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The diel vertical migration of zooplankton in the hypoxia area observed by video plankton recorder

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Temperature, salinity, fluorescence, and dissolved oxygen were investigated together with the vertical distribution of four taxa to discuss the reason for diel vertical migration (DVM). Copepods and chaetognatha performed typical DVM, but only a small part of the population appeared under 40 m. Gelatinous zooplanktons aggregated at the surface water layer shallower than 30 m. DVM of euphausiacea remained uncertain because of the small number of individuals investigated in the study. Our study confirmed that VPR could be used as a valuable tool to study zooplankton DVM. DVM of most zooplankton living in the coastal area of the East China Sea might be affected by multiple environmental elements, such as feeding activities, predator presenting, stratification of water column, and energy utilization.

[**Keywords:** Video Plankton Recorder, Zooplankton, DVM, East China Sea]

Introduction

Many marine zooplankton perform diel vertical migrations (DVM) in oceans[1,2]. DVM is considered as a common behavior, which has an adaptive significance to zooplankton, and has various consequences on the ecosystem[1,3]. Various potential reasons are discussed for different terms of DVM involving herbivorous and omnivorous zooplankton. Species will differ in their DVM based on factors such as their feeding mode and predation risk. Meanwhile, measuring the distribution of plankton in the pelagic environment is a challenging task. Vertical net tows are the most frequently used apparatus. However, individuals collected using this approach are pooled within depth intervals, which weaken the precision of our knowledge about their position, thereby reducing the power when testing for differences in depth distributions during the day and night[4,5]. In addition, plankton surveys can generate hundreds or thousands of samples, requiring long, time-consuming analysis[6,7] and still may not have sufficient sample density for the quantification of patchiness[8]. Another preferable research tool is the acoustic method that can provide precise depth position; however, it also suffers from uncertainties regarding imprecise species information that is obtained[9]. Hence, video recording and photography are alternatives to these traditional approaches.

Numerous video techniques for in situ plankton observation have been developed in the past decades. Among them, the video plankton recorder (VPR)[10-19], underwater video profiler (UVP)[20], and light frame on-sight key species investigation (LOKI) system are the popular choices[21,22]. These systems have the ability to identify planktonic taxa by simultaneously and continuously measuring distributions nearly over a broad range of scales and sampling the delicate plankton and particulate matter in situ[12].

The autonomous VPR (L × W × H: 127 × 71 × 45 cm^3) is an underwater video microscope system designed for the rapid quantification of plankton taxonomic composition and abundance[23]. This

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equipment can provide exact information about individuals and their depth and provide quantitative estimates of plankton abundance and biomass by imaging a given water volume using a camera. The VPR system has the following advantages: (1) it has a high-resolution, (1024 × 1024) 10 bit color digital camera, (2) can be towed at reasonable speeds (2–2.5m/s), and (3) has improved user-friendly image processing and data analysis/display software for observing abundance patterns of plankton[13].

VPR research areas are located in Canada at the following locations[18]: Disko Bay on the Arctic peninsula[17], Marguerite Bay on the Antarctic Peninsula[14], the Georges Bank[24], the Great South Channel (GSC)[12], and the Gulf of Maine[13] in USA, and the Japan/East Sea (JES)[25]. The zooplankton and copepod species include *Calanus finmarchicus*[26], plankton[27], larval krill[14], larval fish[24], pteropod and larvacean[28], and other taxa[17].

The East China Sea continental shelf is complicated hydrographically by a high dynamic. The region represents the confluence caused by the Taiwan Warm Current, the Yellow Seawater, and water from Changjiang River brought by the China Coast Current. Anoxia and hypoxia are observed in the region continually during summer and autumn over decades[29]. All the environmental elements referred above should be considered for understanding the zooplankton DVM in this shallow-water region, requiring studies based on a refined scale. Studies on zooplankton DVM in this region have not been published yet. Therefore, we employed VPR to study DVM of different zooplankton in a station near Zhejiang Province, East China Sea, to shed light on the strategies of zooplankton living in complex environments.

Materials and Methods

VPR used in the study was rated for a maximum operating depth of 1000 m. VPR comprised two pressure cases. One case contained a Uniq UC-1830CL camera and lenses, which uses four stepper(S0-S3) motors for an accurate and a repeatable positioning of camera lens extension and the other case contained a high-powered strobe in a ring configuration. The frame rate of compressed digital images is 15 of times per seconds via an RS232 interface. Each VPR tow produced a file comprising compressed images captured and recorded by the embedded computer stack; the ancillary CTD data can get off the VPR to a processing computer via a USB adapter or an Ethernet cable. Regions of interest (ROIs) were extracted from the images employing a set of extraction parameters using the software AutoDeck (Seascan Inc) and saved to the computer disc as TIFF files. In this way, each ROI was time-stamped for subsequent spatial mapping (time in milliseconds within the day)[23].

Typically, VPR is calibrated prior to each cruise[12,23]. For S3 stepper, the camera was focused such that the field of view of each image was within 42 × 42 mm^2, the lens was adjusted to provide a field of view of 1.7 cm, and the calibrated imaged volume was 300 ml. The VPR undulated manually between the surface and 50 m below the surface with an average vertical velocity of 0.6 m/s; the total volume sampled was 7500 ml per vertical meter. The area imaged by consecutive frames during sampling did not overlap[16,30,31]. Zooplankton numbers of each drop were calculated from the VPR data using AutoDeck, which uses brightness, sharpness, texture, and size thresholds to isolate and extract ROIs from the images[12,32]. We attached SBE-49 CTD on VPR. Fluorescence (Wetlabs ECO Puck) and DO sensors (SBE-43) on SBE-911 CTD were used to study the DVM of zooplankton. VPR was deployed four times at the DH2-1 station (123.11°E, 29.47°N) located offshore of Zhejiang Province (Fig. 1); the sampling was taken during the day and at night (03:09 AM: 15:21 PM) on June 2014 (Table. 1).

The detected ROIs were stored in a special data directory structure. Remaining ROIs, which were <3% of the total number of ROIs, were deleted

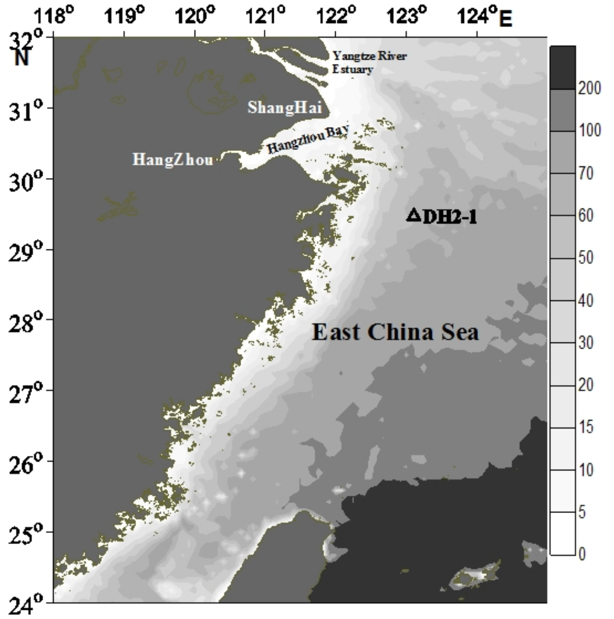

Fig. 1 — Location of the sampling site

Table 1 — Time and depths of VPR deployed on June 2014

Cast	Data	Local time	Depth (m)	Bottom depth (m)	Number of tows
Night1	06/06/2014	21:00	0–35	61	1
Night2	07/06/2014	03:00	0–40	61	3
Day1	07/06/2014	09:00	0–50	61	3
Day2	07/06/2014	15:00	0–50	61	3

because of unidentified and unclear images. ROIs were sorted automatically into different taxa using classifiers trained with a set of manually sorted images. Then, the grouped ROIs were checked manually to confirm if they belonged to the same special taxonomic category and counted. Math works (MATLAB 2010) was used to link the pictures to time and depth of observation via time stamping. The hydrographic parameters (temperature and salinity) could also be related to the ROIs using time stamping[17,23]. For the stand-alone CTD, we used depth and sampling events to link the data. List of observation times for different taxon images were binned into the 1-s time bins of the sensor data, and the number in each bin was divided by the total volume imaged during each 1-s period to obtain the average abundance (number/m^3) per bin[11-13]; the results were plotted with vertical profiles of physical parameters to examine meter-scale variability. Vertical distributions of dominant taxa/particles of DVM follow the method[18,33]. The formula to calculate the abundance was as follows:

$$\mathrm{Abu} = \frac{\mathrm{N}_{\mathrm{ind}}}{\mathrm{N}_{\mathrm{frame}} \times \mathrm{Volume}} \times 10^{-3}, \qquad \dots (1)$$

where Abu is the number of individuals per cubic meter, $\mathrm{N}_{\mathrm{ind}}$ is the number of individuals observed in a second, $\mathrm{N}_{\mathrm{frame}}$ is the number of frames per second, and volume is the image volume of a single frame (e.g., S3 setting, volume: 300 ml).

Results

The distribution of temperature, salinity, fluorescence, and oxygen along the station is shown in Fig 2. Temperature and DO decreased, whereas salinity increased as the depth increased. High-salinity water (about 34.5 PSU) occupied the depth from ~35 m to the seafloor during the survey, and low-salinity water occupied the surface with depth <10 m. The thermocline was at the depth of 15–25 m.

Fluorescence and DO generally decreased with increasing depth. The fluorescence was in the range of

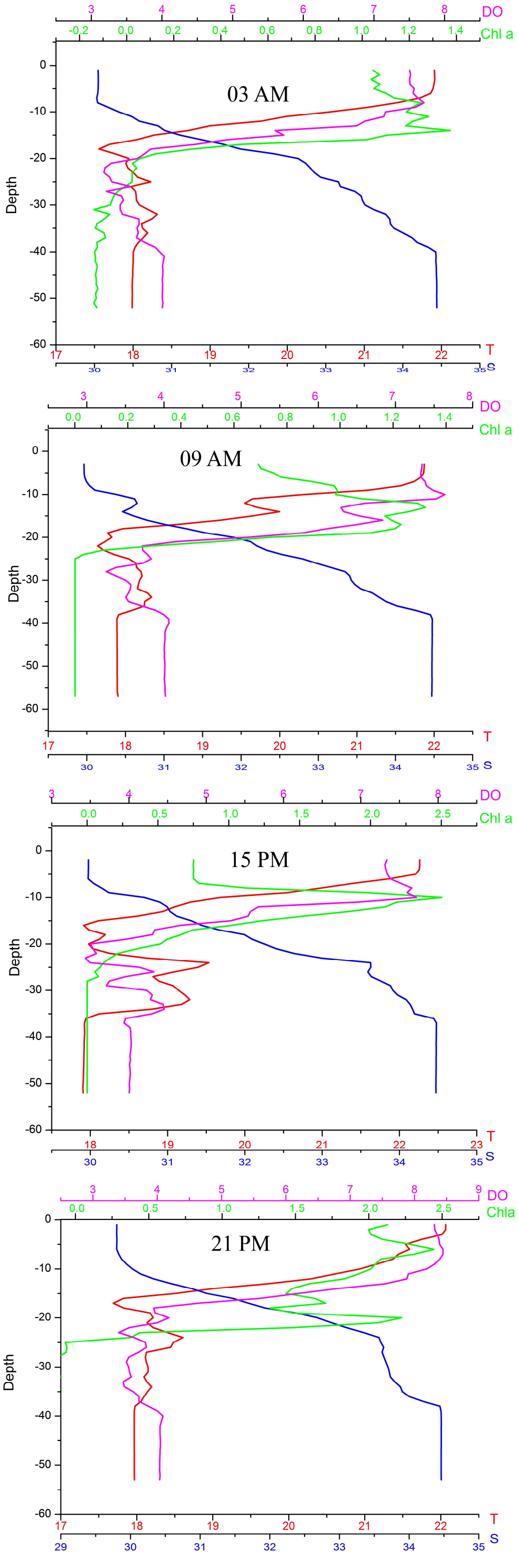

Fig. 2 — Fluorescence (μg·L^{-1}), temperature (°C), salinity(PSU), and DO (mg·L^{-1}) at the sampling site during the day and at night. These parameters were measured using the CTD fitted on the VPR, except for the fluorescence and DO, when measurements were performed using a stand-alone CTD.

0–2.5 μg·L^{-1} Chl (the fluorescence range of the instrument was 0–50 μg·L^{-1} Chl) and appeared as a single peak at around 15 m, except 21 pm. In 21 pm, fluorescence value was consistently high from 25 m to the surface, showing two peaks at 5 m and 20 m, respectively. Generally, the fluorescence value remained high during four drops in the upper 25 m. However, it was extremely low (<0.2 μg·L^{-1}) in water deeper than 25 m. Distribution of DO changed similarly with fluorescence, decreasing steeply under thermocline of ~20m. In our study, DO was in the range of 3.2–8.5 mg/l (the measurement range is 120% of surface saturation in all natural waters). DO was stably at a value <4mg/L under ~40 m.

Fourteen taxa, genera, or particle types were identified and were divided into seven categories for further statistics. Typical images of the main taxa recognized in the study are shown in Fig 3. Major zooplankton groups identified gelatinous zooplanktons (most groups were medusa and few of the species were doliolidae and ctenophore), copepods, chaetognatha, euphausiacea, creseis, larval fish, and particles (e.g., marine snow, unknown). Discrimination of developmental stages of the species was not considered in our study due to the existence of many ambiguous images (Table 2).

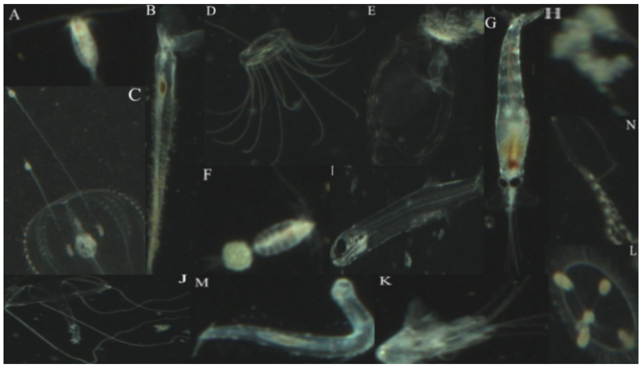

Fig. 3. Selection of images captured using the VPR as a part of the study. A. *Calanus* spp without eggs, B. *Creseis* acicula, C. Ctenophora, D. Cyaneidae, E. Doliolidae, F. *Euchaeta* spp. with eggs, G. Euphausiid, H. Irregular marine snow, I. Larvae fish, J. *Liriope tetraphylla*, K. Pteropoda or unknown, L. *Obelia*.sp, M. *Sagitta* spp., and N. Siphonophora.

As S3 was chosen to be the main stepper used to illuminate the taxa of zooplankton community, the length of zooplankton that appeared in our images was mainly between 1.8–16 mm. These mesozooplankton were identified on the PC and affirmed by the specialists of zooplankton identification after examining the vertical sample taken at the station. Our results indicated that copepods and gelatinous zooplankton dominated in the zooplankton community. The sample mainly was composed of *Calanus sinicus, Euchaeta* spp.*, Flaccisagitta enflata, Zonosagitta nagae, Solmaris* spp., and *Obelia* spp. according to the images and the vertical sample. *Calanus spp*., *Euchaeta spp*., and *Paraeuchaeta* spp. dominated in copepods; these species together with other copepods were classified as "copepods." *C. sinicus* was composed of >60% of the copepods in the sample and in our image sets. Ctenophora, Hydrozoa (containing Hydromedusae and Siphonophora), and Doliolum were combined together as gelatinous zooplanktons. *Solmaris* spp. and *Obelia* spp. dominated in the gelatinous zooplanktons. However, there was no report of any large abundance of *Solmaris* spp. in the area. The species might have been dissolved in the preserved sample, thereby decreasing their abundance, or random sampling error may have resulted in the difference. As different zooplankton categories have different abundance and different levels of ecological importance, we mainly focused on four categories (copepods, gelatinous zooplanktons, chaetognatha, and euphausiid) in our study and for further analysis.

Only four categories appeared (copepods, gelatinous zooplanktons, chaetognatha, and euphausiid) in all four drops. Although some zooplankton categories were distinctive and some individuals could be identified to species level, most of the images could

Table 2 — Abundance of different taxa (ind/m^3) & different times

Taxon	21PM (mean ± SD)	03AM (mean ± SD)	09AM (mean ± SD)	15PM (mean ± SD)
Gelatinous zooplanktons	427.4 ± 250.8	410.8 ± 272.4	704.4 ± 397.4	1371.4 ± 1454.7
Copepods	526.6 ± 348.6	313.1 ± 164.6	423.2 ± 359.3	306.3 ± 160.2
Chaetognatha	266.7 ± 99.4	242.4 ± 67	244.4 ± 70.3	266.7 ± 99.4
Euphausiacea	222.2 ± 0	296.3 ± 128.3	222.2 ± 0	222.2 ± 0
Creseis	0	333.3 ± 128.3	666.7 ± 0	0
Larva fish	0	222.2 ± 111.1	0	0

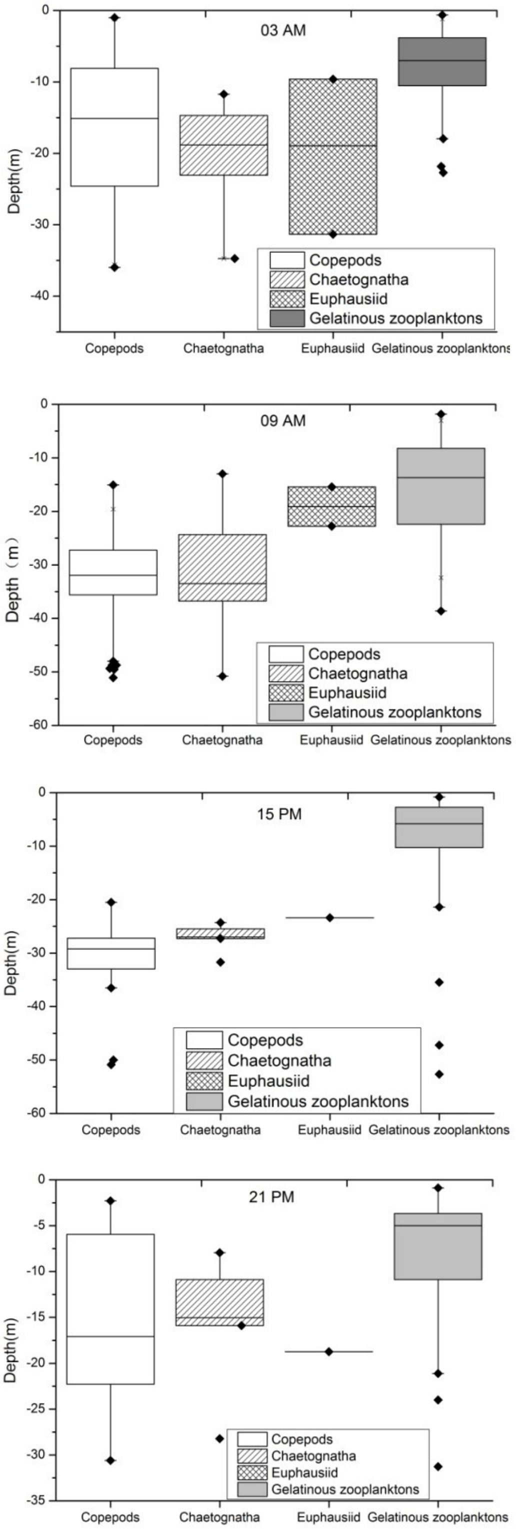

Fig. 4 — Box plot showing the depth distribution of groups and separated four times. The boxes represent the first and third quartile, and the middle bar is the median. The end of the whiskers extends from the hinge to the lowest and highest value within a 1.5 inter-quartile range. The dots represent outliers.

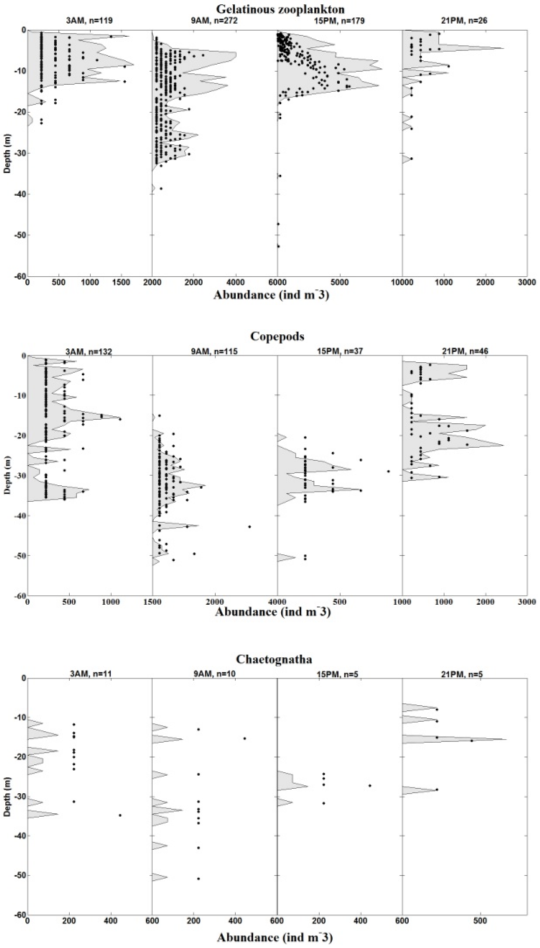

Fig. 5 — The abundance (dots) in all three groups are position by depth and time. Abundance in 5-m deep bins is illustrated (gray shaded areas), n: number of species.

only be identified to a family level or a higher level. The vertical distribution of copepods, gelatinous zooplanktons, chaetognatha, and euphausiid during four deployments are shown in Fig. 4 as a box plot. The DVMs of gelatinous zooplanktons, copepods, and chaetognatha are shown in Fig. 5 as dots plots. Copepods were the most dominant species in the mesozooplankton recorded by VPR; they aggregated at certain depth levels during the day and distributed throughout most of the water column at night. The median depth of copepods was higher during the night (15 m) than during the day (30 m), indicating typical DVM. According to both Fig. 4 and Fig. 5, the most of copepods stayed in the depth above 40 m during the entire day. At night, a considerable part of copepods ascended to an upper layer with the depth <20m (Fig. 5). Fig. 4 also shows that a majority of copepods resided below the thermocline at 20 m but did not descend to a deeper layer during the day. DVM of chaetognatha was similar to that of copepods (Fig. 4 and Fig. 5). The results revealed that nearly all gelatinous zooplanktons (95%–100%) were found on the water surface (<20m) above the thermocline at 3 am, 15 pm, and 21 pm (Fig. 5). However, a portion of gelatinous zooplanktons descended slightly at 9 am; thus, a bulk of gelatinous zooplankton was located in the layer between 5–30 m, deeper than the other three groups. Euphausiid showed no vertical migration behavior in our study probably because their abundance, as determined by VPR, was too low at 15 and 21 pm (Fig. 4) to be plotted in Fig 5.

Discussion

The coastal areas of East China Sea near Zhejiang Province, where our sampling site is located is an important fishery ground for China that exhibits a strongly dynamic and complicated hydrography[34]. This area is also a highly stratified upwelling region with strong thermoclines and haloclines in summer due to the wind[35] (Fig. 2). The upwelling creates a horizontal front in summer that weakens the vertical mix of the water column[36]. The low transparency of the coastal waters restricting the aggregation of the phytoplankton only occurs in the water surface above thermocline. Consequently, high fluorescence values appeared in the upper layer of our sampling site, suggesting that a great amount of phytoplankton inhabited this layer.

Hypoxia of the East China Sea shelf was reported occasionally and has attracted more attention in recent years[37-39]. Due to significant stratification produced by the upwelling, weak vertical mixing, eutrophication, and anoxic KSW[29], the DO of the layer below the thermocline at the sampling site remained between 3–4 mg/L (the Do range of the station was 3.25–8.45 mg/L). On the contrary, at the surface water above the thermocline, the DO was high with the highest value of 8.5 mg/L. High fluorescence detected in the site enhanced the DO.

VPR provides better information about samples with a smaller volume than net and acoustic methods[12]. Compared with VPR, datasets produced by traditional nets were obtained from samples pooled within depth intervals, thus obscuring fine scale/structure information about zooplankton distribution[4,5]. However, VPR can offer abundance, spatial distribution, and taxonomic diversity in situ[11,28]. The fitting sensors of VPR obtained concurrent data on hydrography (temperature, salinity, and density) and phytoplankton biomass (chlorophyll/ fluorescence) from the same parcel of water; thus, it is suitable to resolve the queries regarding zooplankton distributions in relation to the environment[30]

Moreover, VPR is useful for the survey of fragile species, particularly for gelatinous zooplanktons[40]. Some fragile zooplanktons may be damaged during the net tow and cannot be identified. Species also may be dissolved during the preservation process; therefore, they cannot be observed in the samples [41]. The abundance of zooplankton based on images collected via VPR in situ provides more accurate estimates, which can be up to two orders of magnitude greater than the estimates obtained via traditional net and bottle samplers[12]. Although the results of VPRs often show disparity with the results of traditional methods, VPRs and nets always provide comparable information about the concentrations of abundant taxa, such as copepods [28]. In conclusion, video images offered by VPR can offset the deficiency of traditional methods. Therefore, the results obtained via VPR and traditional methods must be compared repeatedly to discuss the difference between them.

VPR also provides other potential advantages. Traditional methods based on stratified sampling of zooplankton always entail much time-consuming work in counting organisms and require skilled researchers for identification. VPR can precisely yield an in situ estimate of taxa and calculate their quantity within microscale patches quickly[40]. Along with technological development, VPR should provide high quantity and high quality data in the future.

To choose an appropriate sampling volume always reflects a compromise between high-resolution image quality and representative sampling of the community[12]. In our research station, the dominate species were macro zooplankton (e.g., copepods and gelatinous zooplanktons); therefore, we used four settings (S0–S3) to investigate all the stations but preferred the S3 setting as the target setting. Since S3 had the largest volume (3×10^{-4} m^{-3}) compared with the other setting in each frame (S0: 2.1×10^{-7} m^{-3}; S1: 5.7×10^{-6} m^{-3}; S2: 4.1×10^{-5} m^{-3}), it could obtain the effective image with a 42 × 42 mm^2 field of view. S3 was considered to be most suitable setting due to the abundance of macrozooplankton in the station. Its sampling volume could be larger and its magnification could be lower, which produces more real time images than other settings. Therefore, the result of S3 would be more suitable for comparison with the traditional sampling result.

As a universal behavior observed by researchers in fresh water and marine environments, various significance and ecological consequence of zooplankton DVM were extensively studied[1]. Consequence of DVM involves zooplankton horizontal dispersal, population distribution, trophic interactions, refined scale community, biochemical courses, and other significant ecological events[1,33,42,43]. Feeding, predators, temperature, halocline, breeding requirement, and light are important impact factors of DVM[1,3,44-49]. Many herbivorous and omnivorous zooplanktons respond to predators by performing classical or normal DVM (leave the productive surface layers and migrate deeper during day)[1,45,47]. Performing normal DVM for utilizing food in the surface layer and avoiding predators were uneconomic with respect to energy consumption[1]. Thus, DVM could be modified using other environmental elements[50].

The hydrological condition was complicated in the study area wherein station was located. Upwelling, unstable thermocline, halocline, occasional low DO, high chlorophyll, and the current probably could alter DVM paradigm of zooplankton. Unfortunately, research in offshore areas of the East China Sea is sparse and often focused on vertical distributions of only several key species in given time[51,52] and insufficiently paid attention on the environmental elements.

Most zooplankton performed classical DVM or normal DVM in our research, which means they ascended at night[2], except for gelatinous zooplankton. Although the light attracted much research attention, it was not one of the important factors impacting zooplankton DVM, given the less transparent offshore seawater at the station[47]. A high fluorescence value existed in the upper 10 m during the 24-h survey, showing the presence of abundant phytoplankton on the water surface. At the station, fluorescence peak (2.5 mg/m^3) was located between 0–15 m. Abundant phytoplankton might be attractive to herbivores and omnivores in the community, such as copepods and euphausiids.

Copepods performed “special” normal DVM according to our result (Fig 4 and 5). They ascended to the upper layer (0–35m) at night and descended in the daytime. But they seldom descended to the water layer deeper than 40m, which was never reported before. *C. sinicus* and *Euchaeta* spp. were dominant at the station based on sample identification and our set of images and performed the same kind of DVM. *C. sinicus* composed more than 60% of copepods. The vertical distribution of copepods seems to correlate with chlorophyll concentrations in our study conducted at night (Fig 4 and Fig 5).

Liu et al found that *Euphausia pacifica* was generally distributed in the layer under 20 m and was mainly concentrated at 30–50 m during the day[53]. However, in our study, only a few individuals were counted in the day time; therefore, the DVM of euphausiid was not considered.

Normal DVM[54-57], abnormal DVM [58], and no DVM[57,59] of *C.sinicus* have been reported in China. In the East China Sea, Wang et al reported *C.sinicus* performed abnormal DVM in autumn and aggregated in the upper 25-m layer showing no DVM during spring[58]. *C.sinicus* was found to perform normal DVM under the strong thermocline, showing no obvious DVM and staying in the cold Yellow sea during the summer[54-57,60], avoiding the extremely hot surface layer because *C.sinicus* could only tolerate environmental temperatures lower than 26.9°C[61]. When the thermocline was weaker, *C.sinicus* performed normal DVM in the entire water column[62]. However, our results were slightly different from the above reports. The DVM range of most copepods (mainly composed of *C. sinicus*) was confined to a layer <40m. The upper layer was narrowed by the Kuroshio Subsurface Water[63], which characterized by minimal food concentration, lower temperature, higher salinity, and moderate hypoxia (Fig 2, Fig 4, and Fig 5).

As food concentration, temperature, salinity, DO, predators, light, and other environmental parameters were considered as factors altering DVM[33,50,57], detailed discussion was essential. Salinity and temperature of the water layer below 40 m did not exceed the scope in which *C. sinicus* could live[64].

DO was consistently low from 20 to 50 m at our station (Fig. 2) as a potential reason impeding the dive of *C.sinicus*. Wang et al found *C.sinicus* would die in 96 h when DO was 3 mg·L^{-1} but would live when DO was 4 mg·L^{-1}, whereas their egg-production rate would be restrained. The results suggested that the physiological activity might be restrained, which implies *C. sinicus* needed to cope with hypoxia; in addition, some adaption mechanism existed, and moderately low DO at the station under 20 m was not lethal for short time exposure [65]. Interestingly, similar case was found in a type of krill, *Meganyctiphanes norvegica*. It often appeared in the hypoxia deep water of fjords. They changed DVM, migrating into deep hypoxic water twice a day, but not traversing the pycnocline. The environmental O^2 tensions it encountered already exceeded its oxy-regulatory ability. Unpublished studies proved that if they migrated deeper or ascended later, they would be killed by their insufficient oxy-regulatory ability[66]. Thus, the krill returned to the oxygenated surface to cope with hypoxia similar to copepod in our study. Therefore, it could be deduced synthetically that stratification was the potential reason why *C.sinicus* preferred to perform normal DVM but did not descend below 40 m. There might be energy trade-off based on several factors for *C.sinicus*. In our study, food concentration was attractive to copepods, inducing DVM, which made them stay within the surface layer during the whole night, thus obtaining a maximum feeding rate and sufficient DO. Another possible reason making *C.sinicus* ascend was breeding[67].During the day, these species required to dive to reduce predation within surface water[1,68]. We suspected that *C.sinicus* preferred to reduce the energy required of their DVM and reduce the time they spent in a hypoxic environment; therefore, they stayed within the medium water layer during the day. However, further studies are required to illustrate the procedure and mechanism.

In many coastal areas and oceanic areas of the world, Oxygen Minimum Zone (OMZ) are common and zooplankton are always found in OMZ regardless of the depth[69-74]. Although behavior effects and physiological response of hypoxia to the zooplanktons always drew attention, few studies concerned how the zooplankton coped with hypoxia [66,75]. Thus, combining two aspects should be essential parts of our exploring study in future.

The pelagic environment hosts a diverse community in which complex interactions and trophic cascades can occur[2]. As the potential predators of copepods, Chaetognatha also performed normal DVM and their abundance peak was consistent with copepods in our study (Fig 5). Migration patterns can be delivered from one to the next trophic level, which was known as “cascading migrations”[76]. Consequently, it could be concluded the DVM of copepods had induced the same DVM of chaetognatha in our study.

An abundance of gelatinous zooplanktons in our study area suggests they were in the process of “blooming;” this trend has not been previously reported in this same area. In our study, gelatinous zooplanktons preferred to reside in the upper water layer with higher temperature and lower salinity, and only a few specimens were observed in the 40–50 m layer. More than 95% of gelatinous zooplanktons (most of them were hydromedusa) were found at salinities <32, suggesting strong salinity stratification may act as a physical barrier.

Different species sometimes preferred different depth ranges to perform their DVM[77,78]. Stratification was also an important factor affecting plankton populations[79] and their DVM behavior[50]. The vertical spreading of gelatinous zooplankton is occasionally reported to be hindered by the salinity stratification or influenced by other environmental variables, e.g., Doliolum (*Thalia democratica*)[80], hydromedusa (*Clytia* spp., *Obelia* spp.)[81], and ctenophore (*Mnemiopsis leidyi*)[33]. Some species are considered as non-migratory; these species always live in the shallowest water layer [82].

The DVM of copepods was modified by gelatinous zooplankton aggregation in zones of higher fluorescence, where they only spent a short time[83], but this was not in accordance with our study. Although hydromedusas were abundant in the surface water, copepods still performed normal DVM and spent almost the entire night in the surface water.

Conclusion

Copepods and chaetognatha performed typical DVM due to food chain requirements. Only a small amount of the copepod population appeared under 40 m because of the lack of DO. Gelatinous zooplanktons aggregated at the water surface layer shallower than 30 m because of salinity stratification. Less euphausiacea individuals were investigated in the study; therefore, their DVM remains uncertain. Applicability of VPR was affirmed herein. DVM of four zooplankton taxa in the coastal areas of the East China Sea might be affected by multiple environmental elements, such as feeding activities, predator–prey relation, water column stratification, and energy utilization.

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Conflict of interest

This manuscript has not been published elsewhere and is not under consideration by another journal. There are no conflicts of interest to declare.

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