ACADEMIA JOURNAL OF BIOLOGY 2023, 45(1): 65–75
DOI: 10.15625/2615-9023/17940

COPEPOD VERTICAL DIEL MIGRATION ON THE CONTINENTAL SHELF OF SOUTH CENTRAL VIETNAM

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Received 7 December 2022; accepted 16 March 2023

ABSTRACT

Zooplankton often migrates within the water column for different purposes but mostly to find food and avoid predators. Vertical migration over 24 hours is called diel vertical migration (DVM). However, knowledge of DVM for different zooplankton species is limited. The present study analysized DVM based on species distribution in the water column at each different times of day at two stations on the central Vietnam shelf. One station was on the shelf (LT2) and another was on the shelf slope (FK002). The results showed that 69 zooplankton species, out of 191 recorded at the two stations, having strong DVM (dz > 15 m). Among them, 38 species were nocturnal and 36 species showed reverse DVM. Species with nocturnal DVM were less on the shelf station than on the shelf slope. Moreover, detailed analysis at LT2 showed 18 species having DVM at dawn and 13 species having DVM at sunrise. This study provides important data for zooplankton ecology in Vietnam and marine tropical waters.

Keywords: Zooplankton, diel vertical migration, central shelf, Vietnam.

Citation: Nguyen Tam Vinh, Huynh Thi Ngoc Duyen, Doan Nhu Hai, 2023. Copepod vertical diel migration on the continental shelf of South Central Vietnam. *Academia Journal of Biology*, 45(1): 65–75. https://doi.org/10.15625/2615-9023/17940

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INTRODUCTION

In marine ecosystems, zooplankton are primary consumers that feed on phytoplankton. They are widely distributed with high diversity that makes them important in different processes in the ocean. Zooplankton community features (e.g. species composition and biodiversity) can be influenced by environmental factors such as temperature (Edmondson, 1965), salinity (Egborge, 1994), pH (Sprules, 1975), tidal processes (Li et al., 2006) and light (Haney, 1987). In the estuary, for example, variation in the size structure of zooplankton communities was controlled by the season or the freshwater impacts from land (Hitchcock et al., 2012; Nguyen Tam Vinh & Doan Nhu Hai, 2020, 2021; Bellier et al., 2022).

Diel vertical migration (DVM) of zooplankton has been investigated for 200 years (Bandara et al., 2021). Vertical migration can occur on short time scales (e.g., 24 hours (DVM)) or seasons. Diel migration has been hypothesized as occurring for food and escape from predation since the late 19th century. Seasonal migration allows zooplankton to complete their life cycle and also relates to food and predators, but over a much longer time scale. Research on zooplankton migration has provided an understanding of several ecological roles in various marine habitats. One of the most discussed was its contribution to carbon flux into the deep ocean. This contribution is thought to be important to reduce the impacts of climate change by bringing the atmospheric CO_2 to depth and burying it in sediment. The DVM is better well-studied than the SVM (seasonal vertical migration) (Bandara et al., 2021). However, the DVM of zooplankton is complex. Hypotheses on how (proximate control, e.g. Cohen & Forward, 2009) and why (adaptive significance, e.g. Hays, 2003) DVM happens have been offered. Despite the large knowledge of DVM in zooplankton, our understanding of its link(s) to seasonal vertical migration is still limited. Moreover, there is needed interdisciplinary research to better understand zooplankton migration (Bandara et al., 2021).

Studies of zooplankton in Vietnam have occurred since the establishment of the Institute of Oceanography in Nha Trang in 1922 with main focuses on taxonomy, biodiversity, and biogeography. However, research on the vertical migration of zooplankton in Vietnam is limited. Cho & Ky (1994) found the impacts of tide and seasons on the vertical migration of zooplankton in Nha Trang Bay. Recently, trait-based research on copepods revealed DVM patterns of 4 copepodite genera and 8 copepod species in south Vietnam (Doan Nhu et al., 2022). In the present stud, our investigation was conducted to understand and/or confirm the diel migration of zooplankton species in Vietnam and to understand zooplankton structure changes over 24 hours as a result of vertical migration.

MATERIALS AND METHODS

Zooplankton were collected for DMV analysis at two stations in the south central shelf of Vietnam (Fig. 1). At station FK002 (on the shelf slope), two samples were taken day and night. At station LT2 (on the shelf), 7 samplings occurred every 4 hours. Environment parameters were measured at each sampling using calibrated CTD-rosette systems (SBE 9+ and SBE 19+, Sea-Bird Electronics Inc., USA). The parameters estimated were temperature, salinity, and chlorophyll-a.

Quantitative and qualitative samples were taken using vertical net tows (Juday net, 200 µm mesh size) equipped with a release mechanism. Four depth intervals were sampled: 100 - 50 m, 50 - 25 m, 25 - 10 m, and 10 - 0 m. At station LT2, the interval of 100 - 50 m was replaced by 70 - 50 m due to the station depth being 76 m. The samples were fixed with formaldehyde (5% final concentration) and returned to the lab for later analysis. In the laboratory, samples were washed with fresh water and handpicked trash fragments were removed. A 500 µm sieve was used to separate the samples into two portions: large (> 500 µm) and small

(< 500 µm). The large sized samples were counted to species level under a stereomicroscope (40 - 160x magnification) or compound microscopy (Olympus BX53, Japan). The small size samples were diluted in filtered freshwater and one-milliliter subsamples were counted. Zooplankton species were identified based on the literature: Chen (1965, 1974), Owre (1967), Nishida (1985), Khoi (1994), Boltovskoy (1999) and Mulyadi (2002, 2004). Taxonomic information was updated based on (Walter & Boxshall, 2022).

Diel vertical migration (DVM) of zooplankton was calculated by the changes in their density over 24 hours. The weighted mean depth (WMD) for each taxon in each sample was calculated following Frost & Bollens (1992):

$$WMD = \sum(n_i \times z_i \times d_i) / \sum(n_i \times z_i)$$

Where: d_i is the mid-point depth of the depth interval of sample i; z_i is the thickness of the stratum; and n_i is species density (individuals per 1,000 m^3) at that depth.

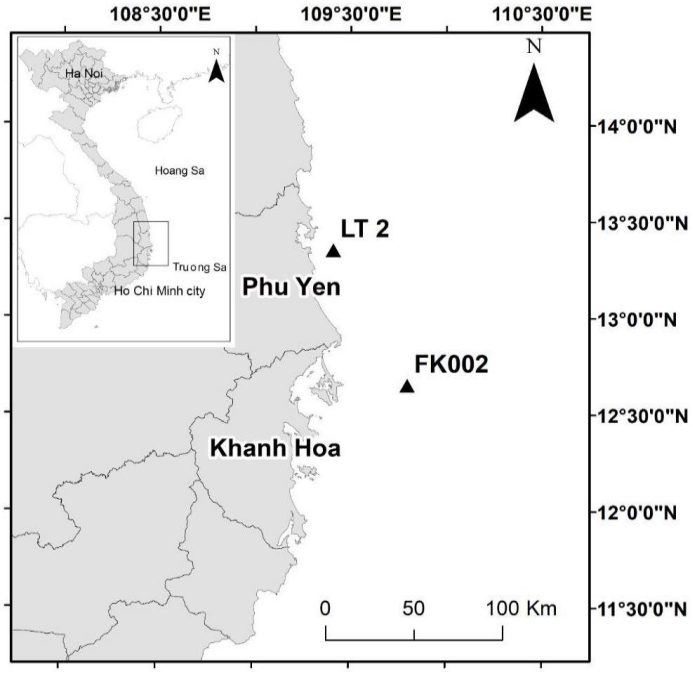

Figure 1. Map showing sampling locations and stations

RESULTS

Environmental setup

The on-shelf station LT2 was 76 m deep and was impacted by coastal water and tides in the upper water column. In the day, the sun warmed up the surface water to a depth of 5 m to 10 m to 28 ^oC while at night, this water layer cooled by 1–1.5 ^oC (Fig. 2). Salinity at the 10 m of surface water was greatest during the highest tide (day 1600 and 1200). During low tide, salinity was low at the upper 20 m (Fig. 2). At LT2, the mixed layer depth seemed to be around 20 m. The chlorophyll maximum was thick, ca 30 m, and moved up and down between 30 m and 40 m.

At station FK002, subsurface chl-max (SCM) was around 40–50 m but a second, smaller peak occurred at 60–80 m. The second SCMs deepened to ca. 120 m during the day while they occurred at 100 m during the evening and night. The TS profiles indicated consistent strong stratification with a mixed layer of about 40 m (Fig. 3).

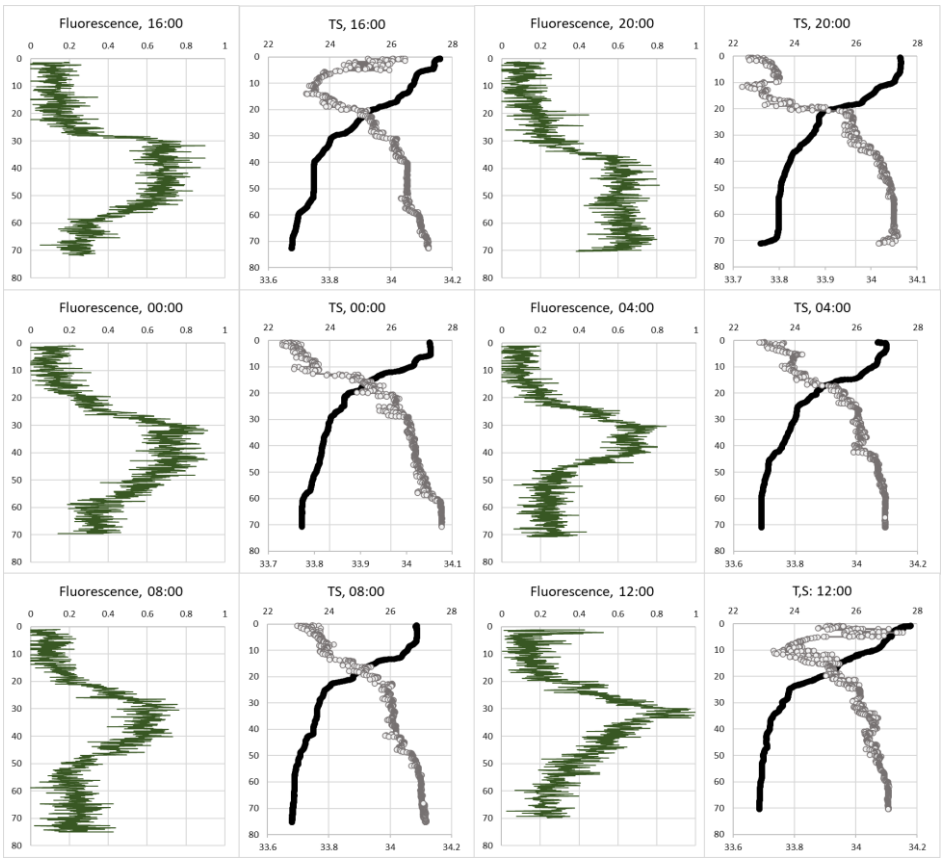

Figure 2. Vertical profiles of Temperature (T, ^{o}C, black line), Salinity (S, grey line) (TS graphs), and fluorescence (mg Chl-a/m^3) at different observations at station LT2

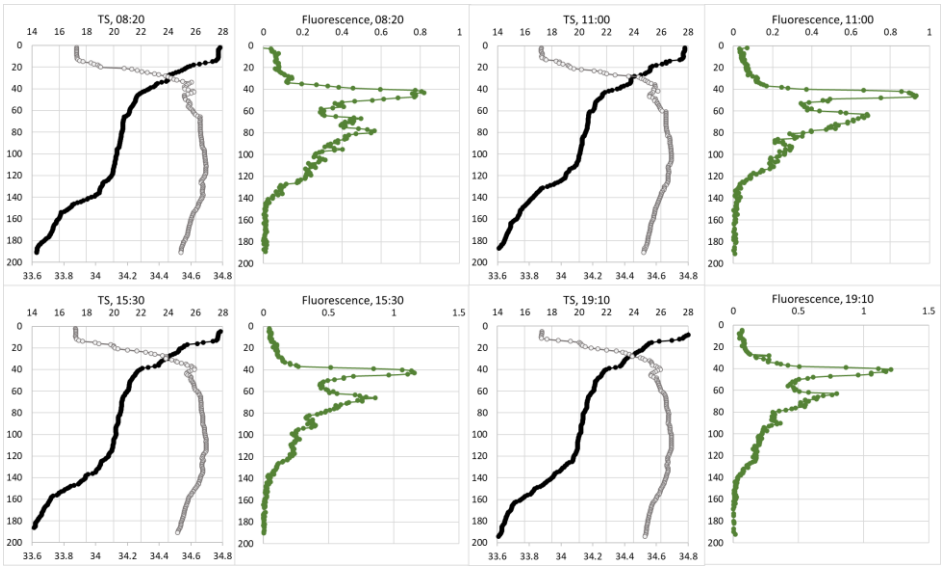

Figure 3. Vertical profiles of Temperature (T, ^{o}C, black line), Salinity (S, grey line) (TS graphs), and fluorescence (mg Chl-a/m^3) at different observations at station FK002

Zooplankton diversity and abundance

The total number of species/subspecies recorded at two anchored stations was 191 belonging to 7 phyla. The highest number of taxa was 139 in the Arthropoda phylum (mainly in subclass Copepoda), followed by Cnidaria, Chordata, and Mollusca with 12, 13, and 10 taxa, respectively. The total species number was not different between the two stations except in Arthropoda and Cnidaria (Table 1).

Table 1. Number of taxa recorded at two stations in the central shelf of Vietnam

Phyla/Stations	FK002	LT2	Total
Annelida	4	6	6
Arthropoda	110	94	139
Chaetognatha	6	3	6
Chordata	11	12	13
Cnidaria	7	15	15
Ctenophora	0	2	2
Mollusca	5	8	10
Total	143	140	191

There was a clear vertical distribution of zooplankton at both stations, especially at night. At station LT2, Copepoda contributed 75% of the total zooplankton density and was deeper in the water column, near the bottom layer to 25 m depth. During the day the Copepoda tend to move to deeper water (Fig. 4). At FK002, at night, zooplankton were more abundant at the surface and between 50−25 m (Fig. 5).

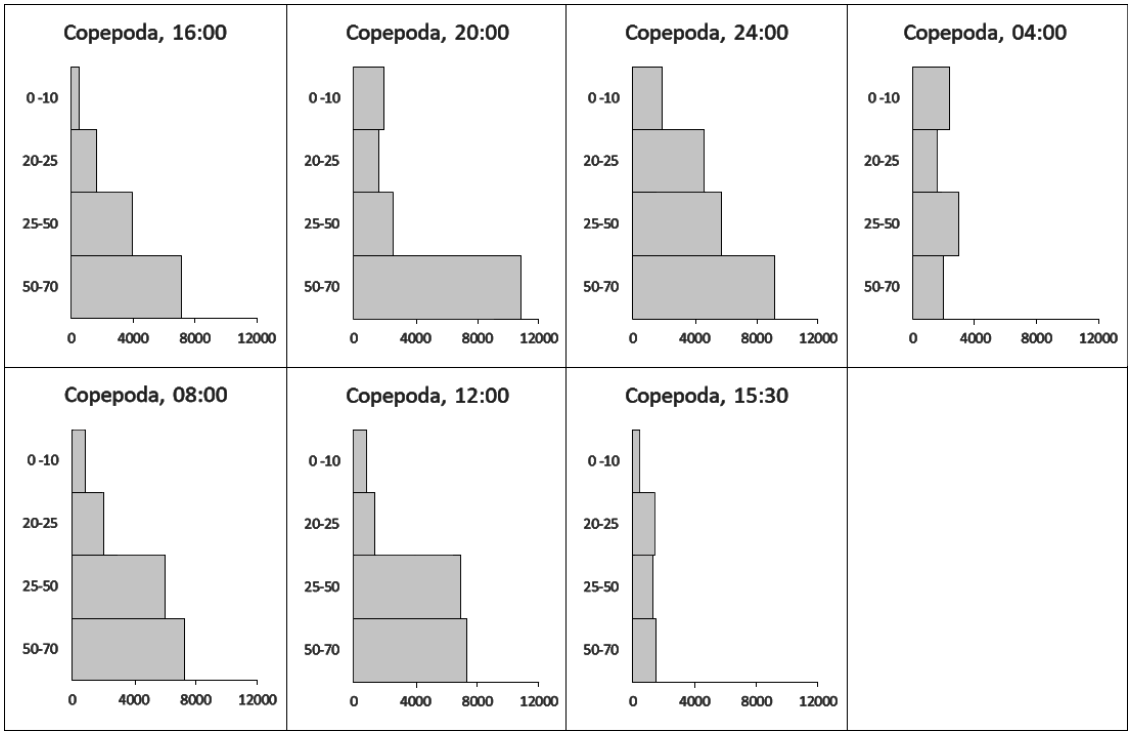

Figure 4. Vertical distribution of Copepoda abundance (individual/m^3) at station LT2

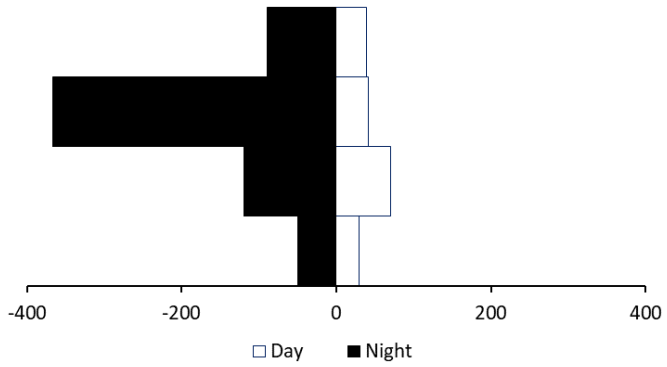

Figure 5. Vertical distribution of zooplankton abundance (individual/m^3) at station FK002

Diel vertical distribution

Station FK002

37 species showed DVM with absolute dz greater than 15 m. Three larval groups and 5 copepod juveniles also have absolute dz greater than 15 m. Most of the species and groups (28) showed nocturnal upward migration but much lesser species and groups (17) had reverse DVM (Table 2).

29 copepod species showed DVM with distances over 15 m. Other zooplankton species including species in Gastropoda, Ostracoda, Branchiopoda, Polychaeta, and Appendicularia also showed DVM but only 1 species for each group. Only three larval groups of Decapoda, Ophiura, and Bivalvia but 5 copepod genera showed high dz (Table 2).

At station LT2, 26 species and groups were found to have DVM with dz larger than 15 m including 4 copepodite genera and 5 species belonging to classes other than Copepoda. Among them, 17 taxa had nocturnal DVM and 9 taxa had reverse DVM. Appendicularian were all reverse DVM (Table 3). In addition, there were 16 taxa were found to have medium DVM with dz ranging from 10 to < 15 m (data not shown).

At both stations, the total taxa recorded to have DVM was 69 including 38 nocturnal and 36 reverse DVM. Only two copepod species, *Corycaeus speciosus* and *Lucicutia ovalis*, were found to have DVM at both stations. Four copepod species, *Ditrichocorycaeus andrewsi*, *Farranula gibbula*, *Oithona setigera*, and *Scolecithricella longispinosa*, had different diel migration types at the two stations.

Table 2. WDM at day and night of a 24-hour period and amplitude of the migration (dz, m) of selected taxa (dz > 15 m) at station FK002

No.	Class/Group	Species	WMD (m)		dz
			Day	Night	
Reverse DVM					
1	Copepoda	*Acrocalanus gibber*	32.1	10.5	21.5
2		*Copilia mirabilis*	75.0	32.5	42.5
3		*Corycaeus speciosus*	30.0	5.0	25.0
4		*Ditrichocorycaeus andrewsi*	37.5	21.3	16.3
5		*Ditrichocorycaeus dahli*	70.6	44.5	26.1
6		*Euchaeta longicornis*	57.0	37.5	19.5
7		*Lucicutia ovalis*	55.0	31.7	23.3
8		*Microsetella norvegica*	58.8	38.3	20.4
9		*Oithona robusta*	75.0	56.3	18.8
10		*Scolecithricella nicobarica*	60.0	32.5	27.5

No.	Class/Group	Species	WMD (m)		dz
			Day	Night	
1	Ostracoda	*Euconchoecia bifurcata*	30.0	12.5	17.5
2	Gastropoda	*Limacina trochiformis*	22.5	5.0	17.5
1	Larvae/Juvenile	Bivalvia larvae	28.5	7.9	20.7
2		*Candacia* (Juvenile)	30.8	9.5	21.3
3		*Lucicutia* (Juvenile)	71.7	40.8	31.0
4		*Oncaea* (Juvenile)	42.9	27.1	15.7
5		*Paracalanus* (Juvenile)	42.7	26.1	16.6
Nocturnal DVM					
1	Copepoda	*Acrocalanus gracilis*	5.0	41.6	-36.6
2		*Calanopia elliptica*	5.0	75.0	-70.0
3		*Canthocalanus pauper*	8.8	34.8	-26.0
4		*Clausocalanus arcuicornis*	20.2	37.4	-17.2
5		*Clausocalanus furcatus*	16.8	32.9	-16.1
6		*Clausocalanus pergens*	31.3	52.5	-21.2
7		*Cosmocalanus darwinii*	29.4	46.0	-16.6
8		*Euchaeta indica*	5.0	46.0	-41.0
9		*Farranula gibbula*	7.4	40.0	-32.6
10		*Oithona setigera*	37.5	64.4	-26.9
11		*Onychocorycaeus catus*	5.0	40.0	-35.0
12		*Sapphirina nigromaculata*	21.3	51.9	-30.6
13		*Scolecithricella longispinosa*	27.5	59.7	-32.2
14		*Subeucalanus crassus*	37.5	75.0	-37.5
15		*Subeucalanus subcrassus*	37.5	68.8	-31.3
16		*Temora turbinata*	5.0	67.2	-62.2
17		*Triconia conifera*	25.2	42.4	-17.3
18		*Triconia similis*	29.8	48.1	-18.3
19		*Urocorycaeus furcifer*	40.0	75.0	-35.0
1	Gastropoda	*Creseis clava*	5.0	75.0	-70.0
2	Ostracoda	*Euconchoecia* sp.	40.1	75.0	-34.9
3	Malacostraca	*Euphausia brevis*	37.5	75.0	-37.5
4	Appendicularia	*Oikopleura (Coecaria) fusiformis*	23.5	44.1	-20.6
5	Branchiapoda	*Penilia avirostris*	19.8	37.5	-17.7
6	Polychaeta	*Tomopteris* sp.	37.5	66.1	-28.6
1	Larvae/Juvenile	*Neocalanus* (Juvenile)	47.7	75.0	-27.3
2		Ophiura larvae	25.3	46.2	-20.9
3		Decapoda shrimp larvae	44.3	66.9	-22.6

Table 3. WDM at every 4 hours of a 24-hour period and amplitude of the migration (dz, m) of selected taxa (dz > 15 m) at station LT2. The dz of night/day was calculated between noon

and midnight; the Dawn dz was calculated between 1,600 and 20,000 and sunrise between 0400 and 0800

Class	Species	WDM (m)							dz (m)		
		1600	0800	1200	1600	2000	2400	0400	Day - Night	Dawn	Sunrise
Appendicularia											
	Fritillaria formica	52.5	37.5	12.5	34.1	35.9	29.2	12.2	-16.7	16.6	-25.3
	Oikopleura (Juvenile)	18.6	57.9	5.0	10.0	24.2	28.2	60.0	-23.2	-5.7	2.1
Copepoda											
	Corycaeus (Juvenile)	38.8	22.4	27.0	36.8	30.9	59.1	49.8	-32.1	7.9	27.4
	Calocalanus pavoninus	NA	60.0	12.5	29.2	NA	33.3	NA	-20.8	NA	NA
	Corycaeus sp.	31.7	41.9	30.0	45.4	49.7	49.4	42.4	-19.4	-18.1	0.5
	Ditrichocorycaeus andrewsi	29.2	29.6	37.5	37.5	NA	52.5	31.4	-15.0	NA	1.8
	Farranula concinna	29.8	48.8	39.6	36.0	NA	60.0	46.4	-20.4	NA	-2.3
	Onychocorycaeus pacificus	37.5	37.5	37.5	NA	45.6	53.5	37.5	-16.0	-8.1	0.0
	Limacina sp.	56.1	46.2	31.2	41.7	42.3	56.1	49.2	-24.9	13.8	3.0
Copepoda											
	Canthocalanus (Juvenile)	57.5	47.8	55.5	40.4	38.3	40.1	25.2	15.4	19.2	-22.7
	Centropages (Juvenile)	37.5	NA	60.0	5.0	60.0	10.0	10.0	50.0	-22.5	NA
	Calocalanus pavo	21.1	24.6	60.0	12.5	5.0	37.5	20.7	22.5	16.1	-3.9
	Canthocalanus pauper	50.1	49.6	53.6	54.7	34.5	38.3	28.5	15.3	15.7	-21.1
	Corycaeus speciosus	12.5	NA	58.1	37.5	NA	31.0	5.0	27.1	NA	NA
	Ditrichocorycaeus erythraea	45.5	42.0	60.0	42.5	60.0	44.8	50.8	15.2	-14.5	8.8
	Farranula gibbula	12.5	12.1	43.1	17.8	12.5	21.8	30.1	21.4	0.0	18.0
	Lucicutia ovalis	57.1	58.1	56.3	60.0	33.3	36.3	46.6	20.0	23.8	-11.6
	Oithona attenuata	37.5	NA	60.0	37.5	60.0	11.5	NA	48.5	-22.5	NA
	Oithona brevicornis	NA	21.8	37.8	38.3	12.5	5.0	NA	32.8	NA	NA
	Oithona setigera	33.3	48.8	48.8	55.5	60.0	5.0	37.5	43.8	-26.7	-11.3
	Scolecithricella longispinosa	53.1	57.0	56.0	54.4	28.1	15.7	45.9	40.3	25.0	-11.1
	Undinula vulgaris	56.3	45.0	60.0	NA	21.0	5.0	5.0	55.0	35.3	-40.0
	Creseis acicula	34.1	41.1	47.8	28.8	47.5	24.5	29.2	23.3	-13.4	-11.9
Malacostraca											
	Pseudeuphausia latifrons	51.7	7.5	47.4	5.0	34.6	17.9	17.0	29.5	17.0	9.5
Polychaeta											
	Pelagobia longicirrata	48.5	45.5	48.8	60.0	40.1	28.4	31.1	20.3	8.4	-14.4
Sagittoidea											
	Aidanosagitta neglecta	37.5	NA	60.0	NA	12.5	10.0	NA	50.0	25.0	NA
	Total								26	18	13

DISCUSSION

The present study revealed the DVM of zooplankton in the narrow shelf area of central Vietnam to the species level. Among the 191 zooplankton species identified, there were 69 species having DVM with dz >15 m, including 38 nocturnal and 36 reverses DVM. The number of species having DVM was not high. Characterizing traits of zooplankton species is increasing (e.g. Benedetti et al., 2002) as is the use of the trait-based approach in zooplankton ecology. However, similar to other traits, species DVM is an ecological characteristic and more observations are needed to confirm the status of that species. The DVM database for zooplankton is limited and our results provide significant inputs to the database, especially in tropical waters.

Species diversity and abundance

The number of species recorded at the two stations was high (191), with the average of the shelf slope (FK002) 54 ± 12 species lower than at the station on the shelf (LT2, 87 ± species). Although the total number of species at each station was the same, the larger variation of species composition at FK002 was expected because of its location

close to the shelf break front. FK002 is located off Cape Varella and can be at the boundary between the two eddies in the Bien Dong (Li et al., 2017). The abundance of zooplankton at the two stations was similar in magnitude (over 20.000 individuals/m^3), similar to the western tropical Atlantic (De Figueiredo et al., 2020).

Diel Vertical Migration

In addition to the four copepodite genera, we found many other copepod juveniles also having DVM (Tables 2, 3). Previous research (Longhurst,1985; Doan Nhu et al., 2022) revealed the juvenile copepod migrated around the Chl-a max layers. In the present study, Chl-a max was at 20−100 m and as was the high abundance of juveniles.

In a previous publication (Doan Nhu et al., 2022), two copepodite genera had short migrations, *Paracalanus,* and *Oncaea,* while *Oithona* and *Corycaeus* migrated long distances (dz = 25.6). The present study confirmed the two copepodite genera to have short to long DVM while *Oithona* and *Corycaeus* only showed migration at LT2. LT2 was sampled 7 times for 24 hours so there is a possibility that the sampling time did not match well with the migration time. However, all four copepodite genera were having DVM in the central shelf waters (Table 4).

For adult copepods, there were 39 species reported to have strong DVM with dz > 15 m. In addition, there were 47 species of copepod having DVM. Four species, *Ditrichocorycaeus andrewsi, Farranula gibbula, Oithona setigera,* and *Scolecithricella longispinosa*, had opposite DVM at two stations, so confirmation for the type of DVM is needed. Previously (Irigoien et al., 2004), C5 juvenile of *Paracalanus parvus* and C1-C3 of *Acartia* and *Calanus* performed both nocturnal and reverse migrations and that was at different sampling times. This can possibly be a normal situation in copepod giving these four species were all omnivore-herbivore species that depend largely on the depths of Chl-a maximum.

Compared to the previous study (Doan Nhu et al., 2022), our results confirm the DVM behavior of four copepod genera *Corycaeus, Oithona, Oncaea,* and *Paracalanus*. Furthermore, *Corycaeus* copepodite and *Oncaea mediterranea* can migrate during sunrise and *Oithona* copepodite at dawn (Table 4). For adult copepods, *Oithona nana* seemed not to have DVM but other seven species, *Oithona plumifera, Oncaea media, O. mediterranea, Paracalanus parvus, Parvocalanus crassirostris, Triconia conifera,* and *Triconia minuta* do migrate.

Among the adult copepod previously reported as having strong migration (*Oncaea media* and *Triconia conifera*), Doan Nhu et al. (2022) found that *Triconia conifera* migrated, but we confirmed that both species (Table 4) have medium DVM (dz ~ 14−17 m). There was probably no DVM for *Oithona nana, Paracalanus parvus,* and *Parvocalanus crassirostris* as they had inconsistent dz in migration (Table 4).

Diel vertical migration of zooplankton on the Vietnam central shelf based on their distribution in the water column over 24 hours periods was observed. There were both normal and reverse DVM reported for 69 species having strong DVM (dz >15 m). At the shelf station, there were fewer species having nocturnal DVM than at the shelf slope station (9 vs. 29 species). There were an equal number of species (17) having reverse DVM at both stations. There was also a possibility of 18 species having DVM at dawn and 13 species having DVM at sunrise. This study provides important data for zooplankton ecology in Vietnam and marine tropical waters. The vertical changes of zooplankton abundance over 24 hours were impacted by DVM. However, other factors (e.g. lateral advection) need to be investigated in the future.

Table 4. Comparison dz (m) of 8 adult copepod species and 4 copepodite genera at two stations in the present study with previous publication. The negative value indicated nocturnal DVM and a positive for reverse DVM. Numbers in bold indicate moderate to strong DVM

Taxa	FK002	LT2			Doan-Nhu et al. (2022)
	Day/Night	Day/Night	Dawn	Sunrise	Day/Night
Corycaeus (Juvenile)	-1.6	-32.1	7.9	27.4	25.6
Oithona (Juvenile)	-0.3	-0.4	-13.6	-6.1	-17.1
Oncaea (Juvenile)	15.7	-2.0	12.4	-2.1	14.1
Paracalanus (Juvenile)	16.6	-0.2	-15.4	-9.2	1.2
Oithona nana	-2.5	NA	NA	NA	-4.5
Oithona plumifera	-2.9	-0.5	-11.0	-6.3	-12.4
Oncaea media	-5.4	14.6	0.1	-7.3	-3.2
Oncaea mediterranea	-4.5	-5.6	-5.2	-15.5	24
Paracalanus parvus	-4.8	3.0	1.1	-6.4	-30.3
Parvocalanus crassirostris	1.2	3.7	-7.9	-2.3	-18
Triconia conifera	-17.3	10.2	9.2	-9.7	-14.7
Triconia minuta	-7.4	NA	NA	NA	14.1

Acknowledgements: The study was funded by Vietnam Academy of Science and Technology via project No. KHCBBI.01/20–22.

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