 11B).

If we limit the analysis to calanoid copepods only, the effect of both location and season were very significant (p =0.0001 and p = 0.0003 respectively) but the interaction between the factors was not significant (p = 0.4462) (Table 5). Both Arabian Sea communities and Sea of Oman communities show similar patterns; with similar communities in the FIM and NEM periods and progressively different communities in the SIM and particularly the SWM (Figure 11C). Salinity here is also the environmental variable that best correlates with the pattern of similarities observed between locations (Figure 11C).

For the non-copepod zooplankton, the effect of both location and season were very significant (p =0.0001 and p = 0.0057 respectively) but the interaction between the factors was not significant (p = 0.1313) (Table 5). Both Arabian Sea communities and Sea of Oman communities show similar patterns; with similar communities in the fall (FIM) and winter (NEM), and progressively different communities in the spring (SIM) and particularly the summer (SWM) (Figure 11D). We see also during the SWM, in the Arabian Sea, a movement on the MDS plane towards higher chlorophyll-a values. Salinity is also the environmental variable that best correlates with the pattern of similarities observed between locations (Figure 11D).

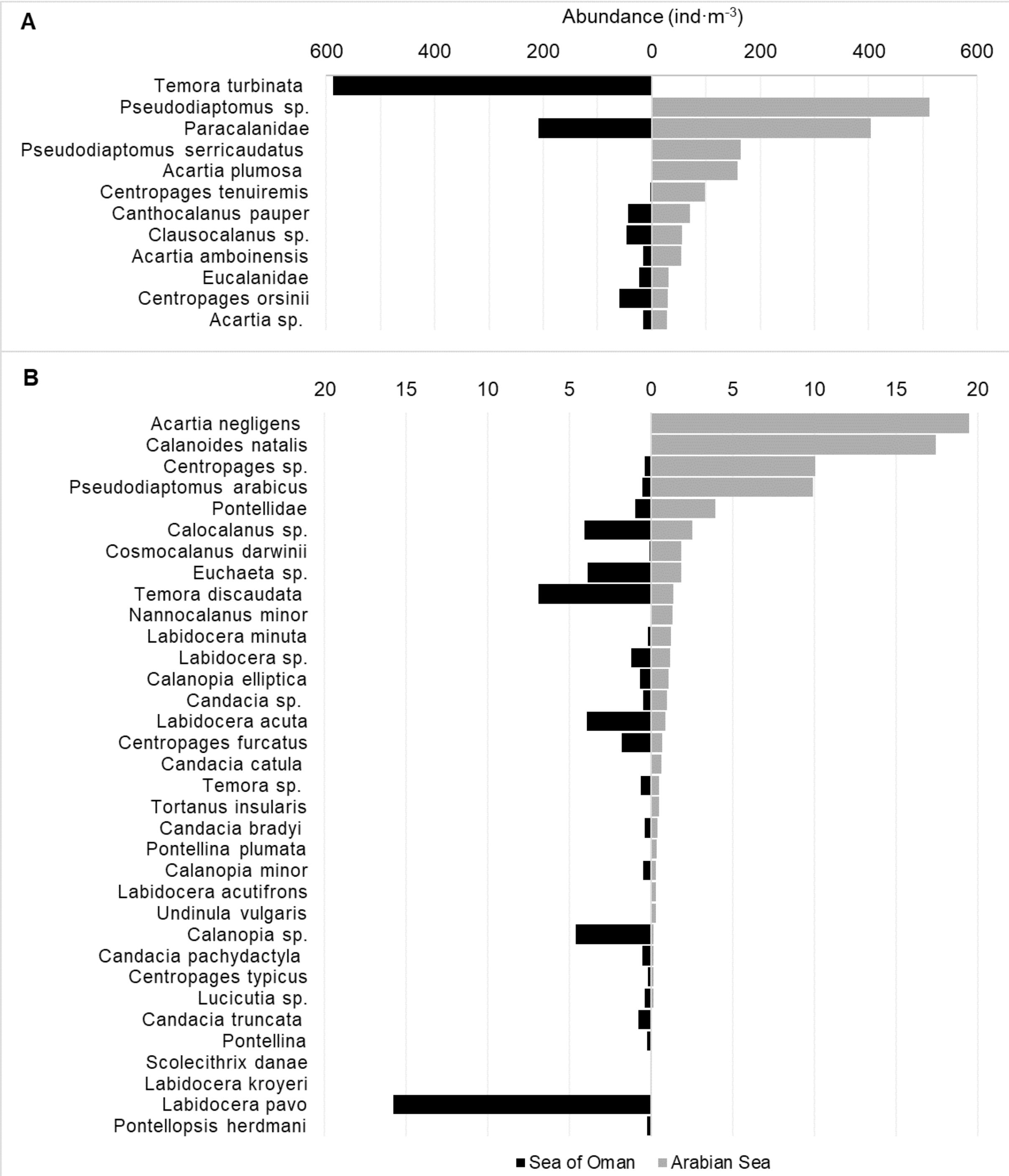

Figure 5. Monthly average abundance of calanoid copepods in the Sea of Oman and the Arabian Sea. (A) denotes the highly abundant and (B) the less abundant species

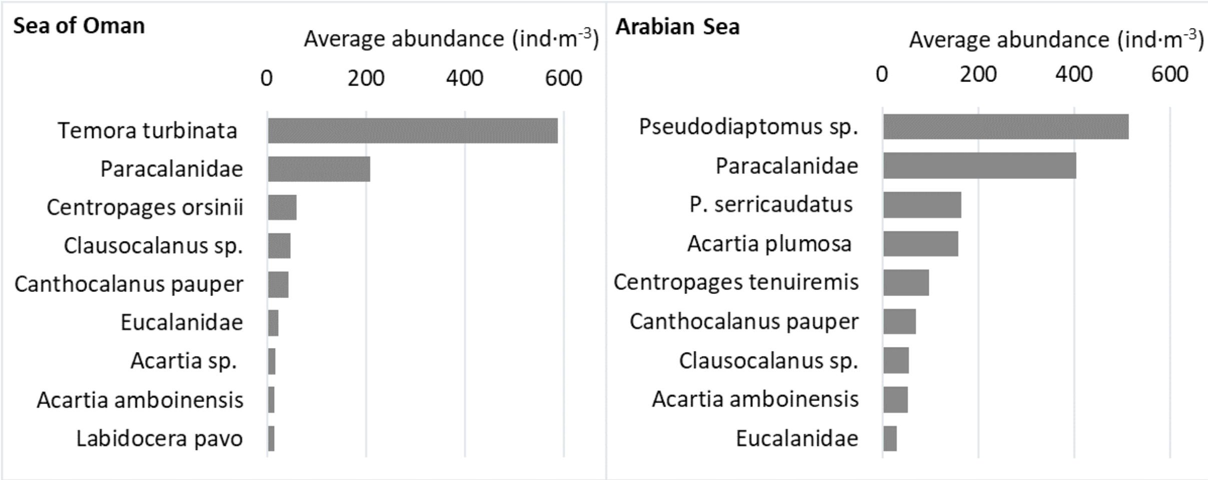

Figure 6. The most abundant calanoid copepods in both locations (monthly average abundance)

Indicator species analysis: The indicator species analysis indicated that 25 species had significant indicator values in separating the Sea of Oman from the Arabian Sea communities (Table 6). Most species (20) were indicators of the Arabian Sea. Among the most significant, Temora turbinata appeared characteristic of the Sea of Oman with *Penilia avirostris* and *Evadne sp*. The species most characteristic of the Arabian Sea communities were *Centropagus tenuiremis, Oithona* sp., *Euterpina* sp., and *Acartia* sp.

Discussion

Environmental variability: Cool temperatures in Salalah during June-September are caused by wind-driven upwelling along the Arabian Sea as a result of strong winds blowing from the SW. The upwelling brings up cold water from depth to the surface (Madhupratap et al., 1996b). In Muscat, the small dip that takes place both years in July-August resulted from the effects of a series of short and irregularly spaced coastal upwelling events along the south coast of the Sea of Oman (Claereboudt, 2018), that raise the thermocline closer to the surface and allow some wind mixing of the surface water with much cooler water below the thermocline resulting in small changes in SST.

In addition to the clear cycle of temperature, the salinity also shows a seasonal pattern. In the Sea of Oman, the higher salinities observed during the summer correspond likely to higher evaporation of the surface water. On the other hand, the progressive decline of salinity during the Khareef (i.e., during months of the SWM) in southern Oman is likely the result of a progressive dilution by the rainfall and occasional river discharge combined with the upwelling of lower salinity waters (Anonymous, 2022).

Peaks of chlorophyll-a in the Sea of Oman during the NEM (typically December-March) are linked to a seasonal bloom of *Noctiluca scintillans* that takes place (Al-Azri et al., 2007; do Rosário Gomes et al., 2014) and coincides with the annual drop in the sea surface temperature. In

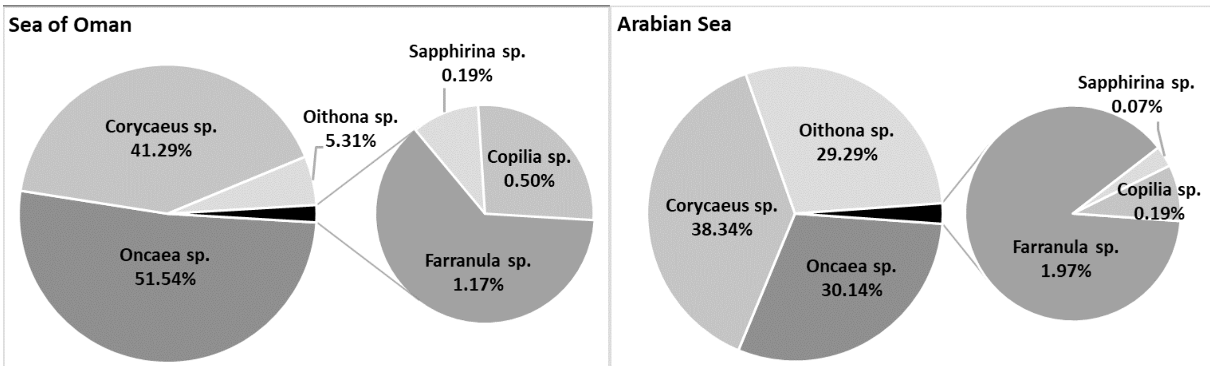

Figure 7. Relative proportions of the different species of cyclopoid copepods in the Sea of Oman and the Arabian Sea

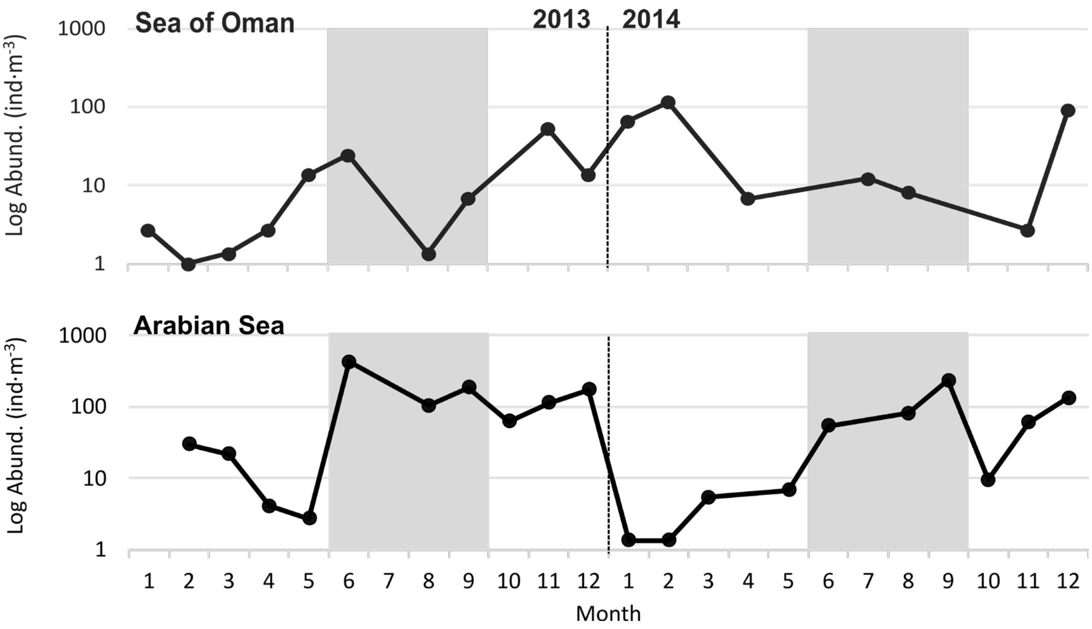

Figure 8. Monthly abundance distribution of Oithona in the Sea of Oman and the Arabian Sea. Y-axis in logarithmic scale. The shaded area denotes to southwest monsoon (SWM).

Salalah, chlorophyll-*a* progressively increases during the SWM (Figure 2) as a direct response to the injection of nutrients in coastal water by the seasonal upwelling.

Species abundance and distribution: The calanoid copepod species *Temora turbinata* (family Temoridae) was the most abundant calanoid copepod in the Sea of Oman (Figure 5). It was also one of the 5 species with a very high indicator value for this geographic area (Table 6). This confirms previous observations in the same area (Al-Azri et al., 2009; Fazeli and Zare, 2011; Piontkovski et al., 2013; Fazeli et al., 2015), and the Arabian Sea (Jemi and Hatha, 2019). This planktonic and epipelagic species is widely distributed in tropical, subtropical, temperate waters (Tseng et al., 2011), and lagoons (Almeida et al., 2012) sometimes in high abundances. The monthly average abundance was 588 ind m^{-3}, whereas the average abundance of females in northeastern Taiwan was 606-34 ind m^{-3} (Wang et al., 2021).

If in Taiwan, the abundance of *T. turbinata* showed a positive correlation with seawater temperature (Tseng et al., 2011), in the Sea of Oman, this correlation with temperature was weak at best (R^2 =0.184, p =0.047) and appear driven by a single high abundance count measured on a hot day in June 2014. There was no clear seasonality in the abundance of *T. turbinata* in the Sea of Oman as it was observed all year round in high abundance. This might be explained by its feeding behavior. This copepod can diversify food items to include even the smallest heterotrophic nanoflagellates (i.e., microbial loop) when the preferred diatoms become scarce (Chang et al., 2014) and therefore can withstand periods of limited phytoplankton abundance.

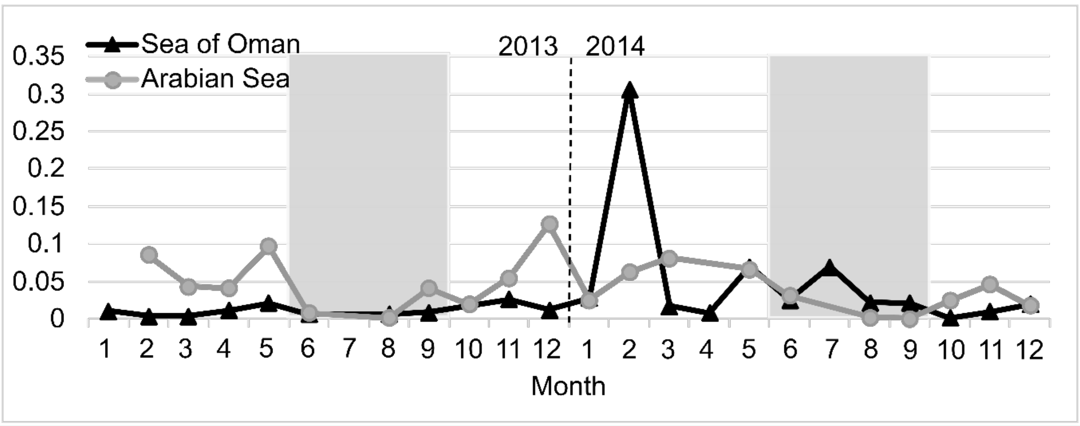

Figure 9. Ratio of Meroplankton to Holoplankton in the Sea of Oman and the Arabian Sea. The shaded area denotes to southwest monsoon (SWM).

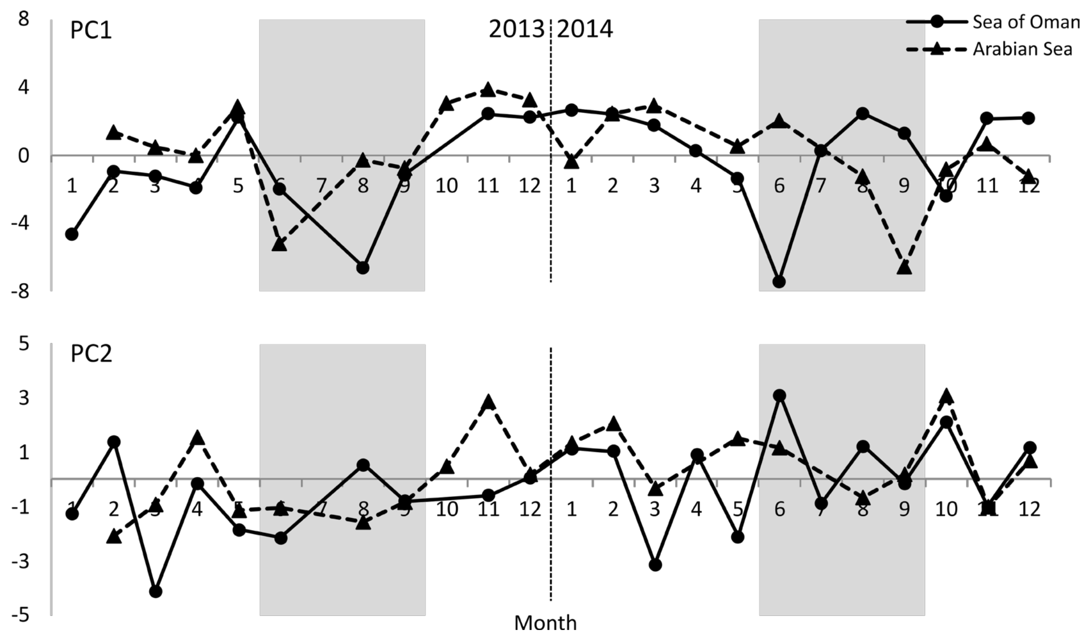

Figure 10. First two principal components (PC) over time. The shaded area denotes the southwest monsoon (SWM).

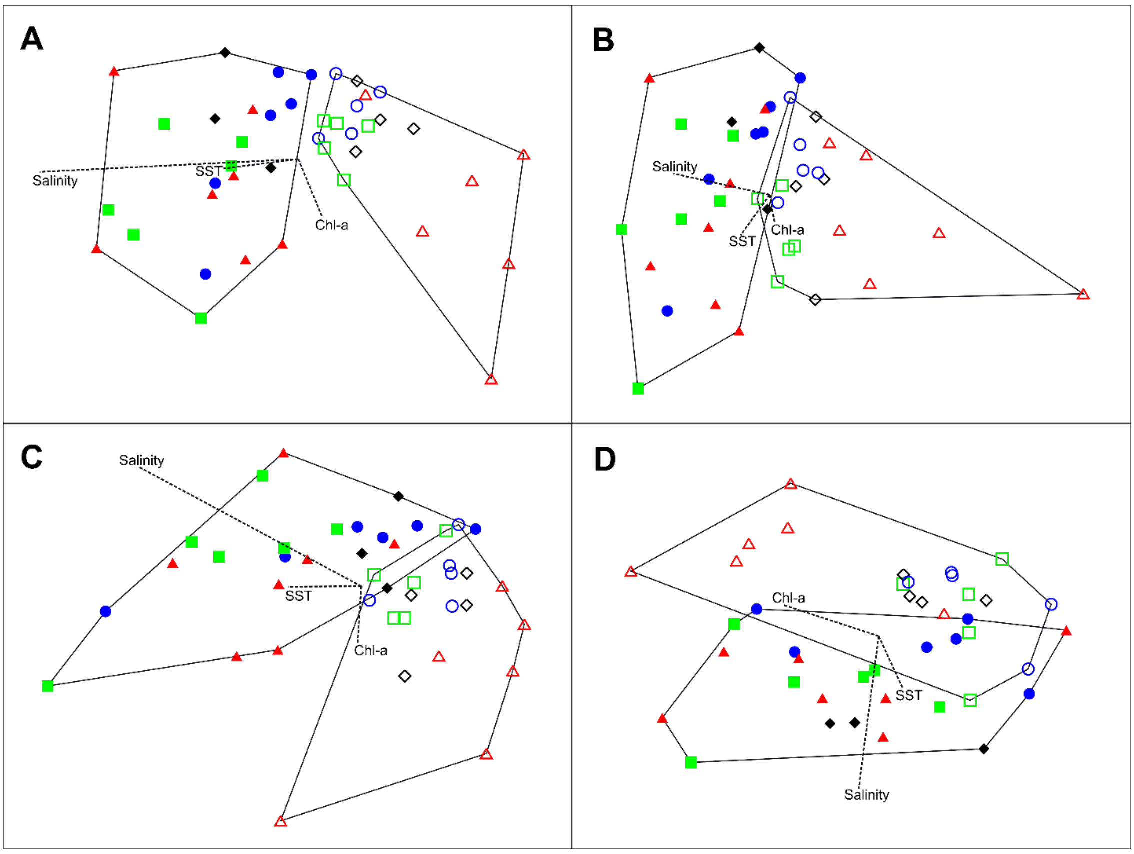

Figure 11. MDS representation of the 42 samples. A, referred to all zooplankton, B, copepods, C, calanoid copepods and D, non-copepod zooplankton. Filled symbols correspond to the Sea of Oman, and empty symbols to the Arabian Sea. Blue disks indicate (NEM), green squares (SIM), red triangles (SWM), and black diamonds (FIM).

Cladocerans (*Penilia avirostris* and *Evadne* sp.) were good indicator species that separated the zooplankton community of the Sea of Oman from the Arabian Sea (Table 6). In the coastal waters of Kochi, southeastern Arabian Sea, these cladocerans flourish in warmer environments with high sea surface temperature, particularly during high stratification periods (Atienza et al., 2006). During the summer monsoon, these two cladocerans constituted up to 50% of the whole zooplankton (Ezhilarasan et al., 2018). A comparison of the seasonality of *P. avirostris* in five different water masses (the Black Sea, the Adriatic Sea, the Atlantic, the Mediterranean basin, and the Sea of Oman) concluded that sea surface temperature played a key role in high abundance during warmer months (>22 ^{o}C). In our study, the peaks of *P. avirostris* corresponded with summer months in the Sea of Oman and support these earlier findings in the Black Sea, the Adriatic Sea, and the Mediterranean basin. In an upwelling area of the north-eastern Atlantic, the abundance of *P. avirostris* was very low arguably because the sea surface temperature was cooler (<22 ^{o}C) even during summer (Piontkovski et al., 2012). This resembles the situation in the Arabian Sea where the abundance of cladocerans, in general, and *P. avirostris*, in particular, was very low in comparison to the Sea of Oman and this could be, also, linked to the seasonal upwelling event in the Arabian Sea. In addition to its association with higher water temperatures, *Penilia avirostris* shows a diet spanning a large range of species and sizes spanning small flagellate to large diatoms, (Piontkovski et al., 2012) which made this cladoceran able to thrive by grazing on many food sources regardless of their dimensions (Atienza et al., 2006).

The copepod *Centropages tenuiremis* (family Centropagidae) was identified as one of the indicator species of the Arabian Sea communities (Table 6) with a monthly average abundance of 98.5 ind m^{-3} (only 3 ind m^{-3} in the Sea of Oman). The peak abundances of *C. tenuiremis* were recorded in August and September, i.e., towards the end of SWM, which also corresponded with the lowest sea surface temperature. In Xiamen Harbor, China, *C. tenuiremis* is considered a dominant copepod during winter and reached a maximum abundance (80.2 ind m^{-3}) in the spring (Wang et al., 2005). This species, also, reached its highest abundance (between 50-100 ind m^{-3}) during late SWM on the southwest coast of India (Jemi and Hatha, 2019). *C. tenuiremis* may respond well to conditions of high nutrients and low temperatures similar to upwelling areas that led to the high peak during SWM.

Cyclopoid species Oithona and harpacticoid Euterpina were indicators of the Arabian Sea samples. They seem to be associated with areas characterized by low oxygen concentrations (Jyothibabu et al., 2018). Meanwhile, with no clear pattern in the Sea of Oman, the abundance of Oithona copepods in the Arabian Sea sharply increased with the onset of the SWM and continued till the end of the Fall intermonsoon (FIM) before dropping. This finding was documented before (Smith and Madhupratap, 2005) and corresponded perhaps to the progressive exhaustion of its ciliate prey as the biomass of the summer monsoon progressively sinks below the thermocline. With its diet consisting mostly of bacteria eating ciliates, Oithona was particularly well adapted to tapping into the microbial loop.

Calanoides natalis, although it had a low indicator value (probably because of its low abundance in surface water where the samples were collected), is typically considered a unique and characteristic species in the Arabian Sea upwelling area due to its ontogenetic vertical migration from deep water to the surface during the SWM and, hence, is considered as an upwelling indicator species (Smith et al., 2020). During seasonal surveys in 2007-2008, *C. natalis* populated the Omani shelf from Ras Al-Hadd to Salalah in the south during the SWM (Piontkovski et al., 2015). It was also reported in regions of upwelling such as Hadhramout coast of Yemen, (Mukhaysin et al., 2017), and Somalia (Smith, 1982) during SWM. In this study, the existence of *Calanoides natalis* near the surface is coupled with drops in SST and an increase in chlorophyll-a, which are related to the summer upwelling. A combination of strong winds and low temperatures (the typical condition of SWM) are the preferred conditions for high abundances of *Calanoides natalis* (Smith et al., 2020). The sea surface temperature in the Arabian Sea during August-September ranged between 23.50-26.13^{o}C, which is within the most favorable range (18-27^{o}C) found in a study off Masirah Island, Oman, during 2007-2016 (Smith et al., 2020). The high abundance of *C. natalis* at the upper layers during SWM was sustained by predominant diatoms (Garrison et al., 1998). In a single day, this herbivorous species can ingest half the diatoms in a water column (Smith et al., 2020) to the extent it can suppress diatom blooms (Smith and Madhupratap, 2005).

Meroplankton

The abundance pattern of Meroplankton in the Arabian Sea (abundant during the winter and scarce during the Southwest monsoon) reflects the likely outcomes of pelagic larvae hatching during the SWM: a dispersal bringing larvae towards the center of the Arabian sea where appropriate benthic substrates are rare or inexistent. For instance, the abalone *Haliotis mariae* seems to reproduce mostly in March-April, before the onset of the SWM (Al-Hafidh, 2006). A similar reproductive period was recorded for the sea cucumber *Holothuria scabra*, east of Mahout Island (Al-Rashdi and Claereboudt, 2018). The absence of seasonality in Meroplankton abundance in the Sea of Oman, reflects perhaps the relatively favorable conditions observed in this area. For instance, the reef scallop *Laevichlamys ruschenbergerii* showed two periods of reproduction, one in February-March (corresponding to the spring phytoplankton bloom) and one in the Fall (Al-Barwani, 2001).

Community structure

In the Sea of Oman (Muscat) the total number of copepod species was 50 of which 38 were calanoid copepods. In comparison, 66 species of copepods were identified in Chabahar Bay, Iran, among which 34 were calanoids (Fazeli et al., 2015), and in an earlier study (Fazeli et al., 2013) among the 48 copepods recorded in the same area, 32 were calanoids. In this area of the northern Sea of Oman (Chabahar Bay), the total abundance of copepods in February (NEM), May (Pre-SWM), August (SWM), and November (Post-SWM) ranged 487-890, 572-1254, 613-713, and 474-594 ind m^{-3} respectively (Fazeli and Zare, 2011; Fazeli et al., 2013). However, our total copepod abundances for the same periods were 1151, 412, 1092, and 2421 ind m^{-3} respectively. These differences in copepod abundances might be due to a combination of factors, such as environmental conditions and the geographical nature of sampling locations.

The total number of copepod species in the Arabian Sea (Salalah) was 57, of which 44 (43%) were calanoid copepods. During the John Murray expedition (Sewell, 1948), they observed a very similar number of copepod species (60) but the JGOFS programs only identified 47 species (Smith and Madhupratap, 2005). In comparison to other upwelling areas, the total number of copepod species in Cochin, India, was 37, where calanoids represent 21 (36%) species (Jemi and Hatha, 2019). However, on the Hadhramout coast of Yemen, the total number of copepod species was 171, of which 121 (41%) were calanoids (Mukhaysin et al., 2017). The total copepod abundance during the seasonal upwelling period (SWM) was 2932 ind m^{-3}, which is close to what was recorded in Cochin (3211 ind m^{-3}) and the Hadhramout coast of Yemen (2660 ind$\cdot m^{-3}$). In areas of persistent upwellings, such as Chile, the number of copepod species was 77 and the total abundance reached a value of 2228 ind m^{-3} (Gonzalez et al., 2015).

This variation in numbers of copepods in the samples can be affected by factors such as mesh size, towing technique (vertical, horizontal, or oblique), the nature of sampling locations (open water, semi-enclosed bay, or estuarine system), number of sampling locations, speed of the boat and number of samples.

Communities differ between the Sea of Oman and the Arabian Sea but also differ significantly with the season. The two communities were closest to each other in the winter and showed the largest differences in the summer. The community structure of zooplankton, in general, and copepods, in particular, were different between both locations during the summer months (SWM). The Sea of Oman community was mainly dominated by a few species, especially *Temora turbinata*, whereas several copepod species alternated dominance during the same period in the Arabian Sea (Figure 4) which widened the minimum polygon of the MDS plots. Dominance of few species through different seasons and accounted for the majority population was also noted in previous study (Madhupratap et al., 1996a). The atmospheric conditions during SWM are totally different between the two basins. In the summer (during SWM), the Sea of Oman is hot and shows intense stratification. Winds are slow and, hence, mixing in the water column is weak which strengthens the stratification and prevents deep water nutrients from reaching the surface (Madhupratap et al., 1996b). The upwelling phenomenon in the Arabian Sea, which is caused by the southwesterly winds during SWM, creates an optimum condition to support the high growth of mesozooplankton (Smith and Madhupratap, 2005) and can affect the community structure (Gonzalez et al., 2015). On the other hand, during the second half of the summer (Aug-Sep), local upwellings driven by high-frequency changes in the wind direction create small localized phytoplankton blooms (Claereboudt, 2018) that likely drive short pulses in zooplankton production and changes in species composition.

Conclusion

The species composition of the mesozooplankton communities varied significantly between the Arabian Sea and the Sea of Oman. The two communities were the closest in winter (NEM) and showed the largest differences in composition in summer (SWM). Seasonal differences in the zooplankton communities were also identified in all four datasets (zooplankton, copepods, calanoid copepods, non-copepods). The seasonal changes in community structures were most significant for copepods and calanoid copepods and less significant for non-copepods suggesting that the relative abundances of the three orders of copepods responded also to seasonal environmental changes. Out of the total of 91 zooplankton taxa, a few species (17 in the Sea of Oman and 20 in the Arabian Sea) represented more than 90% of the total zooplankton abundance. There was a distinct abundance pattern in the Arabian Sea, especially for copepods and meroplankton but no such pattern in the Sea of Oman. Some species such as *Temora turbinata* and *Penilia avirostris* in the Sea of Oman, and *Oithona spp*. in the Arabian Sea seem able to exploit a wide range of prey from phytoplankton to small ciliates and thus feed through the microbial loop.

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