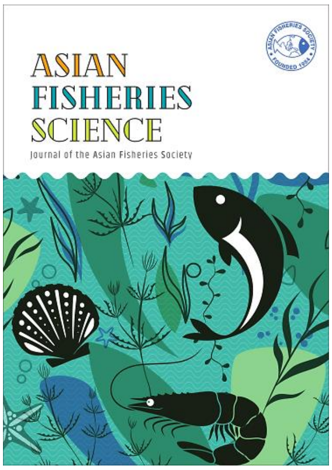

Abundance, Distribution and Species Composition of Cyclopoid Copepods Along a Transect Traversing the Upwelling Zone off Northern Zamboanga Peninsula, Philippines

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Abstract

The abundance, distribution and species composition of cyclopoids were studied in the largest sardine fishing ground in the Philippines during a coastal upwelling event in March 2014. Zooplankton samples were collected in six stations along a transect extending from the coast to about 50 km offshore in Dipolog Bay, Northern Zamboanga Peninsula, Mindanao. A 100 μm NORPAC net was hauled vertically to sample successive depth strata (0–65 m, 65–135 m, 135–200 m). Out of 28 zooplankton groups, cyclopoids made up 12.2 % of mean total zooplankton density. Forty-two cyclopoid species (overall mean density: 503.6 ind.m^{-3}) were identified, with *Oncaea clevei* Früchtl, 1923 (25.4 %) as the most abundant, followed by *Oncaea scottodicarloi* Heron and Bradford-Grieve, 1995 (13.6 %), *Triconia conifera* (Giesbrecht, 1891) (9.2 %), *Oncaea media* Giesbrecht, 1891 (7.2 %) and *Corycaeus dahli* Tanaka, 1957 (7.0 %). The higher abundance (732.9 ind.m^{-3}) of cyclopoids at 0–65 m than at 135–200 m (220.2 ind.m^{-3}) was attributed to the high abundance of phytoplankton in the upper euphotic zone. Cyclopoid density was highest in station 4 (938.3 ind.m^{-3}) at the margin of the upwelling zone. This is attributed to the time lag between phytoplankton and zooplankton build-up and the dispersive effects of wind-driven drift.

Keywords: zooplankton, *Oncaea*, Dipolog Bay

Introduction

Non-calanoid microcopepods specifically cyclopoids are among the more abundant and diverse groups of zooplankton in the pelagic community (Böttger-Schnack, 1987). Cyclopoid copepods are ecologically important but compared to other zooplankton, studies of their species composition and vertical distribution are rare due to their small size, subtle morphological characteristics, and underrepresentation in conventional plankton sampling nets using 0.3 mm mesh (Böttger-Schnack, 2001). The term "cyclopoids" is used to include both orders Cyclopoida and Poecilostomatoida, based on recent ordinal classification of the Copepoda (Boxshall and Halsey, 2004). They generally have shortened antennae, paired egg sacs and their anterior part is broader than the posterior part (Smith, 1977). Males are very similar to the females, except they are smaller, have more urosomal segments and possess geniculate antennae (Torke, 1976).

The coastal waters off the Zamboanga Peninsula in southwest Philippines exhibit seasonal upwelling driven by winds of the northeast monsoon (Villanoy et al., 2011) and support the largest sardine fishery in the country (Rola et al., 2018) dominated by the Bali sardine, *Sardinella lemuru* Bleeker, 1853. This species is the most common zooplanktivore in the area, generally preferring small to medium-sized zooplankton, particularly cyclopoids as prey. *Oncaea* species were preferred by late larvae and juvenile sardines with an Ivlev index of prey selectivity of 0.80 and 0.66, respectively— higher compared to other prey items (Metillo et al., 2018). Hence, knowing the abundance of cyclopoids in the area where sardines dominate may help us understand their significance to the production of sardines. This study aims to characterise the vertical and spatial patterns of abundance and species composition of cyclopoids during upwelling as it is essential in understanding the mechanisms by which physical and biological processes structure marine ecosystems.

Materials and Methods

Study area

Dipolog Bay is located on the northeastern coast of Zamboanga Peninsula. Zooplankton samples were collected from six stations along a transect extending from the coast to about 50 km offshore (Fig.1). Selection of sampling stations was part of an oceanographic survey conducted by the Department of Science and Technology-funded SarDyn Research Program on board the RV DA-BFAR in March 2014 (Campos et al., 2016).

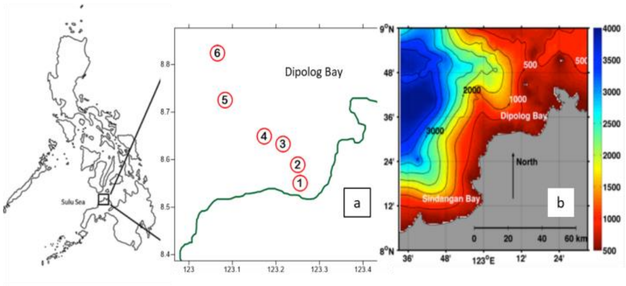

Fig. 1. Map of the study area (a) showing station locations in Dipolog Bay, northern Zamboanga Peninsula, Philippines and (b) with 9 km resolution bathymetry from GEBCO, updated 2010 (BODC, 2016).

Field sampling

Sampling was performed between 21:40–22:30 h at station 1 on 3 March 2014; between 03:00–20:00 h at four sampling stations (stations 2–5) on 4 March 2014; and at 01:10–01:50 h at station 6 on 5 March 2014. Zooplankton samples were collected using a paired North Pacific (NORPAC) net with a mouth diameter of 0.45 m, with 100 µm and 200 µm mesh net fitted to each ring, and equipped with a mechanical flow-meter. In each station, the net was hauled vertically to sample successive depth strata (0–65 m, 65–135 m, 135–200 m). The nets were set up on a series of 2 opening-closing double trip mechanism (1000DT Model, General Oceanics, Miami, USA) to sample discrete depth strata. The length of the towing cable and its angle of declination were used for the determination of the depth of the net. The volume of water filtered was computed by multiplying the vertical distance covered as measured by the flow-meter and the area of the net's mouth. Samples were preserved in 10 % formalin-filtered seawater solution buffered with borax. Physico-chemical parameters such as temperature, salinity, depth and chlorophyll *a* were measured at each sampling station using a CTD Profiler (SBE 911plus Model, SeaBird Scientific, Washington, USA) equipped with sensors taking continuous measurements from the surface to the designated depth and back. Physico-chemical data was provided by the Physical Oceanography Group of the University of the Philippines, Marine Science Institute (Villanoy et al., 2014).

Sample processing

Only the samples using the 100 µm net were used in this study. After determination of the displaced volume, samples were subsampled using a Folsom plankton splitter. Subsamples ranging from 1/2 to 1/16 of the original sample, depending on the displaced volume, were utilised for sorting.

Zooplankton were sorted out manually under a dissecting microscope (SMZ168 Series, Motic, Hong Kong). The sorted organisms from each of the samples were kept in their respective vials with 10% formalin solution. Zooplankton were identified into major taxonomic groups following the taxonomic descriptions of Smith (1977). A more detailed taxonomic analysis was then carried out for cyclopoids using the identification keys of Nishida (1985), Böttger-Schnack (2001), Boxshall and Halsey (2004), Japan Society for the Promotion of Science and Census of Marine Zooplankton: Census of Marine Life (2004), Richardson et al. (2013), and Razouls et al. (2005–2018).

Data analysis

Densities were computed as no. of individuals per cubic meter using this formula:

$$\text{Ind.m}^{-3} = \frac{Total\ count\ in\ sample}{Vol.\ of\ water\ filtered\ (m^3)}$$

Subsample raising factors (RF) were used to compute total counts in each sample. Cyclopoid counts from aliquots were further raised using RF2 below.

$$\text{RF1} = \frac{Sample\ displaced\ vol.\ (mL)}{Subsample\ vol.\ (mL)}$$

$$\text{RF2} = \frac{No.\ of\ cyclopoids\ in\ the\ subsample\ vol.}{No.\ of\ cyclopoids\ identified\ to\ spp.\ level}$$

Species Richness (*S'*) = number of species in a sample

Shannon-Wiener diversity (Shannon index of general diversity *H'*)

$$H' = -\sum_{i=1}^{s}\left(\frac{n_i}{N}\right) log\frac{n_i}{N}$$

where: n_i = importance of values for all species
N = total of importance values
S = total number of species in a sample

Surfer® 10 (Golden Software, LLC) was utilised to produce maps showing the density and distribution of cyclopoids in the study area.

For horizontal distribution, densities were integrated over the first two depth strata because the deepest layer in stations 4 and 5 (135–200 m) were excluded from the analysis because faulty preservation made the data unreliable.

One-way analysis of variance (ANOVA) was used to examine vertical (between depth strata) and horizontal (between stations) variation of cyclopoid density at $\alpha = 0.05$. Tukey's post hoc analysis was used to determine which samples differed from the other. Linear regression analysis was done to investigate the changes in abundance with depth. Possible relationships between cyclopoid density and physico-chemical parameters were analysed using stepwise multiple regression routine in SPSS v.16.

Results

Hydrography

Figure 2 shows the vertical distribution of temperature, salinity, and fluorescence (chlorophyll *a*) in Dipolog Bay, Zamboanga del Norte. Surface (0–65 m) temperatures ranged from 25.0 to 26.6 °C, whereas the temperature in the deepest layer of the water column ranged from 15.8 to 21.5 °C (Fig. 2a). The thermocline was much less steep in stations 2 and 3 due to upwelling-driven vertical mixing in the water column. The difference in temperature between these stations and the other stations, including station 1, started at about 75 m, just below the first sample stratum (0–65 m).

Chlorophyll *a* and fluorescence serve as an indicator of phytoplankton biomass. Surface (0–65 m) mean chlorophyll *a* levels ranged between 0.59 and 1.92 μg.L^{-1}, which were highest in station 3 and lowest in station 4 (Fig. 2b). High nutrient concentrations in the inshore most station (station 1) was likely due to terrestrial run-off while relatively high concentrations in stations 2 and 3 away from the coast are likely due to upwelling. In contrast, offshore stations (4, 5 and 6) had less chlorophyll *a*.

In terms of salinity, high values were observed in the surface layer (0–65 m) of offshore stations and in the deeper layers in all stations, whereas the lowest values were recorded only in inshore and surface layers (Fig. 2c). Stations 2 and 3 showed somewhat lower salinity from the surface to 200 m depth, consistent with vertical mixing from upwelling. The zone of upwelling is thus between stations 1 and 4.

Zooplankton taxonomic composition

A total of 28 major groups of zooplankton were identified from the samples, with copepods (92.3 %) dominating the entire assemblage. Suborder Cyclopoida was the second most abundant group, comprising 12.2 % of all zooplankton collected (Fig. 3). The other major groups observed were copepod nauplii (4.6 %), Harpacticoida (3.3 %) and Larvacea or Appendicularia (2.2 %). The remaining 5.5 % was comprised of Euphausiacea, Foraminifera, Thaliacea, Ostracoda, Polychaeta, Chaetognatha, Hydromedusae, Decapoda, Tintinnid, Siphonophora and others.

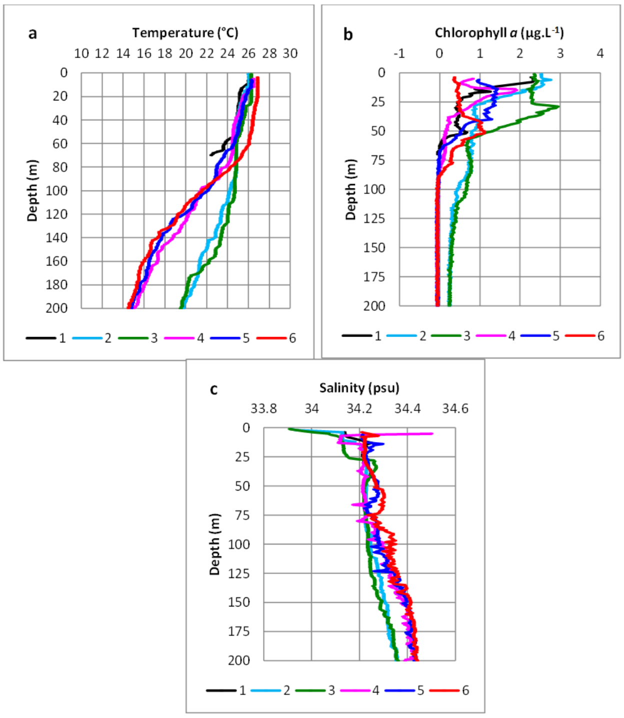

Fig. 2. Vertical profiles of (a) temperature, (b) chlorophyll *a* and (c) salinity in the six stations surveyed in Dipolog Bay, Zamboanga del Norte (Villanoy et al., 2014). Profiles with black, light blue, green, pink, blue and red lines represent Station 1, 2, 3, 4, 5 and 6, respectively.

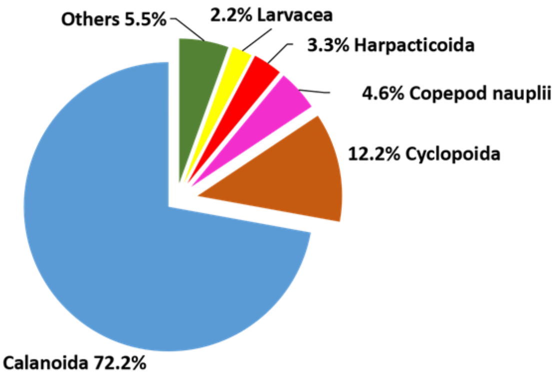

Fig. 3. Overall taxonomic composition (%) of zooplankton in Dipolog Bay, Zamboanga del Norte from surveys conducted in March 2014.

Cyclopoid composition and abundance

Out of 4,047 specimens of cyclopoids examined, a total of 42 species were identified (Table 1). Overall cyclopoid species richness ranged from 26 to 34, with

Table 1. Cyclopoid species densities (ind.m^{-3}) by station and percentage abundances in Dipolog Bay, Northern Zamboanga del Norte in March, 2014. Percentage abundance values of the top 10 cyclopoid species are in boldface. Juveniles are not included since they were only identified to genus level.

	Station						Overall mean density	%
	1	2	3	4	5	6		
Family Oncaidae								
Genus *Oncaea*								
Oncaea clevei Früchtl, 1923	55.5	49.5	166.7	195.8	52.3	46.7	94.4	**25.4**
Oncaea paraclevei Böttger-Schnack, 2001	3.6	1.7	22.3	19.5	4.4	4.7	9.4	2.5
Oncaea media Giesbrecht, 1891	35.3	4.3	12.0	30.6	30.6	48.0	26.8	**7.2**
Oncaea scottodicarloi Heron & Bradford-Grieve, 1995	10.2	19.8	67.3	147.7	31.5	26.7	50.5	**13.6**
Oncaea mediterranea (Claus, 1863)	33.9	13.5	11.4	30.6	14.0	4.9	18.0	**4.9**
Oncaea ovalis Shmeleva, 1966	0.3	1.6	3.2	5.8	4.4		2.5	0.7
Oncaea ornata Giesbrecht, 1891	0.4	6.0	22.0	41.8	21.0	6.5	16.3	**4.4**
Oncaea venusta Philippi, 1843						1.2	0.2	0.1
Genus *Triconia*								
Triconia conifera (Giesbrecht, 1891)	48.2	25.2	24.7	12.4	47.2	47.1	34.1	**9.2**
Triconia dentipes (Giesbrecht, 1891)	3.8	14.9	2.8	14.5	5.3	5.8	7.9	2.1
Family Oithonidae								
Genus *Oithona*								
Oithona simplex Farran, 1913	4.6	8.9	5.3	8.3	9.5	2.1	6.5	1.7
Oithona rigida Giesbrecht, 1896	7.8	0.5	7.3	6.0	3.1		4.1	1.1
Oithona attenuata Farran, 1913	2.7	4.1	1.3	0.8	6.0	2.4	2.9	0.8
Oithona setigera (Dana, 1849)	5.3	9.9	6.3	4.7	6.7	12.1	7.5	2.0
Oithona nana Giesbrecht, 1893	32.4	2.5	9.7	3.0	5.3	9.9	10.5	**2.8**
Oithona brevicornis Giesbrecht, 1891	3.5	2.3					1.0	0.3
Oithona decipiens Farran, 1913	16.6	7.2	3.8	14.7	2.9	22.2	11.2	**3.0**
Oithona fallax Farran, 1913	3.1	2.3	4.7	3.6	1.3	0.5	2.6	0.7
Oithona tenuis Rosendorn, 1917	1.6	2.2	0.8	1.4	5.3	1.5	2.1	0.6
Oithona plumifera Baird, 1843	1.3	4.8	3.2	6.6	4.4	4.0	4.1	1.1
Oithona sp. 1	2.9		1.0	9.4	4.5	3.1	3.5	0.9
Family Corycaeidae								
Genus *Corycaeus*								
Corycaeus dahli Tanaka, 1957	12.2	5.4	19.2	60.3	24.4	35.1	26.1	**7.0**
Ditrichocorycaeus asiaticus (Dahl F., 1894)		0.1	0.8			0.8	0.3	0.1
Corycaeus speciosus Dana, 1849						1.2	0.2	0.1
Urocorycaeus longistylis (Dana, 1849)					1.6	1.3	0.5	0.1
Ditrichocorycaeus andrewsi (Farran, 1911)						2.0	0.3	0.1
Onchocorycaeus pacificus (Dahl F., 1894)			0.8	1.4	1.6	2.8	1.1	0.3
Ditrichocorycaeus tenuis (Giesbrecht, 1891)	2.6		0.8			2.1	0.9	0.3
Corycaeus clausi F. Dahl 1894		0.5	0.5	8.9	2.7		2.1	0.6
Agetus limbatus (Brady, 1883)			0.5				0.1	0.0
Corycaeus sp. 6	2.0		1.7		10.4	0.8	2.5	0.7
Corycaeus erythraeus Cleve, 1904	1.3					5.8	1.2	0.3
Urocorycaeus lautus (Dana, 1849)				1.4		0.5	0.3	0.1
Corycaeus sp. 1	0.3		1.7		5.5	1.0	1.4	0.4
Corycaeus sp. 2			0.8			5.6	1.1	0.3
Corycaeus sp. 3	3.4	0.1	3.5	24.8	14.9	10.1	9.5	**2.6**
Corycaeus sp. 4	0.7		0.3				0.2	0.0
Corycaeus sp. 5		0.1	0.3				0.1	0.0
Genus *Farranula*								
Farranula curta (Farran, 1911)		0.1	2.3	16.0			3.1	0.8
Farranula gracilis (Dana, 1849)	0.3			1.6	3.1	2.0	1.2	0.3
Farranula rostrata (Claus, 1863)		0.1	1.7	1.4	2.7	3.8	1.6	0.4
Farranula gibbula (Giesbrecht, 1891)				2.9		5.0	1.3	0.4
Juvenile *Oncaea*	10.4	15.7	66.1	167.7	66.0	47.6		
Juvenile *Corycaeus*	5.4	1.0	6.8	14.5	37.5	9.5		
Juvenile *Oithona*	2.9	0.4	4.6	6.3	7.1	1.3		
Juvenile *Triconia*	6.4	14.8	27.6	42.2	18.6	27.1		
SUM	321.0	219.7	515.9	906.8	455.6	415.0	371.1	100.0
H' (Shannon-Wiener Diversity index)	2.7	2.7	2.5	2.6	2.9	2.9		
Number of species	28	26	33	28	28	34	42	

station 6 showing the highest and station 2 the lowest. Station 3 had the second highest species richness with 33 cyclopoids whereas the rest of the stations (stations 1, 4 and 5) recorded 28 cyclopoid species each. This is consistent with Shannon-Wiener diversity index which was highest ($H' = 2.9$) in offshore stations (stations 5 and 6) and the lowest ($H' = 2.5$) in station 2. The overall mean density of cyclopoids across all stations including juveniles was 503.6 ind.m^{-3} (SD = 170.35). The top 10 species made up 80 % of the assemblage with six belonging to genus *Oncaea*. *Oncaea clevei* Früchtl, 1923 was the most abundant (25.4 %), followed by *Oncaea scottodicarloi* Heron and Bradford-Grieve, 1995 (13.6 %), *Triconia conifera* (Giesbrecht, 1891) (9.2 %), *Oncaea media* Giesbrecht, 1891 (7.2 %) and *Corycaeus dahli* Tanaka, 1957 (7.0 %), respectively.

Cyclopoid vertical distribution

Total abundance of marine cyclopoids was generally highest in the upper layer of the water column and decreased with increasing depth (Fig. 4). Near surface water showed the highest mean density with 732.9 ind.m^{-3} (SD = 360.5), followed by the midlayer with 393.5 ind.m^{-3} (SD = 221.7) and the lowest was found in the deepest layer with 220.2 ind.m^{-3} (SD = 72.8).

One-way ANOVA showed a significant difference in mean density across depths ($P < 0.03$). A Tukey's post hoc analysis revealed that cyclopoid density was significantly higher at 0–65 m depth strata compared to 65–135 m and 135–200 m depth strata. There was no significant difference among stations. The stepwise multiple regression showed only depth as among the factors determining cyclopoid density. The regression model was significant ($F = 8.647$, $P = 0.012$, $r^2 = 0.419$). The inverse relationship between depth and density ($r = -0.647$) is consistent with the results of ANOVA.

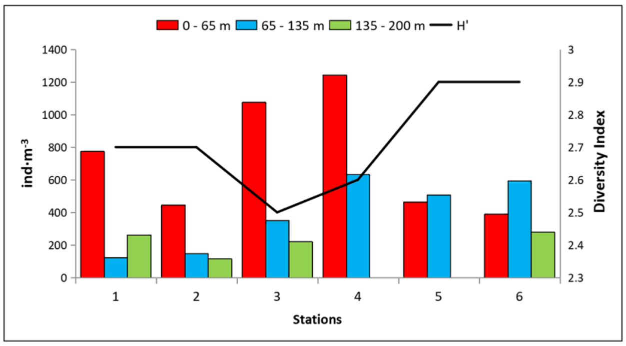

Fig. 4. Comparison of cyclopoid overall mean density (ind.m^{-3}) by depth layer and Shannon-Wiener diversity index in Dipolog Bay, Zamboanga del Norte, Philippines in March 2014.

Cyclopoid horizontal distribution

The distribution of cyclopoids along the transect corresponded roughly with that of the upwelling. Mean cyclopoid density in station 2 (297.2 ind.m^{-3}), within the upwelling zone, was notably low compared to those in other stations (Fig. 5). It was almost four times lower than in station 4, which yielded the highest mean density (938.3 ind.m^{-3}). However, station 3, which is also within the upwelling zone, had the second highest cyclopoid density (713.66 ind.m^{-3}). The inshore stations, including station 1 (449.21 ind.m^{-3}), had lower mean densities compared to the offshore stations.

Oncaea clevei was dominant only in stations 2 and 3 (Fig. 5). In all other stations inshore or offshore of the upwelling zone, the abundance of *O. clevei* was similar to one or two other species such as *T. conifera* and *O. media* in stations 1 and 6, and with *O. scottodicarloi* only in station 4. The lowest level of dominance was in station 1 and in stations 5 and 6, the offshore most stations, whereas the highest was in stations 2 to 4, within the upwelling zone.

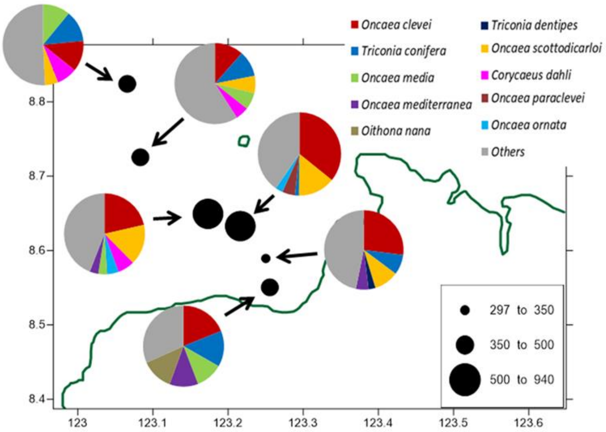

Fig. 5. Map showing the horizontal distribution of cyclopoid density (ind.m^{-3}) in Dipolog Bay, Zamboanga del Norte. Densities are integrated over the first two depth strata. The pie charts refer to the top five species in each station.

Discussion

Based on CTD profiles during the transect survey, upwelling was most extensive at stations 2 and 3, about 15 to 20 km away from the coast. The weaker thermocline at deeper water (Fig. 2a), the elevated chlorophyll *a* above 50 m (Fig. 2b) and the difference in salinity from 80 m below (Fig. 2c) observed in stations 2 and 3 are the indicators of upwelling. Vertical mixing occurs when high saline, cold and nutrient rich water from the deep rises towards the surface and displaces as well as mixes with the warmer surface water (Villanoy et al., 2011). This reduces the temperature difference between the surface and deep water layers, making the thermocline less evident.

Another indicator of upwelling is the elevated chlorophyll *a* which signals high productivity of the area (Villanoy et al., 2011). Chlorophyll *a* is the dominant pigment found in marine phytoplankton such as diatoms and dinoflagellates. They provide food for a wide range of marine organisms, especially the zooplankton. Stations 2 and 3 exhibited high fluorescence values in the upper 50 m of the water column, consistent with upwelling.

The present study recorded a total of 42 adult cyclopoid copepod species belonging to three families (Table 1). This number is lower compared to reports from the Central Red Sea (Böttger-Schnack, 1988) with 45 cyclopoid species recorded. Both studies used 100 µm mesh size and vertical tows. However, in the Red Sea, samples were taken from depths of up to 450 m while in the present study samples were only collected from depths of up to 200 m. The number of samples or stations surveyed will also affect species richness estimates. This may explain the slightly higher diversity in the former. Melo et al. (2014) recorded only 12 cyclopoid species using 300 µm mesh size net, off the northeast coast of Brazil. This result may due to the bias produced in the collection using coarse nets.

Oncaea species found in this study are generally similar to those species found in other tropical areas. Three out of the five top cyclopoid species in this study (*O. clevei*; *O. scottodicarloi*; and *O. media*) (Table 1) belong to genus *Oncaea* which accounted for 6.9 % of the total copepod population. The results on *Oncaea* abundance are in close agreement with those reported by Rezai et al. (2004) in which *O. clevei* and *O. media* were also two of the most common species, contributing about 11.7 % of the total copepod population on average for all cruises in the Strait of Malacca. Possibly, this trend can be attributed to their salinity and temperature that are almost at similar range.

Interestingly, the observed distributions of *Oithona* are consistent with the groupings of Nishida (1985). For example, *Oithona brevicornis* Giesbrecht, 1891, categorised as an inlet species found in embayment waters, was only found in inshore stations (stations 1 and 2). Most of the oithonids recorded in the present study were most abundant in the inshore station as well (Table 1; Fig. 3), including *Oithona nana* Giesbrecht, 1893 which is somehow expected as this species is considered as a tolerant, opportunistic and widely adapted species (Nishida, 1985) occurring in sea ports, near urban wastes and in brackish water (Richard and Jamet, 2001).

The various *Corycaeus* species were more abundant and diverse in offshore stations than in inshore stations (Table 1; Fig. 3). Most corycaeid copepods recorded in this study were rare, except for *C. dahli*, which were found in relatively high numbers. This agrees well with findings in the Northern Taiwan Strait, which recorded only 10 species of corycaeids including two *Farranula* species. However, the occurrence of each species was not frequent (Hsieh et al., 2004). The epipelagic *C. dahli* is also one of the top species in Taiwan Strait, contributing 2.79 % and 3.83 % of the total relative abundance of copepods collected from the West and East Strait, respectively (Hsieh and Chiu, 2002). *Corycaeus* are generally carnivorous with many reported as ingesting nauplii, copepodites and adults of other copepods (Turner, 1986). This suggests that these carnivorous cyclopoids can survive even in areas with low chlorophyll concentrations in offshore stations.

The overall trend of decreasing mean density of cyclopoids with depth (Fig. 4) is consistent with the overall decrease in phytoplankton or chlorophyll *a* concentration (Fig. 2b), which is primarily a function of light and is typical of most oceans. In the Strait of Malacca, for instance, zooplankton biomass is highest in the surface and decreases with depth (Rezai et al., 2011). Most zooplankton are concentrated in the uppermost layer because conditions are most favourable in the surface layer.

Zooplankton typically disperse at night, ascending towards the surface, but descend during the daytime when they are concentrated in deeper waters. However, this diel vertical migration is sometimes variable (Bayly, 1986). Most of the stations were sampled during dark except stations 3 and 4 (8:00–14:00). However, these two stations had higher zooplankton density in the surface (0–65 m) layer than the other stations (Fig. 4) suggesting that zooplankton in these two stations were abundant and do not seem to be affected by diel vertical migration. Finer scale investigations may reveal the influence of diel vertical migration.

In the present study, the highest cyclopoid densities did not completely overlap with the upwelling area. Other studies have documented a similar situation. In the Northern Taiwan Strait upwelling area, high zooplankton abundance did not always correspond with high chlorophyll *a* concentrations (Shih and Chiu, 1998). According to Kämpf and Chapman (2016) one of the reasons for the lack of correspondence between phytoplankton and zooplankton abundance in an upwelling area is due to eddies, the movements of water which disperse heat anomalies, organic matter, fish larvae and zooplankton from the upwelling center to the offshore. Primary production is in its fastest rate when wind stress is relaxed and the water column is stabilised, because it allows nutrients to accumulate and permits phytoplankton to utilise nutrients brought to the surface during periods of high intensity winds (Peterson and Miller, 1977; Lalli and Parson, 1993). Usually, the phytoplankton population responds rapidly to increased nutrients, whereas the biological response of zooplankton is slower. The increase in zooplankton density in response to phytoplankton build-up can be seen in the margins of upwelling zones because of the drift that disperses them offshore (Villanoy et al., 2014). This may be the reason why cyclopoids in the present study were more concentrated in station 4 on the margin of the upwelling zone.

Small-sized copepods, particularly the cyclopoid genera *Oithona*, *Oncaea* and *Corycaeus*, and Calanoid families Clausocalanidae and Paracalanidae are abundant in subtropical-tropical regions and may represent more than 50 % of the total number of copepods (Böttjer et al., 2010). In this study, cyclopoids made up 12.2 % of total copepod abundance, next to calanoids with 72.2%. All the cyclopoid species found in the present study have been reported in other tropical-subtropical waters (Razouls et al., 2005–2018). They have also been reported to be conspicuous in zooplankton communities in upwelling zones (Hidalgo et al., 2010). Among the characteristics of cyclopoids that allow population stability and widespread distribution in the ocean are their effective feeding strategy (low rates of feeding), adaptability to scarce food conditions by reducing their energy consumption (low rates of growth and reproduction), and consequently, low rates of mortality (Paffenhöfer, 1993; Gallienne and Robin, 2001). These characteristics allow them to thrive and survive even in unstable areas such as in the upwelling zone. Furthermore, upwelling areas in the world are known to be important fishing grounds of sardines which prefer small-sized zooplankton (Ganias, 2014).

Previous studies in the area show that juvenile and adult sardines are generally located in waters within 15-km from the coast of northern Zamboanga Peninsula where sardine fishing operations were also concentrated (Willette et al., 2011; Villanoy et al., 2014). It can be hypothesised that the low density of cyclopoids in stations 1 and 2 (Fig. 4), despite high chlorophyll *a* concentrations (Fig. 2b), may be caused by sardine predation. This is consistent with the study of Metillo et al. (2018) who reported that sardine larvae and juveniles in inshore stations prefer small-sized cyclopoids such as oncaeids as prey.

Cyclopoids abundance and composition directly influence feeding of sardines and indirectly affects their fisheries through influencing growth, survival and recruitment. Off the coast of Peru, the shift in zooplankton diversity towards smaller-sized copepods, such as *Oncaea* and *Oithona* is favourable to sardines, particularly in El Niño events (Lehodey et al., 2006). Off northern Zamboanga, sardine catches are also highest during El Niño years (Villanoy et al., 2011). Thus, knowledge on cyclopoid assemblages, not only the presence or absence of specific species but also their relative abundance between water masses with which they are associated, provide insight and comprehensive understanding of oceanic ecosystem dynamics and the functioning of an epipelagic copepod community. The results of the present study are significant as they are linked to the local sardine fishery and will be useful for further studies.

Conclusion

This study provided a thorough identification of cyclopoid species in relation to their spatial and vertical distribution in the northern Zamboanga upwelling region during the northeast monsoon. Cyclopoid species composition was dominated by the genus *Oncaea* (58.1 %), oithonids were common in inshore stations while corycaeids were common in offshore stations. Depth and its influence on light and consequently on phytoplankton production, are important factors determining cyclopoid density. The concentration of cyclopoids was highest in the offshore margin of the upwelling zone (station 4) consistent with drift and the time lag between phytoplankton production in the upwelling zone and zooplankton build-up.

The key role played by cyclopoids in the coastal waters of the Sulu Sea needs further ecological studies on sampling deeper strata and spatio-temporal aspects to further account for their distribution, feeding behaviour and reproductive patterns that would further enhance our understanding about them.

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References

Bayly, I.A.E. 1986. Aspects of diel vertical migration in zooplankton, and its enigma variations. In: Limnology in Australia, DeDeckker P., Williams, W.D. (Eds.) Commonwealth Scientific and Industrial Research Organization, Melbourne. pp. 349–268. https://doi.org/10.1007/978-94-009-4820-4_22

BODC. 2016. GEBCO general bathymetric chart of the oceans. http://www.gebco.net/data_and_products/gridded_bathymetry_data/gebco_30_second_grid/ (Accessed 01 March 2016).

Böttger-Schnack, R. 1987. The vertical distribution of micro-and small mesozooplankton in the central Red Sea. Biological Oceanography 4:383–402.

Böttger-Schnack, R. 1988. Observations on the taxonomic composition and vertical distribution of cyclopoid copepods in the central Red Sea. Hydrobiologia 47:311–318. https://doi.org/10.1007/978-94-009-3103-9_31

Böttger-Schnack, R. 2001. Taxonomy of Oncaeidae (Copepoda: Poecilostomatoida) from the Red Sea. II. Seven species of *Oncaea* s. str. Bulletin of the Natural History Museum London (Zoology) 67:25–84.

Böttjer, D., Morales, C.E., Ultrich, B. 2010. Trophic role of small cyclopoid copepod nauplii in the microbial food web: a case study in the coastal upwelling system off central Chile. Marine Biology 157:689–705. https://doi.org/10.1007/s00227-009-1353-4

Boxshall, G., Halsey, S. 2004. An introduction to copepod diversity. The Ray Society, London. Vol 166. 421 pp.

Campos, W.L., Acabado, C.S., Metillo, E.B., Naguit, M.R.A., Bagarinao, A.A., Almaquer, C.J., Felix, L.R., Piloton, D.R. 2016. Development of robust tools for managing sardine fisheries in the Philippines: Zamboanga Upwelling-Bohol Sea System: 3. Estimating early life stage mortality and sources of recruits. Terminal report submitted to DOST-PCAARRD. UP Visayas, Miag-ao, Iloilo, Philippines. 56 pp.

Gallienne, C.P., Robins, D.B. 2001. Is *Oithona* the most important copepod in the world's oceans? Journal of Plankton Research 23:1421–1432. https://doi.org/10.1093/plankt/23.12.1421

Ganias, K. 2014. Biology and ecology of sardines and anchovies. CRC Press, Taylor & Francis Group, USA. 394 pp. https://doi.org/10.1201/b16682

Hidalgo, P., Escribano, R., Vergara, O., Jorquera, E., Donoso, K., Mendoza, P. 2010. Patterns of copepod diversity in the Chilean coastal upwelling system. Deep-Sea Research Part II 57:2089–2097. https://doi.org/10.1016/j.dsr2.2010.09.012

Hsieh, C., Chiu, T. 2002. Summer spatial distribution of copepods and fish larvae in relation to hydrography in the northern Taiwan Strait. Zoological Studies 41:85–98.

Hsieh, C., Chiu, T., Shih, C. 2004. Copepod diversity and composition as indicators of intrusion of the Kuroshio Branch current into the Northern Taiwan Strait in spring 2000. Zoological Studies 43:393–403.

Japan Society for the Promotion of Science, Census of Marine Zooplankton: Census of Marine Life. 2004. Identification manual for Southeast Asian coastal zooplankton. Training course on methods of zooplankton ecology and identification. University of the Philippines Los Baños, Laguna, Philippines. 98 pp.

Kämpf, J., Chapman, P. 2016. The functioning of coastal upwelling systems. In: Upwelling systems of the world, a scientific journey to the most productive marine ecosystems, Kämpf, J., Chapman, P. (Eds.), Springer International Publishing, Switzerland. 31–65 pp. https://doi.org/10.1007/978-3-319-42524-5_2

Lalli, C.M., Parson, T.R. 1993. Biological oceanography: an introduction. Oxford: Pergammon Press, New York. 337 pp.

Lehodey, P., Alheit, J., Barange, M., Baumgartner, T., Beaugrand, G., Drinkwater, K. 2006. Climate variability, fish and fisheries. American Meteorological Society Journal of Climate - Special Section 19:5009–5030.

Melo, P., Junior, M.M., Macedo, S.J., Araujo, M., Neumann-Leitao, S. 2014. Copepod distribution and production in a Mid-Atlantic Ridge archipelago. Annals of the Brazilian Academy of Sciences 86:1719–1733. https://doi.org/10.1590/0001-3765201420130395

Metillo, E.B., Campos, W.L., Villanoy, C.L., Hayashizaki, K., Tsunoda, T., Nishida, S. 2018. Ontogenetic feeding shift and size based zooplanktivory in *Sardinella lemuru* (Pisces, Clupeidae) during an upwelling in southeastern Sulu Sea, The Philippines. Fisheries Management and Ecology 25:441–455. https://doi.org/10.1111/fme.12319

Nishida, S. 1985. Taxonomy and distribution of the family Oithonidae (Copepoda, Cyclopoida) in the Pacific and Indian Oceans. Bulletin of the Ocean Research Institute, University of Tokyo, Japan 20:1–167.

Paffenhöfer, G.A. 1993. On the ecology of marine cyclopoid copepods (Crustacea, Copepoda). Journal of Plankton Research 15:37–55. https://doi.org/10.1093/plankt/15.1.37

Peterson, W.T., Miller, C.B. 1977. Seasonal cycle of zooplankton abundance and species composition along the central Oregon coast. Fishery Bulletin 75:717–724.

Razouls, C., de Bovée, F., Kouwenberg, J., Desreumaux, N. 2005–2018. Diversity and geographic distribution of marine planktonic copepods. http://copepodes.obs-banyuls.fr/en (Accessed 02June 2018).

Rezai, H., Yusoff, F.M., Arshad, A. Kawamura, A., Nishida, S., Ross, O.B.H. 2004. Spatial and temporal distribution of copepods in the Straits of Malacca. Zoological Studies 43:486–497.

Rezai, H., Yusoff, F.M., Othman, B.H.R. 2011. Vertical distribution of zooplankton and copepod community structure in the Straits of Malacca. Journal of the Persian Gulf 2:17–23.

Richard, S., Jamet, J.L. 2001. An unusual distribution of *Oithona nana* Giesbrecht (1892) (Crustacea: Cyclopoida) in a Bay: the case of Toulon Bay (France, Mediterranean Sea). Journal of Coastal Research 17:957–963.

Richardson, A.J., Davies, C., Slotwinski, A., Coman, F., Tonks, M., Rochester, W., Murphy, N., Beard, J., McKinnon, D., Conway, D., Swadling, K. 2013. Australian Marine Zooplankton: Taxonomic Sheets. 294 pp.

Rola, A., Pulhin, J., Hall, R. 2018. Water policy in the Philippines: issues, initiatives and prospects. Springer International Publishing. 285 pp. https://doi.org/10.1007/978-3-319-70969-7

Shih, C., Chiu, T. 1998. Copepod diversity in the water masses of the southern East China Sea north of Taiwan. Journal of Marine Systems 15:533–542. https://doi.org/10.1016/S0924-7963(97)00053-5

Smith, D. 1977. A guide to marine coastal plankton and marine invertebrate larvae. Kendall/Hunt Publishing Company, Dubuque Iowa. 161 pp.

Torke, B.G. 1976. A key to the identification of the cyclopoid copepods of Wisconsin with notes on their distribution and ecology. Wisconsin Department of Natural Resources Research Report 88. 16 pp.

Turner, J. 1986. Zooplankton feeding ecology: contents of fecal pellets of the cyclopoid copepods *Oncaea venusta, Corycaeus amazonicus, Oithona plumifera* and *O. simplex* from the Northern Gulf of Mexico. Marine Ecology 7:289–302. https://doi.org/10.1111/j.1439-0485.1986.tb00165

Villanoy, C.L., Cabrera, O.C., Yñiguez, A., Camoying, M., de Guzman, A., David, L.T., Flament, P. 2011. Monsoon-driven coastal upwelling off Zamboanga Peninsula, Philippines. Oceanography 24:156–165. https://doi.org/10.5670/oceanog.2011.12

Villanoy, C., Yniguez, A., David, L., Deauna, J.D., del Prado, J., Pata, P., Camoying, M., Borja, R. 2014. Capturing the dynamic linkages between small pelagic fisheries and primary production through satellite images and models for better resource management in the Bohol Sea and Zamboanga Peninsula. Marine Science Institute, University of the Philippines Diliman, Quezon City. 84 pp.

Willette, D.A., Bognot, E.D.C., Mutia, M.T., Santos, M.D. 2011. Biology and ecology of sardines in the Philippines: a review. Bureau of Fisheries and Aquatic Resources, National Fisheries Research and Development Institute. Technical Paper Series 13:1–18.