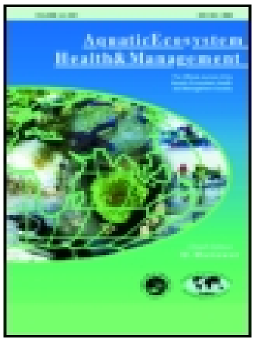

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Seasonal dynamics of microzooplankton communities in the Sea of Oman (Arabian Sea)

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Abstract

Seasonal dynamics of microzooplankton and changes in environmental condition were analysed during a one-year field sampling campaign in the Sea of Oman at two different stations. Monsoon winds in this region cause distinct seasonality patterns with high primary productivity during the south-west monsoon in summer (June to October) and north-east monsoon periods in winter (November to March). Microzooplankton in the Sea of Oman showed several biomass peaks throughout the year. In general, higher biomass occurred during the south-west monsoon when compared to the north-east monsoon period with maxima of 190 µg C l^{-1} at the inshore station Bandar Al-Khyran at 1m and 308 µg C l^{-1} at 10m water depth. At the offshore-station, peaks of 372 µg C l^{-1} (1m) and 256 µg C l^{-1} (20m) occurred during the south-west monsoon. A strong coupling between phytoplankton and microzooplankton was observed during monsoon periods but some microzooplankton peaked during inter-monsoon periods when chlorophyll concentration was low (Bandar Al-Khyran: 372 µg C l^{-1} at 1m and 196 µg C l^{-1}, 10m; Offshore-station: 419 µg C l^{-1}, 20 m). The initiation of phytoplankton blooms in the Sea of Oman was bottom-up controlled due to strong seasonal nutrient influx during south-west and north-east monsoon periods. Highest microzooplankton biomass occurred during monsoon periods with a dominance of Noctiluciphyceae and peaks of 7596 µg C l^{-1} at Bandar Al-Khyran (1m) and 5942 µg C l^{-1} (10m). *Copepod nauplii*, Amoebozoa and Larvacea contributed substantially to microzooplankton biomass throughout the year. Ciliophora contributed low proportion to the total microzooplankton biomass peaking both during monsoon and inter-monsoon periods. During the spring inter-monsoon, choreotrich ciliates (tintinnids) showed distinct peaks of 15.9 µg C l^{-1} at Bandar Al-Khyran (1m) and 17.7 µg C l^{-1} (10m) as well as 18.2 µg C l^{-1} at Offshore-station (20m). The interplay between bottom-up controlled primary production and top-down control mechanisms regulates the phenology patterns of specific microzooplankton groups in the Sea of Oman thus pointing at complex trophodynamic interactions at the lowermost food-web level in this low-latitude ecosystem.

Keywords: protozoa, protozooplankton, *nauplii, appendicularia*, Noctiluca, tintinnid

Introduction

Zooplankton plays a key role in the functioning of marine foodwebs as it acts as the major grazer of phytoplankton and serves as a trophic link between primary producers and higher trophic levels such as fish. Furthermore, its role in terms of nutrient cycling and the transfer of matter and energy up the foodweb is crucial. Previously, studies on plankton communities primarily focused on mesozooplankton (size fraction: 200-2000 µm) as consumers of phytoplankton (Richardson, 2008) which led to the assumption of a linear food chain (phytoplankton-copepods-fish). Only after Azam et al. (1983) coined the term 'microbial loop', the role of microzooplankton (MZP) (size fraction: 20-200 µm) has been acknowledged. MZP comprising of protozoa (heterotrophic dinoflagellates, ciliates, rotifers) and small metazoa (e.g. meroplanktonic larvae, appendicularians, copepod nauplii) which act as a major consumer of autotrophic production (Calbet, 2008; Landry and Calbet, 2004; Loeder et al., 2012) and serve as a trophic intermediary between primary producers and mesozooplankton (Calbet, 2008; Figueiredo et al., 2009; Sherr et al., 1986). Especially the MZPs role in terms of energy transfer to higher trophic levels has been stressed recently (Bils et al., 2017; Montagnes et al., 2010).

Despite intensive studies on pelagic marine systems and alterations of plankton communities in relation to changes in environmental conditions, some marine regions are investigated at a low spatial and temporal resolution although they are subject to substantial environmental changes at present. For example, most studies dealing with global warming impacts on plankton communities focussed mainly on cold and temperate pelagic systems rather than on low latitude regions (Richardson, 2008). This is astonishing since several low latitude regions like the Indian Ocean (Rao et al., 2012) and the Arabian Sea more specifically (Goes et al., 2005; Piontkovski and Claereboudt, 2012) are facing pronounced sea surface warming at present with substantial impacts on e.g. ocean productivity (Boyce et al., 2010).

In addition to global warming scenarios, natural weather phenomena can affect the environmental conditions of the ocean such as nutrient conditions. While temperate regions usually show distinct seasonality patterns in relation to light and nutrient conditions which in turn translate into changes in zooplankton communities, regions close to the equator are considered as less seasonal. In some low latitude regions, however, upwelling and monsoonal wind systems can cause distinct seasonality patterns as described for example for the North-East Monsoon (NEM) period in the Sea of Oman (SoO), Arabian Sea (Al-Azri et al., 2012; Al-Azri et al., 2010). The NEM causes low-latitude upwelling and convective mixing leading to eutrophic conditions during winter (November to March) in contrast to oligotrophic conditions during the South-West Monsoon (SWM) period in summer (June to October). Such upwelling and convective mixing events induce changes in the nutrient regime thus changing autotrophic and heterotrophic production considerably.

The present study focused on plankton communities in the SoO, an area which is experiencing one of the strongest warming scenarios at present (Piontkovski and Chiffings, 2014). Since warming is considered as one of the most important factors affecting MZP growth and grazing due to an increased metabolism, rapid growth and generation times at elevated temperature conditions (Aberle et al., 2007; Aberle et al., 2015; Rose and Caron, 2007), an integration of MZP into foodweb analyses in oceanic and coastal regions of the Arabian Sea like the SoO is essential. To our knowledge, this is the first comprehensive study accounting for trophodynamic interactions between primary producers and consumers and the pronounced role MZP in the coastal planktonic foodweb in the SoO in relation to seasonal nutrient and temperature changes.

Methodology

Samples of microzooplankton and environmental parameters were collected during a monthly sampling campaign in the Sea of Oman (SoM) during the period from April 2010 to April 2011. Two different stations were sampled: (1) Inshore station at Bandar Al-Khyran (BK) and (2) Offshore station (OFF) located 30 km off Muscat, Oman, Fig. 1) and small metazoa ranging between 20-200 µm were analysed and MZP biomass estimated using calculated volume of various geometric objects (sphere, cone, cylinder, etc.) to which the observed microzooplanton organisms in a counting chamber were equalized.

Chlorophyll *a*, temperature, salinity and nutrient measurements were obtained from surface water samples at BK (water depth of ~15 m) and OFF (water depth of ~100m).

Temperature, salinity, and chlorophyll *a* were measured with an Idronaut-Ocean Seven 316 CTD probe fitted with a chlorophyll *a* fluorescence sensor. Nutrient samples were filtered using Whatman GF/F filters. Frozen samples were later analysed with SKALAR FlowAcccess auto-analyser following procedures described in manuals (Skalar, 1996; Strickland and Parsons, 1972).

Statistical analyses

To show correlations between microzooplankton and environmental variables, non-parametric Spearman rank correlations were performed using STATISTICA 14.0 with a significance level of $p < 0.05$. Data from the April 2010 to April 2011 was used for the Spearman rank correlations in order to assess the relationship between microzooplankton community characteristics and environmental variables (e.g. chlorophyll a, nutrients, oxygen, temperature, phytoplankton groups) and to gain further understanding on ecological interactions between phytoplankton and microzooplankton and their environmental drivers

Results

Biotic and abiotic parameters

At the inshore station Bandar Al-Khyran (BK) and the offshore-station (OFF), two distinct peaks of chlorophyll *a* occurred throughout the year, each during the two monsoon periods (Fig. 2). The highest chlorophyll *a* peak (up to 2.7 mg m^{-3}) occurred during the SWM period at the inshore station Bandar Al-Khyran (BK) followed by a lower peak during the NEM (Fig. 2a). Chlorophyll *a* peaks were lower at the OFF station reaching maximum values of 1.3 mg m^{-3} during the NEM period.

Sea surface temperature reached a maximum during the SWM period with up to 31.0°C (BK) and 31.5°C (OFF) at the end of June 2010 (Fig. 2a+b). Lowest sea surface temperatures of 23.4°C were observed at the end of the NEM period at BK and OFF at the end of February 2011 (Fig. 2a+b).

Salinity showed a maximum of 37 during the inter-monsoon period in October 2010 at BK and OFF and low salinities in February/March 2011 (Fig. 2a+b).

Nutrient concentration during the SWM period at BK and OFF was generally low. However, silicate concentrations before and after the 1st phytoplankton bloom (chlorophyll *a* peak, July-September 2010) where comparably high and remained at a similar level during the NEM period thereafter (Fig. 2c+d). An increase in nitrogen compounds (NO_X) and PO_4 was observed during the inter-monsoon period (October 2010). Concentrations remained comparably high during the NEM until the 2nd phytoplankton peak developed.

Microzooplankton biomass and community composition

The highest MZP biomass (excluding *Noctiluca* sp. and Amoebozoa, given in µg C l^{-1}) was found at the inshore station Bandar Al-Khyran (BK) at 1m (Fig. 3b) and 10 m water depth (Fig. 3b) as well as at the offshore-station (OFF) at 20 m water depth (Fig. 2d) when compared to the offshore-station (OFF) at 1m water depth (Fig. 3c). In general, higher biomass occurred during the SWM period when compared the NEM period (Fig. 3). The inter-monsoon period during spring (SIM= spring inter-monsoon) was characterized by relatively high MZP biomass especially at the inshore station Bandar Al-Khyran (BK) (Fig. 3a+b) as well as at the offshore-station (OFF) at 20 m water depth (Fig. 3d).

MZP biomass was dominated by Noctiluciphyceae. The highest *Noctiluca* sp. biomass (µg C l^{-1}) was found at the inshore station Bandar Al-Khyran (BK) during the period of NE monsoon with maximum biomass of 7600 µg C l^{-1} at 1m in January 2011 (Fig. 4a) and 5900 µg C l^{-1} at 10m in December 2010 (Fig. 4b). *Noctiluca* sp. biomass at the offshore-station (OFF) reached much lower values with peaks occurring during the NE-monsoon period (Fig. 4c+d). Amoebozoa did not show clear seasonality patterns but relatively high biomass occurred during the inter-monsoon period in fall (FIM= fall inter-monsoon) especially at the inshore station Bandar Al-Khyran (BK) (Fig. 4a+b).

Copepoda (nauplii) contributed to a high share to the total MZP biomass at all stations throughout the year and no distinct seasonality patterns could be observed (Fig. 5). Copepod nauplii were of relevance both during the monsoon and the inter-monsoon periods showing in total a higher biomass at the BK when compared to the OFF station. In general, Larvacea (class Appendicularia) occurred at higher biomass during the NEM and the inter-monsoon periods while they were of minor relevance during the SWM period.

Ciliophora showed relatively low biomass at all stations throughout the year (Fig. 6). Choreotrichia and Oligotrichia biomass was in general higher at BK (Fig. 6a+b) when compared to OFF station (Fig. 6c+d) and no distinct seasonality patterns could be observed. However, it must be noted that the present data on Ciliophora must be treated with caution since reverse filtration might have caused a loss in some delicate, aloricate ciliate species (Gifford and Caron, 2000; Gowing et al., 2003).

Interaction between microzooplankton and environmental variables

To show correlations of microzooplankton with environmental parameters, the Spearman rank correlation coefficient ρ was calculated for the entire data set. Only the results that are statistically significant are presented here ($p < 0.05$). At BK, the Spearman rank correlation for total microzooplankton was negative with nitrate ($\rho = -0.55$, $p < 0.05$) and nitrite + nitrate ($\rho = -0.53$, $p < 0.05$). Ciliophora were negatively correlated with nitrite ($\rho = -0.49$, $p < 0.05$) whereof Oligotrichia were negatively correlated with nitrite (ρ= -0.59, $p < 0.05$). For Arthropoda the correlation was negative with nitrate (ρ= -0.58, $p < 0.05$) and nitrite (ρ= -0.58, $p < 0.05$).

At OFF, the Spearman rank correlation for total microzooplankton was positive with ammonium (ρ =0.53, $p < 0.05$). For Amoebozoa a negative correlation with salinity was observed (ρ= -0.64, $p < 0.05$) while Oligotrichia and Arthropoda showed positive correlations with ammonium (ρ= 0.59, $p < 0.05$ and ρ= 0.58, $p < 0.05$ respectively).

Discussion

Water column hydrography, chlorophyll and nutrient conditions

The hydrography of the Arabian Sea is strongly influenced by the prevailing wind systems in the Indian Ocean. During the NEM period in winter, upwelling and convective mixing occur thus leading to changes in the nutrient, temperature and salinity regime, especially in coastal regions of the Arabian Sea like the SoO. During the SWM in summer, meso-to oligotrophic conditions and temperatures >30°C occur (Piontkovski et al., 2011). However, coastal upwelling caused by the SWM can lead to an intrusion of cool water into the upper water column in the SoO leading to an abrupt decline in sea surface temperature (<25°C) and a strong thermohaline stratification (Al-Azri et al., 2010). This causes more stable conditions for phytoplankton to grow thus in turn stimulating secondary production such as micro- and mesozooplankton. During the present seasonal study, the two stations OFF and BK in the SoO showed distinct nutrient, salinity and temperature patterns throughout the year with an abrupt decline in temperature, salinity and silicate concentrations at the beginning of the SWM period 2010. The drop in silicate concentrations points at a heavy uptake of silicate by primary producers thus pointing at a dominance of diatoms during the SWM period which is in line with observations from 2004-2006 (Al-Azri et al., 2010) and reflect the typical pattern of SWM summer conditions. In contrast, autotroph and heterotroph standing stocks usually remain low during the calm, oligotrophic inter-monsoon periods in autumn and spring. Only with the start of the NEM monsoon period in winter, the water column gets mixed again as a result from north-easterly winds (Burkill et al., 1993). Similar to the SWM period, coastal upwelling promotes a decrease in temperature and salinity while nutrient conditions increase thus stimulating autotroph productions.

Monsoon-derived changes in the wind regime thus affect the hydrography of the SoO considerably. This results in seasonal upwelling at the coastal zones of Oman thus leading to nutrient inputs to the uppermost water column. The high nutrient availability stimulates autotrophic productions in the surface waters thus leading to high chlorophyll *a* concentrations, a proxy used for biomass estimates of autotrophs. In this study, chlorophyll *a* concentrations reached a maximum both during SWM and NEM periods. In general, total chlorophyll *a* at the OFF station where lower than at BK. At BK, chlorophyll *a* peaks where almost twice as high during the SWM period as during the NEM period. At OFF, chlorophyll *a* reached similar concentrations during SWM and NEM periods. Phytoplankton communities at both stations were dominated by dinoflagellates throughout 2010/2011 and diversity was generally high both at BK and OFF (Al-Hashmi et al., 2014). During SWM, nutrient concentration in the water column showed similar concentrations at BK and OFF and the dinoflagellate community was dominated by *Prorocentrum miniumum* reaching similar abundances at both stations. However, other dinoflagellate species (e.g. *Gynnodinium* spp., *Scripsiella trochoidea*) showed higher cell numbers at BK when compared to OFF. Thus, higher chlorophyll *a* concentrations at BK during the SWM period resulted most likely from higher total dinoflagellate abundances at BK during the SWM period in 2010. In addition, copepods showed higher abundances at OFF during the SWM 2010 (Piontkovski et al., 2013) thus pointing at a strong top-down control of the phytoplankton standing stocks by copepods at OFF compared to BK. During the NEM, both stations showed similar peak heights for chlorophyll *a* although the phytoplankton community at BK was dominated by diatoms during that seasons while at OFF the community comprised mainly of dinoflagellates (Al-Hashmi et al., 2014).

Microzooplankton responses to phytoplankton standing stocks

MZP biomass at BK and OFF showed distinct seasonality patterns with several peaks throughout the year 2010/2011. MZP are considered as important grazers of phytoplankton standing stocks and there is strong evidence that MZP can be considered as primary grazers of phytoplankton consuming up to 60% of primary production per day (Calbet, 2008). In this study, highest phytoplankton standing stocks (indicated by high chlorophyll *a* concentrations) were observed when lowest MZP biomass occurred. This points at a strong predator-prey interactions between phytoplankton and MZP and a strong top-down control of phytoplankton standing stocks by MZP. Periods of less intense MZP grazing might open a 'loophole' sensu Irigoien et al. (2005) thus promoting intense phytoplankton blooms in the SoO due to a release from MZP grazing pressure (Irigoien et al., 2005). Nevertheless, the initiation of phytoplankton blooms is not solely governed by top-down control mechanisms but are rather dependent on bottom-up processes. The negative relationship between specific MZP groups and water-column nutrient concentrations provide thus a clear indication for strong bottom-up mechanisms that determine the onset and the intensity of phytoplankton blooms in the SoO.

Compared to other Indian Ocean studies, MZP biomass in the SoO was high with an average biomass ranging between 69-123 µg C l^{-1} during the sampling year. The high total MZP biomass (excluding *Noctiluca* sp. and Amoebozoa) is considered to be linked to the high productivity in the Northern Arabian Sea compared to the southern regions (Dennett et al., 1999). High MZP biomass in this study can mainly be attributed to high copepod nauplii and larvacean biomass, a pattern also described for the Southern Indian Ocean (Jaspers et al., 2009) and other tropical regions (Hopcroft et al., 1998). This is in contrast to a study by Gowing et al (2003) where microplankton was analysed from mesopelagic zones (250 to 1100 m water depth) during four seasons in the Arabian Sea, off the coast of Oman (Gowing et al., 2003). In this study, microzooplankton assemblages (20-200 µm) were dominated by protozoa and metazoan microplankton contributed only to low shares. The total mean microplankton biomass during the different seasons was <0.07 µg C l^{-1} and thus considerably lower compared to the present data from microzooplankton biomass in the upper water column in the SoO. This points at considerably different microzooplankton assemblages in the upper water column of the Arabian Sea when compared to mesopelagic zones and is in line with observations by Jónasdóttir et al. from the Southern Indian Ocean were peak nauplii abundances where found in the uppermost 100 m of the water column (Jonasdottir et al., 2013).

The ciliate biomass we reported, was similar to that published by Jonasdottir et al. (Jonasdottir et al., 2013) for the southern Indian Ocean during the Fall Intermonsoon season. However, the tintinnid biomass at the BK and OFF stations was considerably higher than that for the southern Indian Ocean regions. However, the actual biomass of ciliates might have been underestimated in the pre3sent study since reverse filtration was used during the sampling process which might have caused a bias in the biomass estimates of delicate, aloricate ciliate species (Gifford and Caron, 2000; Gowing et al., 2003).

Larvaceans are considered as important grazers in low latitude regions consuming up to 40% of the autotroph biomass per day while copepods account only for ~20% of the grazing (Jonasdottir et al., 2013). In this study, we did not find clear relationships between chlorophyll concentrations and copepod nauplii and larvaecean abundances. This is in line with previous studies in the Indian Ocean where no relationship between larvacean biomass and food availability was found (Hopcroft and Roff, 1998; Jaspers et al., 2009). So far, larvacean population dynamics seem to be rather top-down than bottom-up controlled. A negative coupling between copepods and larvaceans as described previously (Lopez-Urrutia et al., 2003; Sommer et al., 2003)could not be confirmed here.

Conclusions

Distinct seasonal changes in plankton community composition where observed during a one-year field sampling campaign in the Sea of Oman (SoO). Phytoplankton and microzooplankton standing stocks showed distinct responses to changes in environmental condition. This was especially true for South-West monsoon (SWM) and North-East Monsoon (NEM) periods when a strong coupling between phytoplankton and microzooplankton was observed. The initiation of phytoplankton blooms in the SoO was bottom-up controlled due to strong seasonal nutrient influx during SWM- and NEM-induced upwelling events. The interplay between bottom-up controlled primary production and top-down control mechanisms regulated the phenology patterns of specific microzooplankton groups in the SoO thus pointing at complex trophodynamic interactions at the lowermost food-web level in this low-latitude ecosystem.

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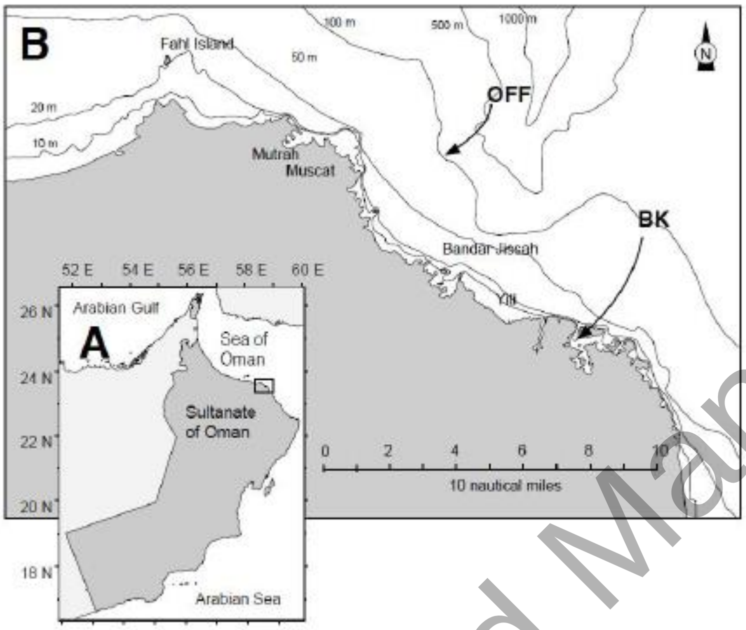
Fig. 1



Sampling sites (from Al-Hashmi et al., 2014).

Fig. 2

Surface water chlorophyll *a* (mg m^{-3}, grey areas) and nutrients at BK (a+c) and OFF (b+d). a+b: temperature, salinity), c+d: nitrogen compounds (NOx), PO4 and silicate taken from samples at 1m depth. Black circles: temperature, white circles: salinity, grey squares: silicate, white triangles: NOx, black diamonds: PO4. Vertical boxes illustrate periods of the SW monsoon (SWM) and the NE monsoon (NEM).

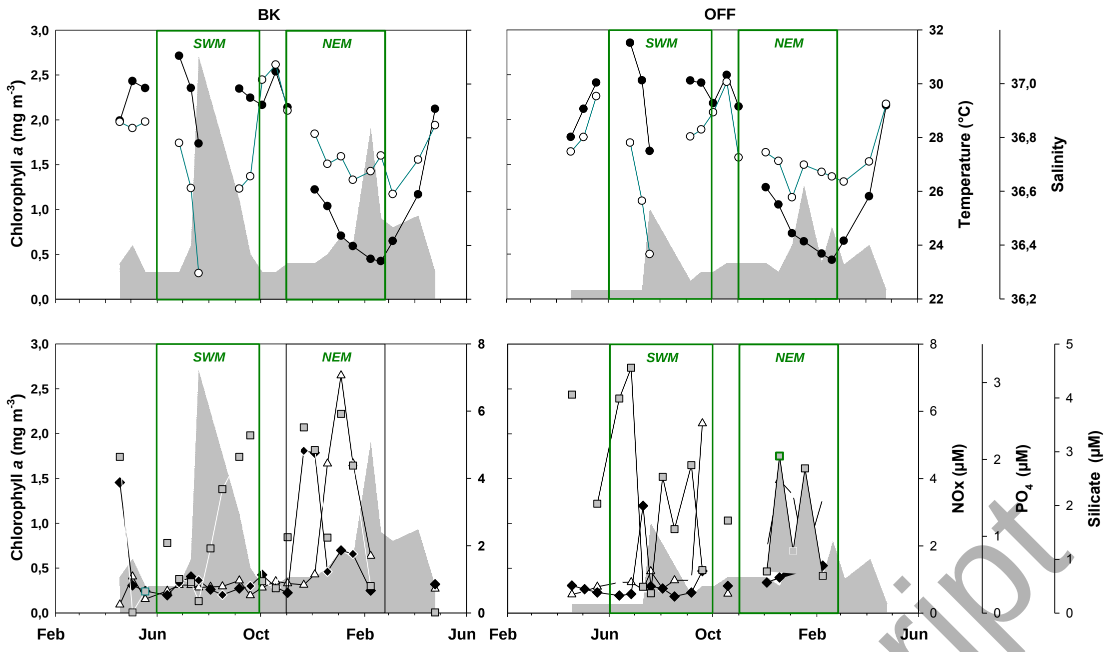


Fig. 3

Total microzooplankton (MZP) biomass (µg C l^{-1}) (excluding *Noctiluca* sp. and Amoebozoa) in relation to chlorophyll *a* (mg m^{-3}, black lines) at the inshore station Bandar Al-Khyran (BK) at 1 m (3A) and 10 m water depth (3B) and at the offshore-station (OFF) at 1m (3C) and 20 m water depth (3D). Vertical boxes illustrate periods of the SW monsoon (SWM) and the NE monsoon (NEM).

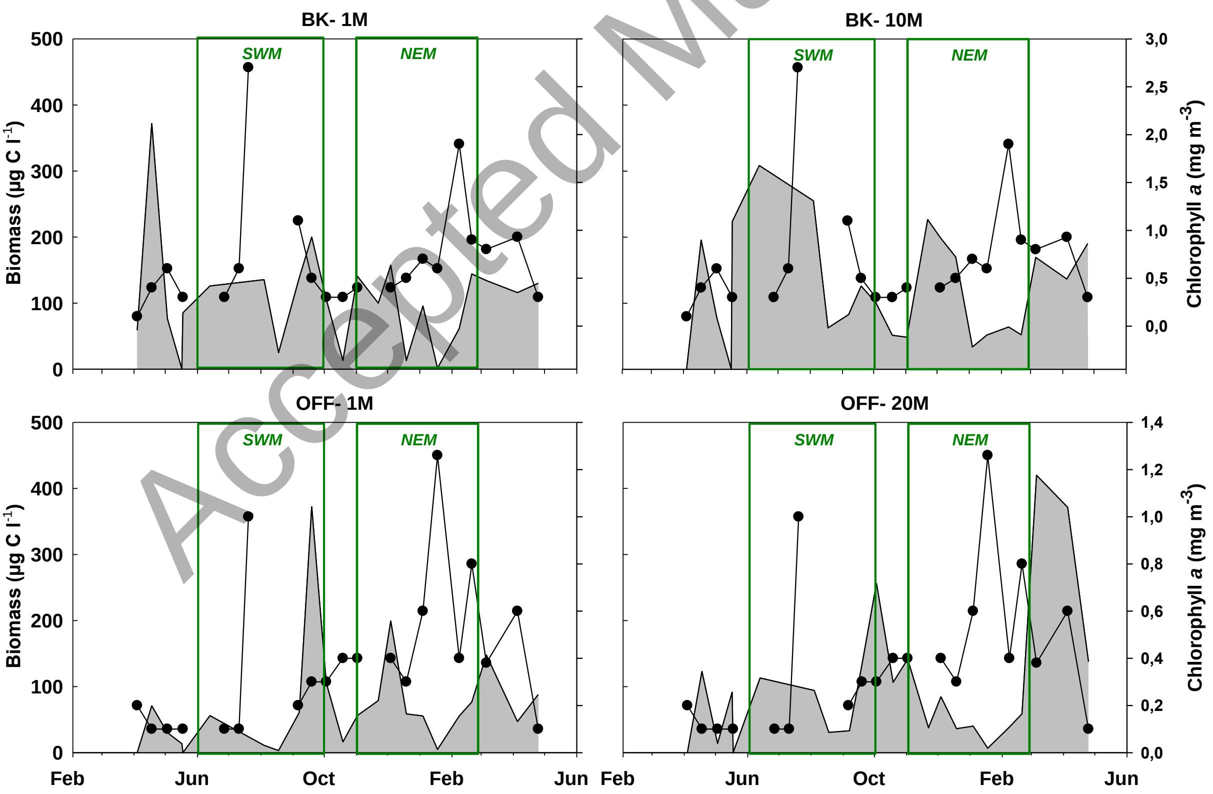


Fig. 4. Biomass (µg C l^{-1}) of *Noctiluca* sp. (black areas) and Amoebozoa (grey areas) at the inshore station Bandar Al-Khyran (BK) at 1m (4A) and 10 m water depth (4B) and at the offshore-station (OFF) at 1m (4C) and 20 m water depth (4D). Vertical boxes illustrate periods of the SW monsoon (SWM) and the NE monsoon (NEM).

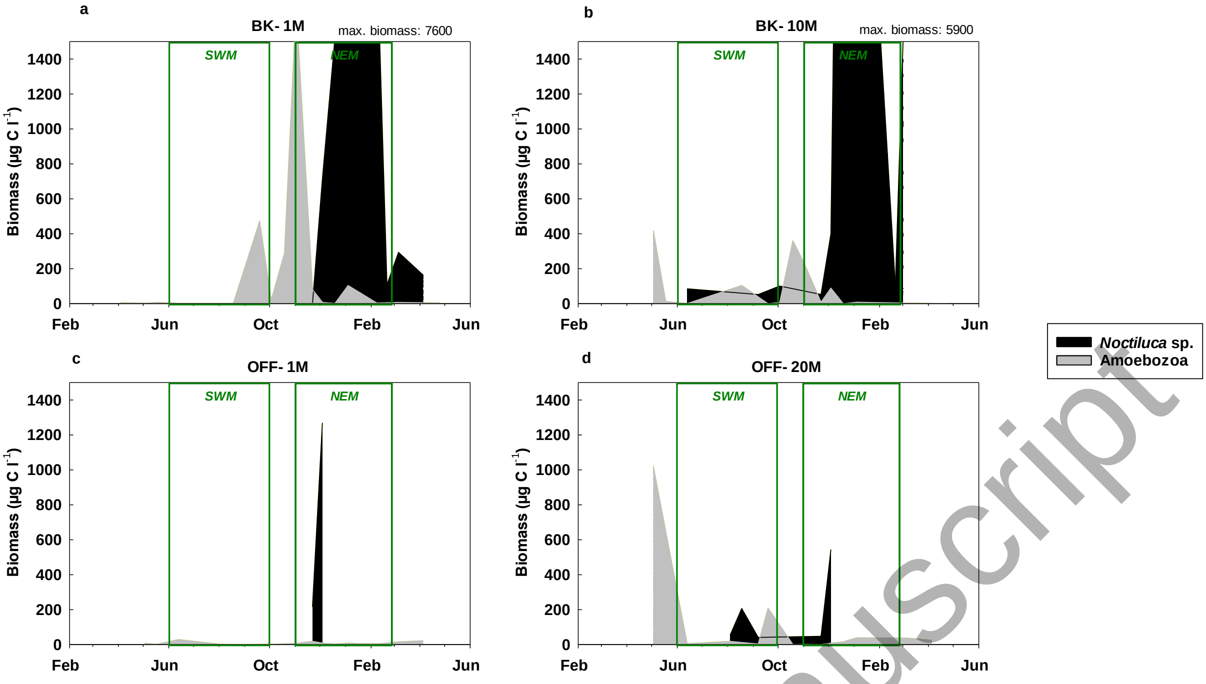


Fig. 5

Biomass (µg C l^{-1}) of Copepoda (nauplii) (black areas) and Larvacea (class Appendicularia) (grey areas) at the inshore station Bandar Al-Khyran (BK) at 1m (5A) and 10 m water depth (5B) and at the offshore-station (OFF) at 1m (5C) and 20 m water depth (5D). Vertical boxes illustrate periods of the SW monsoon (SWM) and the NE monsoon (NEM).

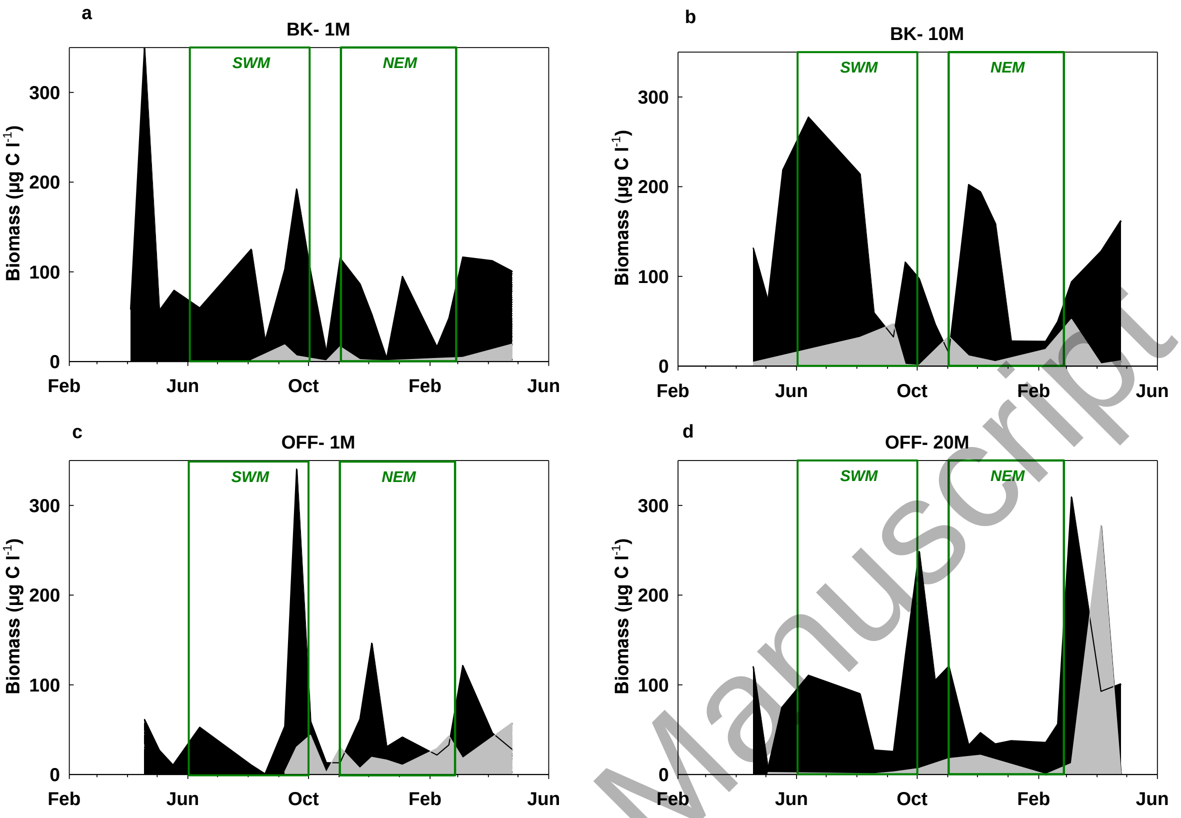


Fig. 6

Biomass (µg C l^{-1}) of the two main groups of Ciliophora (black: Choreotrichia and grey: Oligotrichia) at the inshore station Bandar Al-Khyran (BK) at 1m (6A) and 10 m water depth (6B) and at the offshore-station (OFF) at 1m (6C) and 20 m water depth (6D). Vertical boxes illustrate periods of the SW monsoon (SWM) and the NE monsoon (NEM).