



Diel vertical migration and tidal influences on plankton densities in dynamic coastal systems

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ABSTRACT

Recent increased application of optical imaging devices have facilitated efficient capture of plankton abundance and community composition, enabling the study of plankton distribution *in situ* and at a high spatio-temporal resolution. In this study, we aim to investigate how the abundances and distribution patterns of plankton taxa relate over 24-h periods, covering tidal and diel cycles, in the southern North Sea using data from a WP2 net and a Video Plankton Recorder. In the highly dynamic southern North Sea, we document diel vertical migration patterns in the pelagic zone of both pelagic and hyperbenthic taxa, including Calanoida (Copepoda), Amphipoda, Annelida, and Cumacea. In addition, the densities of plankton taxa showed significant small-scale geographical variation over a 24-h period for which tidal currents played an important role, a source of considerable variation that is typically not accounted for. This study adds to the current understanding of plankton distribution and behaviour, particularly in the context of coastal areas characterised by strong tidal cycles and currents, by using *in situ* imaging techniques.

1. Introduction

Plankton are passive drifters in the water, subject to the effects of wind, waves, and currents. While they lack the ability to swim against these forces, some exhibit limited mobility that allows them to determine their vertical position in the water column. Plankton plays a crucial role in the marine food web by contributing to organic matter flux and nutrient recycling (Steinberg and Landry, 2017). Vertical migration can therefore lead to the mobilisation of a considerable biomass through the water column and acts as a vehicle for carbon export in the marine carbon cycle (Steinberg and Landry, 2017). This flux of organic matter is estimated to account for 4–34% of the total particulate organic carbon flux in various regions worldwide (reviewed in Ducklow et al., 2001).

Both plankton and its predators respond to sunlight. While autotrophic phytoplankton (primary producers) try to maximise sunlight exposure for photosynthesis (Vernet, 2000), fish predators (secondary consumers) often require light to detect their zooplanktonic prey (Guthrie, 1986). Fish, and to some extent also phytoplankton, migrate vertically in response to light availability (Gerbersdorf and Schubert,

2011; Kaartvedt et al., 2012; Solberg and Kaartvedt, 2017; Wirtz and Smith, 2020). The movements of zooplankton (primary consumers) in the water column therefore often relate to the vertical distribution of phytoplankton (their prey) and fish (their predator; Reichwaldt and Stibor, 2005; Haupt et al., 2009). Many zooplankton species perform diel vertical migration (DVM; Bandara et al., 2021) which can be categorised in three general migration patterns (Hutchinson, 1957): nocturnal, twilight, and reversed vertical migration, with zooplankton rising from deeper waters towards the surface during night, at twilight, and during daytime, respectively. Nocturnal or twilight migration is the most common behaviour observed among plankton. The underlying mechanisms driving DVM can be behavioural responses to exogenous factors such as light, gravity, temperature, salinity, oxygen, hydrostatic pressure, the availability of food, and potential mates, or endogenous changes in behaviour and physiology (Cohen and Forward, 2016). Various hypotheses were proposed to explain why these organisms perform DVM, but it is commonly assumed to be primarily driven by a trade-off between predator avoidance and foraging opportunities (Loose and Dawidowicz, 1994). Gut fullness plays a significant role in this

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trade-off and studies observed that fatter or fuller individuals prioritise predator avoidance in deeper waters over risky feeding in upper waters (Hays, 2001) and that DVM behaviour in organisms co-occurred with higher feeding rates at night (Daro, 1985). Furthermore, the size-dependent predation risk caused by visual predators led to a hypothesis suggesting that larger copepods predominantly engage in DVM due to their increased susceptibility to visual predation (Hays, 1995).

The vertical distribution of plankton is traditionally studied with nets. Often, systems consisting of multiple nets that can open and close during a vertical haul (e.g., MultiNet, MOCNESS) are deployed within different depth ranges of the water column (Luo et al., 2000; Keskinen et al., 2004). One limitation of this approach is that organisms are in many cases pooled within depth intervals, resulting in a loss of precision regarding their depth and diminishing statistical power when investigating differences in depth distributions between day and night (Pine-I-Alloul, 1995; Pearre, 2003). Advancements in technology to collect *in situ* data led to the development of optical imaging devices such as the Video Plankton Recorder (VPR; Davis et al., 1992). These devices photograph plankton and other particles within the water column and simultaneously collect depth and environmental data, allowing a tight coupling between the environment and plankton community. As a result, a VPR can efficiently capture variation in zooplankton abundance and community composition in 3D and through time, allowing to study the plankton and hyperbenthic taxa distribution with a high vertical spatial resolution. Due to its capabilities, the VPR proved to be very useful to detect small-scale plankton aggregations (Jacobsen and Norrbin, 2009; Möller et al., 2012).

In this study, we use the VPR technology to investigate the relationships between abundances and distribution patterns of several plankton taxa over 24-h periods, a timescale covering two tidal and one diel cycle, during two seasons, in a shallow coastal region with a (nearly) permanently mixed water column (here: the Belgian part of the North Sea; van Leeuwen et al., 2015). These areas experience strong tidal cycles and currents, resulting in a water column with a very weak salinity and temperature stratification (Fettweis and Nechad, 2010). While in certain areas of the North Sea or neighbouring areas some studies failed to detect diel vertical migration of zooplankton (e.g. in the English Channel by Daro, 1985), migratory patterns in copepods were observed

in the Southern Bight of the North Sea (Daro, 1985) and in the retention basin of a disused scouring sluice in the harbour of Ostend, Belgium, which is only sporadically connected to the sea (Daro, 1974). This study utilizes a compelling combination of zooplankton abundance data collected throughout the entire water column using a WP2 net processed by the ZooScan, alongside zooplankton abundance data obtained by a VPR at different depths. These data, along with a comprehensive set of (a)biotic variables, allow us to analyze how plankton is distributed vertically over fine spatial and temporal scales within the water column. By conducting this research, we aim to gain valuable insights into the dynamics of planktonic communities in well-mixed water columns over 24-h periods, thereby enhancing our understanding of diel vertical migration and other migratory patterns in the marine environment.

2. Methodology

2.1. Study area

The Belgian part of the North Sea (Fig. 1) is located in the southern North Sea and is positioned in the transitional region between the Atlantic Ocean and the North Sea. It is a relatively shallow area with maximum depths of about 40 m. The strong semi-diel tidal currents and the alongshore residual current, flowing towards the northeast, result in a well-mixed water column with very weak salinity and temperature stratification (Fettweis and Nechad, 2010). The tidal currents are dominated by tides ranging from 3 m (neap tide) to 4.5 m (spring tide) and have velocities with maxima up to 1.66 m s⁻¹ (Verfaillie, 2008). They are mainly driven by tides and wind force, resulting in anti-clockwise gyres (Otto et al., 1990).

2.2. Sample collection

Data were collected during two 24-h sampling campaigns in May 2021 (19-05-2021 15:37 to 20-05-2021 14:19) and November 2022 (22-11-2022 14:42 to 23-11-2022 09:30) whilst the RV Simon Stevin laid on anchor at station 330 (2.8091° E; 51.4341° N; red point in Fig. 1). In May 19, 2021, the moon phase was first quarter which produces moderate tides known as neap tides, while on November 22, 2022, the moon

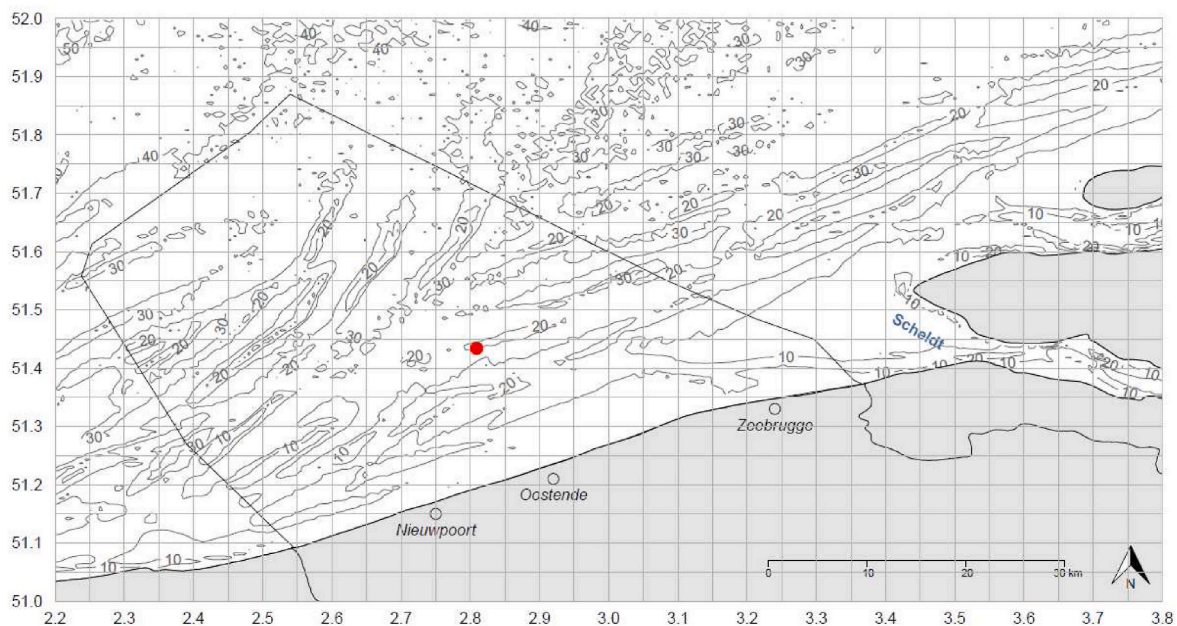


Fig. 1. Sampling station 330 represented as a red point within the Belgian part of the North Sea (black outline). The depth of the water column [m] is represented by the grey lines and values. The X-axis represents longitude [°E] and the Y-axis latitude [°N]. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

phase was a waning crescent, resulting in tidal bulges that are increasing in size until they reach their maximum during the spring tides at new moon phase. Every hour, data on mesoplankton and associated water parameters were collected. Mesoplankton were imaged *in situ* by means of a Real Time VPR (Seascan, Inc.), capable of sampling particles ranging from 100 μm up to a few centimeters. This said, identification of plankton is more efficient for specimen exceeding 400 μm (Ollevier et al., 2022). The VPR was deployed each hour for approximately 15 min, while it was lowered and raised vertically through the water column at a speed 0.15 m s⁻¹. It was deployed 3 m from the seafloor and 3 m beneath the surface to avoid hitting the seafloor or the ship.

The image data was manually classified by sorting the mesoplankton into the categories: Amphipoda, Annelida, Appendicularia, Appendicularia house, Brachyura zoea, Calanoida, Caridea, Chaetognatha, Cirripedia cypris, Cirripedia nauplius, Cnidaria, Ctenophora, Cumacea, Echinodermata, Harpacticoida, *Noctiluca* and *Phaeocystis*. The prymnesiophyte *Phaeocystis* was counted in numbers of colonies, as the VPR has the capacity to detect and observe these collective formations but not individual cells. Other particles were classified as detritus, bubbles, fibres or unknown. Plankton densities were calculated as the number of individuals per sampled volume and then linearly extrapolated to cubic metres of water [ind m⁻³].

During the first hours of the cruise in May, the imaged volume of every VPR frame was 29.564 mL which was calculated as the field of view (magnification setting S1: 20.8 \times 15.2 mm) multiplied by focal depth. The latter was determined by the parameters used with the VPR AutoDeck software: a “segmentation threshold – low” of 0, a “segmentation threshold – high” of 131, a “focus – sobel” of 23, and a “focus – std dev” of 2. From 3 a.m. (UTC+2) onwards, these parameters were accidentally changed, resulting in an imaged volume of 26.345 mL for the remainder of the cruise (a segmentation threshold – low of 0, a segmentation threshold – high of 132, a focus – sobel of 25, and a focus – std dev of 2). As a result of the smaller sampling volume, approximately 10% less organisms were encountered. The second highest magnification, S1, was chosen as a trade-off between image detail and observation chance of particles (Ollevier et al., 2022). In November the imaged volume was 23.391 mL for the whole campaign, based on magnification setting S1, a segmentation threshold – low of 0, a segmentation threshold – high of 135, a focus – sobel of 25, and a focus – std dev of 1. Simultaneously, fluorescence, turbidity, salinity, temperature, and depth data were collected with the ECO Puck FLNTU fluorometer and turbidity sensor (WETLabs), and SBE 49 CTD sensor (Sea-Bird Electronics, Inc.) that was mounted on the VPR, allowing to link plankton images with *in situ* environmental and position data at the moment of collection. Salinity was measured using the Practical Salinity Scale. Data on average current speed and averaged current direction (Average Current Speed TimeSeries - Belgian Coastal Zone - COHERENS UKMO. (n.d.); Average Current Direction TimeSeries - Belgian Coastal Zone - COHERENS UKMO. (n.d.)) were derived from the ERDDAP data server of RBINS (Royal Belgian Institute of Natural Sciences, n.d.).

Mesoplankton were also sampled with a 200 μm WP2 net, which was deployed vertically and equipped with a flowmeter, following the protocol of Mortelmans et al. (2019b). Zooplankton collected in the cod-end were sedated by soda water and fixed in 4% formalin. In the lab, the fixative was changed to 70% ethanol. The samples were digitised by the ZooScan plankton imaging device and processed by ZooProcess and Plankton Identifier in order to detect and classify the digitised objects (Grosjean, 2004; Gorsky et al., 2010). Images were manually controlled and validated to the categories Amphipoda, Annelida, Anomura, Appendicularia, Branchiopoda, Brachyura megalopa, Brachyura zoea, Calanoida, Chaetognatha, Cirripedia cypris, Cirripedia nauplius, Cnidaria, Ctenophora, Cumacea, Echinodermata larvae, Harpacticoida, Mollusca, Mysida, fish egg, artefact, detritus, fibres, and *Noctiluca*.

2.3. Data analysis

Due to adverse weather conditions during the November campaign, VPR data could only be gathered from 2 p.m. till 9 a.m. The weather also hindered the collection of a continuous series of WP2 net samples. Net samples from November are therefore not considered in this study. Plankton densities and distributions through the water column were visually represented in R v4.0.3 (R Core Team, 2020). The depth under which 75% of the community could be found at day and night was represented by the 25th percentile. Nighttime was defined as the period between sunset and sunrise, specifically, between 21:31 and 05:47 in May, and between 16:48 and 08:11 in November. Conversely, observations made outside of these time frames were categorised as daytime. To assess the relative influence of environment, tides and diel cycle on plankton community composition and species abundances, variation partitioning analysis was used. This method allows us to dissect the variance in community data attributed to these factors. For this analysis, plankton community data, aggregated per VPR deployment, was Hellinger transformed (Borcard et al., 2011). The Hellinger transformation is suitable for compositional data, preserving the Euclidian distance and aiding in the analysis of community structure. The model was then built as a function of environmental, tidal and diel cycle parameters using redundancy analysis (RDA). RDA was chosen for its ability to handle complex ecological datasets and is well-suited for modeling relationships between the entire plankton community and multivariate predictor variables. The environmental dataset contained temperature, salinity, turbidity and chlorophyll concentration. The tidal dataset consisted of data on maximum sampling depth (which serves as a proxy for tide, i.e. the alternate rising and falling of the sea), average current direction and average current speed. In the diel effect dataset solar altitude (‘sunAngle’ function from the *oce* v.1.7–2 package; Kelley and Richards, 2022) was included. The number of environmental and tidal predictors was reduced using a forward selection procedure. These final set of predictor variables were used for variation partitioning analysis using the *vegan* v. 2.6–2 package (Oksanen et al., 2022) in R. The role of tidal and diel patterns on the depth distribution of taxa was analysed using generalized additive models (GAMs) with a log-link function assuming a Poisson distribution of the response variables (counts of the individual plankton taxa). Unlike generalized linear models, which are constrained by the assumption that all explanatory variables are linked in a linear combination with the response variable, GAMs can model non-linear relationships between predictors and the response variable by applying smooth functions and uncover complex patterns and relationships in the data (Zuur et al., 2009). However, it is essential to note that in the present study, GAMs were primarily employed for visualizing underlying patterns within the raw data. The emphasis was placed on exploring and understanding complex relationships, as opposed to interpreting the significance of the statistical test, given that certain assumptions required for conventional model interpretation were not met (Zuur et al., 2009). These analyses were carried out with the *mgcv* package (Wood, 2011) in R. The models included ‘depth’, ‘diel’, ‘tides’, and ‘detritus’ as predictors and allowed for an interaction term for ‘depth’, and ‘diel’ (see formulas in Supplementary Table 1). By incorporating ‘detritus’ in the GAMs of the various taxa, the influence of passive particle distribution driven by diel and tidal patterns is taken into account, which allows to distinguish and analyze the distribution patterns of the taxa itself.

3. Results

3.1. Abiotic environment over time

During the 24-h cycle in May it was high tide at 19:11 and 8:10 and low tide at 2:21 and current speed ranged between 0.15 m s⁻¹ and 0.64 m s⁻¹. The CTD upcasts measured temperatures ranging between 11.2 and 11.7 °C and observed no stratification layers in the water column. In

some cases the temperature was homogeneously distributed along the entire water column, although in most cases there were slight surface-bottom differences where the surface part had a maximally 0.1 °C higher temperature than the seafloor. The strongest differences between top and bottom occurred between high and low tide at the turning of the tides, i.e. currents changing direction. Overall, salinity ranged between 32.8 and 33.8, and was not stratified over the water column. Based on the FLNTU and turbidity sensor on the VPR, mean turbidity was 1.43 NTU (Q1: 0.60 - Q3: 2.00) and mean chlorophyll *a* concentration 1.71 µg L⁻¹ (Q1: 1.2 - Q3: 2.05). In November it was low tide at 18:25 and 6:46, and high tide at 0:09, with current speeds ranging between 0.20 and 1.00 m s⁻¹. CTD upcasts revealed water temperatures between 13.3 and 13.6 °C and salinity values between 34.6 and 34.7. These measurements indicated a homogenous water column without stratification. Mean turbidity was 1.75 NTU (Q1: 0.8 - Q3: 2.4) and mean chlorophyll *a* concentration was 1.11 µg L⁻¹ (Q1: 0.90 - Q3: 1.30).

3.2. Species abundance over time

The densities of plankton taxa, represented in Fig. 2 and in Supplementary Tables 2 and 3, showed large variation over the 24-h time period, both for the WP2 and VPR data. Although the order of magnitude of densities differed, similar abundance patterns were often observed by the two methods. The peaks did not coincide with high or low tide, but displayed some time lag in relation to high or low tide occurrences, approximately peaking or declining approximately 2 h prior to changes in tidal patterns. *Noctiluca*, Calanoida and Echinodermata were observed throughout the whole period by both methods and exhibited a pronounced pattern in density over time with two peaks for *Noctiluca* and a third peak for Calanoida and Echinodermata. *Phaeocystis*, only observed by the VPR, displayed a similar pattern with two distinct peaks. *Noctiluca* and *Phaeocystis* were most abundant in the VPR dataset with peak densities of 1320 ind m⁻³ and 1818 ind m⁻³, respectively. Calanoida and Echinodermata had maximum densities of 59 and 24 ind m⁻³, respectively, with the VPR. Calanoida and *Noctiluca* showed the highest peak densities in the WP2 dataset with densities of 14,650 ind m⁻³ and 12,623 ind m⁻³, respectively.

In both observation methods Amphipoda, Annelida, and Cumacea were mainly observed during night-time. Other taxa such as Appendicularia, Caridea, Chaetognatha, Cirripedia cypris, Cirripedia nauplius, Cnidaria, Harpacticoida, and fish egg were sporadically observed with the VPR during the day (Supplementary Table 2). For most of these taxa this was also the case for the WP2 data (Supplementary Table 3), except

for the taxa Cirripedia nauplius, Cirripedia cypris, and Harpacticoida which were observed more frequently throughout the day and had two peaks with sometimes a third smaller peak. Other species that were additionally sporadically observed by the WP2 net were Anomura, Brachyura megalopae, Brachyura zoeae, Mollusca, and Porcellanidae.

3.3. Effect of environmental conditions on species abundances and community composition

The results from the variation partitioning analysis shown in Fig. 3 A indicated that environmental, tidal, and diel predictors together explained 41.4 % (calculated by subtracting the residuals from 1) of the variation in taxa abundances of the plankton community. The selected predictors were chlorophyll concentration (environmental), maximum sampling depth (tidal), and altitude of the sun (diel). The environmental predictors explained 18.0 % ($p < 0.001$). Tidal predictors explained the largest part of the variation and accounted for 28.3 % of which 21.7 % ($p < 0.001$) could be attributed purely to the tidal effect. Diel predictors explained 13.8 %, of which nearly half was shared variation explained by both diel cycle and tides. Diel variation alone accounted for 7.2 % of the variation ($p < 0.05$). The RDA biplot (Fig. 3 B) shows that the first axis is positively correlated with all parameters, but has the strongest association with the tidal parameter. The second axis is positively associated with diel and tidal variables, but negatively with environmental ones. Distinct taxa are Calanoida, *Noctiluca*, and *Phaeocystis* and the cluster of Amphipoda, Annelida, and Cumacea.

3.4. Diel vertical migration

The vertical distribution of plankton are represented in Fig. 4 and reveal that certain taxa in the dataset showed clear displacements through the water column over the observed 24-h period in May. The taxa Amphipoda, Annelida, and Cumacea (Fig. 4 A, B, D) were not or hardly observed during the day, while being observed several times during the night. Calanoida (Fig. 4 C), an abundant taxa in the zooplankton community, on the other hand, were observed during the entire 24-h period, but the majority of calanoids was found in shallower water layers at night compared to their position at daytime. During the day 75% of the calanoid copepod community was present below 9.2 m whereas at night this was at 5.7 m (Supplementary Table 4). In November only Cumacea (Fig. 4 H) were sufficiently present for meaningful statistical analysis in the VPR data and therefore are the only taxa visualised in November. Cumacea were regularly observed at night,

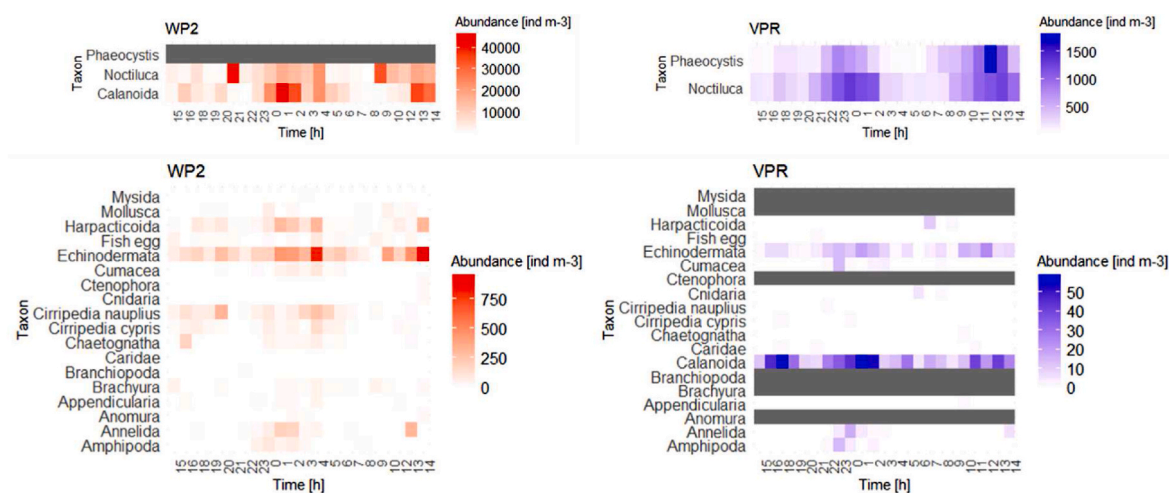


Fig. 2. Plankton densities [ind m⁻³] over a 24-h time period [h] in May as observed by a WP2 net (red) and VPR (blue). Taxa that were not observed by a sampling method are represented in grey. Note that different scales are used for abundance [ind m⁻³] between the plots. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

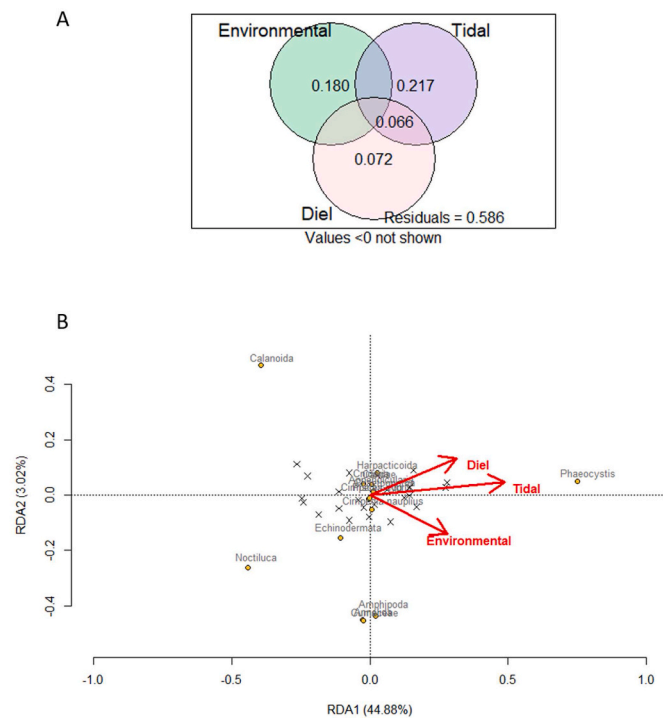


Fig. 3. (A) Venn diagram showing the variation partitioning results for Hellinger-transformed plankton abundance data explained by unique and joint effects of environmental (green), tidal (purple), and diel (pink) factors. Only significant effects ($p < 0.05$) are represented. The overall explained variation in taxa abundances of the plankton community are calculated by subtracting the residuals from 1 which ensures a more accurate assessment of the unique and shared contributions of the explanatory variables, addressing the issue of overestimation (e.g., a portion of the shared variation being counted twice) caused by collinearity. (B) Biplot of RDA showing the effect of the environmental, tidal, and diel variables (red arrows). Species are represented as yellow dots, the sampling times as crosses. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

but because only a limited number of observations were made during daytime in the 17-h period, it is not possible to know if the taxon was present or absent during the unsampled times of the day. Hence, drawing definitive conclusions about DVM patterns of Cumacea in November is challenging. Moreover, the distribution of detritus was visualised (Fig. 4 E) as this provides insights into the dispersion of passive particles within the water column as they are primarily influenced by hydrodynamical forces. Elevated densities were found in the deeper layers and density peaks occur approximately 12 h apart from each other over the course of the 24-h period.

The GAMs (see Supplementary Table 1) explained 6.17, 17.2, 28.7, and 44.9% of the variation in the distribution of Calanoida, *Noctiluca*, *Phaeocystis*, and detritus, respectively. For the hyperbenthic taxa Amphipoda, Annelida, and Cumacea these numbers were 26.4, 22.1, and 21.1% of the variance, respectively. The visualisations of the model for the taxa represented in Fig. 5 show that Calanoida (Fig. 5 C) will be present in the surface layers at night and in the deeper layers during the day and that the hyperbenthic Amphipoda and Cumacea (Fig. 5 A, D) will be more present in the water column during night-time. Annelida (Fig. 5 B) probably follows the same pattern as the latter two taxa, but there is an outlier observation during the day (see Fig. 4 B; between 14:00 and 15:00) that skews the pattern in the visualisation of the predicted distribution. The slightly symmetrical GAM prediction patterns of *Noctiluca*, *Phaeocystis*, and detritus (Fig. 5 F, G, E) suggest semi-diurnal changes in densities.

4. Discussion

Our study detected DVM patterns for Calanoida and observed an upward migration of them at night. This corroborates earlier observations by Daro (1974, 1985) in the southern North Sea which described DVM in the following copepod species: *Acartia bifilosa*, *Pseudocalanus elongatus*, and *Temora longicornis*. Although DVM rhythms are extensively studied for pelagic migrators in the open ocean, they remain relatively unexplored in shallow and well-mixed waters. In the open ocean, organisms are known to undertake migrations spanning distances of tens to hundreds of metres (Ringelberg, 2010). Yet, our study unveiled that DVM patterns also manifest on a smaller scale, with migrations exhibiting only a few metres in amplitude. The results demonstrate that individuals engage in DVM even over short distances, with migrations as narrow as approximately ± 3.5 m, within shallow and well-mixed waters.

Our data shows that DVM rhythms also occur in hyperbenthic taxa. So far, DVM of hyperbenthic organisms in the southern North Sea were described for Annelida (*Polydora ciliata*), Gastropoda (*Crepidula fornicata*), and Bivalvia larvae (*Magallana gigas*; Daro, 1974). Our study confirms DVM for Annelida and extends this list of taxa displaying DVM with Amphipoda and Cumacea for which this behaviour was not yet reported in the southern North Sea. Due to the limitations in the taxonomic resolution of our data, species names cannot be provided for the organisms displaying DVM. It is crucial to note that DVM patterns reflect attributes unique to certain species or individuals and are not representative of entire community (Bollens and Frost, 1991). Therefore, when discussing e.g. Amphipoda and Cumacea, we are referring to specific species or subsets of individuals rather than the entire population. In our study, the hyperbenthic taxa were predominantly observed at night in the VPR and WP2 data, indicating that they actively leave the seafloor and enter the pelagic water column at night. They were observed throughout the whole water column which is particularly useful because being high above the bottom helps their dispersal and habitat selection during settlement (Ullberg and Ólafsson, 2003). Other hyperbenthic organisms migrate to the surface to reproduce (e.g. Annelida; Bartels-Hardege and Zeeck, 1990) or moult (e.g. Cumacea; Anger and Valentin, 1976; Gerken et al., 2022).

Observations over various months within the plankton community hint at the plausible existence of temporal variation in DVM patterns, yet definitive confirmation remains elusive due to the lack of collected data. During the winter months, numerous taxa exhibited low abundances hampering research into their vertical migration patterns. Only Cumacea were sufficiently abundant for analysis in November. Their observations in November seemed to have the greatest abundance during two moments, namely after sunset and before sunrise. Earlier studies, however, did reveal that seasonal changes in DVM patterns in hyperbenthic taxa are not uncommon (Brunel, 1979) and can relate to variations in free-swimming behaviour between species (Wang and Dauvin, 1994), life stages, or sexes (Dauvin and Zouhiri, 1996). This phenomenon described in the literature implies potential variations in the timing or seasonality of DVM behaviour, introducing complexities that warrant further exploration. To gain a deeper understanding of the nuances in DVM patterns, it is imperative to consider the potential influence of varying environmental conditions and temporal dynamics. Our research offers insight into a limited temporal timeframe and observed clear DVM behaviour of certain plankton groups, but this might not be representative of the broader migratory behaviour within the study system. Additional sampling and research efforts could therefore shed more light on the intricacies of DVM patterns under different contexts and temporal intervals.

Plankton and detritus densities exhibited fluctuations within a 24-h timeframe, as evidenced by both net samples and the VPR. Densities differed for samples of the same location taken just a few hours apart from each other. The tidal cycle played a role in this, but peak densities did not necessarily coincide with high or low tide and exhibited a time

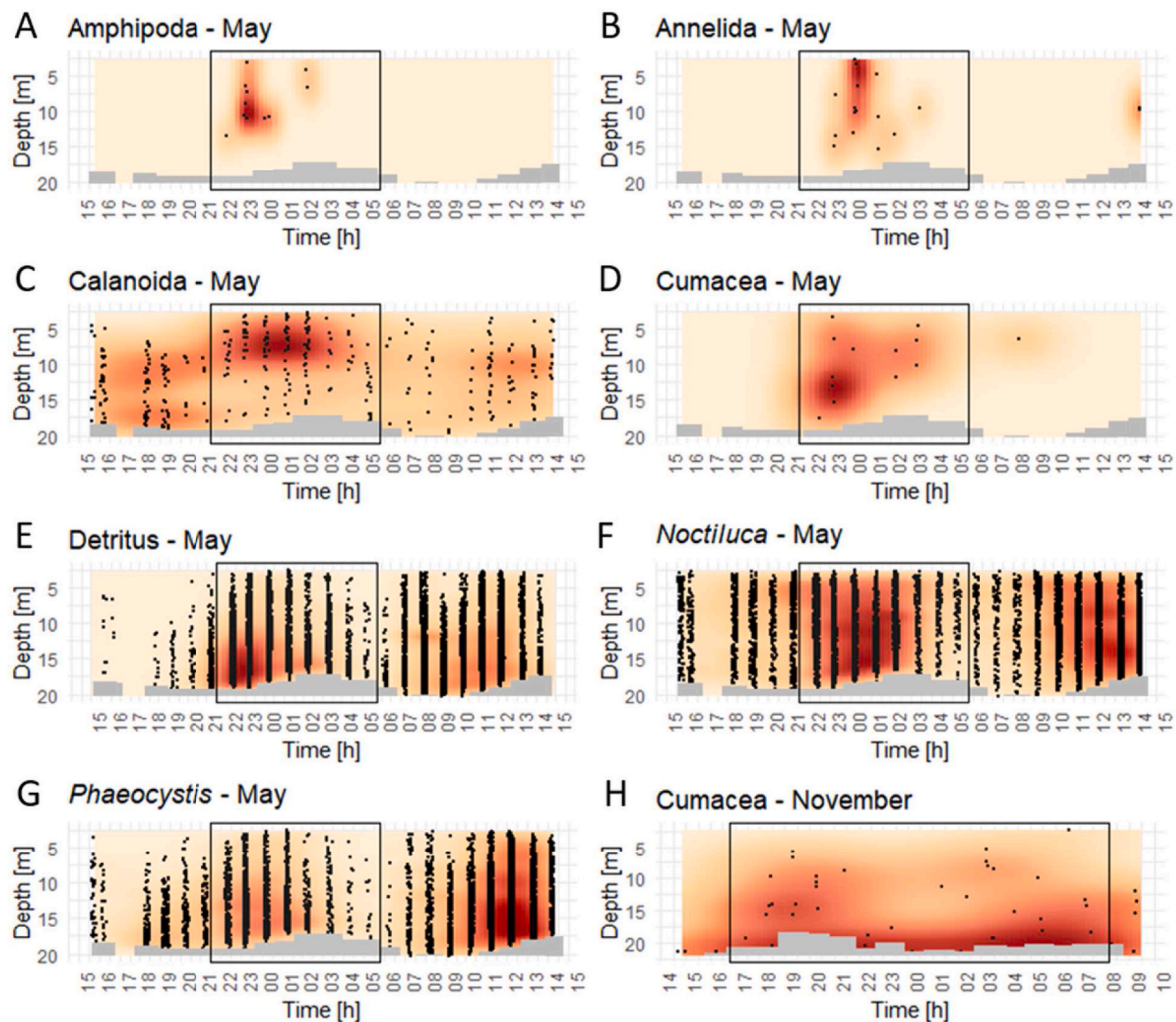


Fig. 4. Kernel density plots for the depth distribution of individual observations (black dots) of (A) Amphipoda, (B) Annelida, (C) Calanoida, (D) Cumacea, (E) detritus, (F) *Noctiluca*, and (G) *Phaeocystis* in May and (H) Cumacea in November over time [h] based on Video Plankton Recorder data. The red areas represent higher interpolated densities for the group under consideration and the rectangular box represents night-time. Remark: from 3 a.m. onwards (in May) a smaller sampled volume was used resulting in $\pm 10\%$ less observed particles. In May there was no data collected at 5 p.m. Note that the depth range varies depending on the tides (the area below the maximum sampling depth is represented in grey). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

lag. While previous studies reported on copepods and amphipods being more abundant in the water column during flood than ebb tides (Hough and Naylor, 1991, 1992), we found plankton densities to be generally less abundant during flood tides. Due to the observed time lag and difference in the timing of peak densities and tidal cycles in different studies, we infer that a plankton patch with higher densities is oscillating back and forth with the (anticlockwise) tidal gyres, rather than the tides themselves having a direct effect on the plankton community. As the tidal currents change direction within the tidal cycle, they usher in new water masses over the sampling location. Considering the local aggregation and small-scale geographical variations of plankton (Benoit-Bird et al., 2013; Robinson et al., 2021), we can observe a distinct waxing and waning pattern of a high-density plankton and detritus patch passing through the sampling site every 12 h, which corresponds to the duration of a tidal cycle. This pattern was observed for most plankton taxa, but was the most distinct for passive particles (detritus; Fig. 4 E) and less mobile organisms (*Noctiluca* and *Phaeocystis*; Fig. 4 F, G). To gain further insight into the potential trajectory and potential distance travelled by the patch, we conducted a simulation at the moment of sampling (from 19 to 05–2021 19:00 to 20-05-2021 07:00) using the OSERIT model (Legrand et al., 2023). This oil spill model simulates the

three-dimensional drift of oil on the sea surface and within the water column. Acknowledging the disparities in characteristics such as buoyancy between plankton and oil, the displacement of both is shaped by environmental factors, leading us to posit that the model's output can provide insights into the potential distance and scale of the distribution of a plankton patch. The model calculates the independent movement of single particles under the combined action of the wind, water current and waves. The simulation depicted that the patch follows an ellipsoid-shaped trajectory over the course of a tidal cycle, with a major axis extending 4.4 km and a total travel distance covering 11.6 km. This suggests that plankton and passive floating marine particles may traverse considerable distances over several kilometres during tidal cycles and that their movements driven by tidal forces may contribute to the spatial heterogeneity of coastal marine communities.

The documented DVM and geographic variation of zooplankton bear implications for both the functioning of the food web and the methodologies employed in plankton sampling. To begin with, zooplankton movements in the water column affect the spatial and temporal overlap of predators and prey resulting in ecosystem-wide implications through changing predator-prey interactions (Reichwaldt and Stibor, 2005; Haupt et al., 2009). Furthermore, the migratory patterns are directly

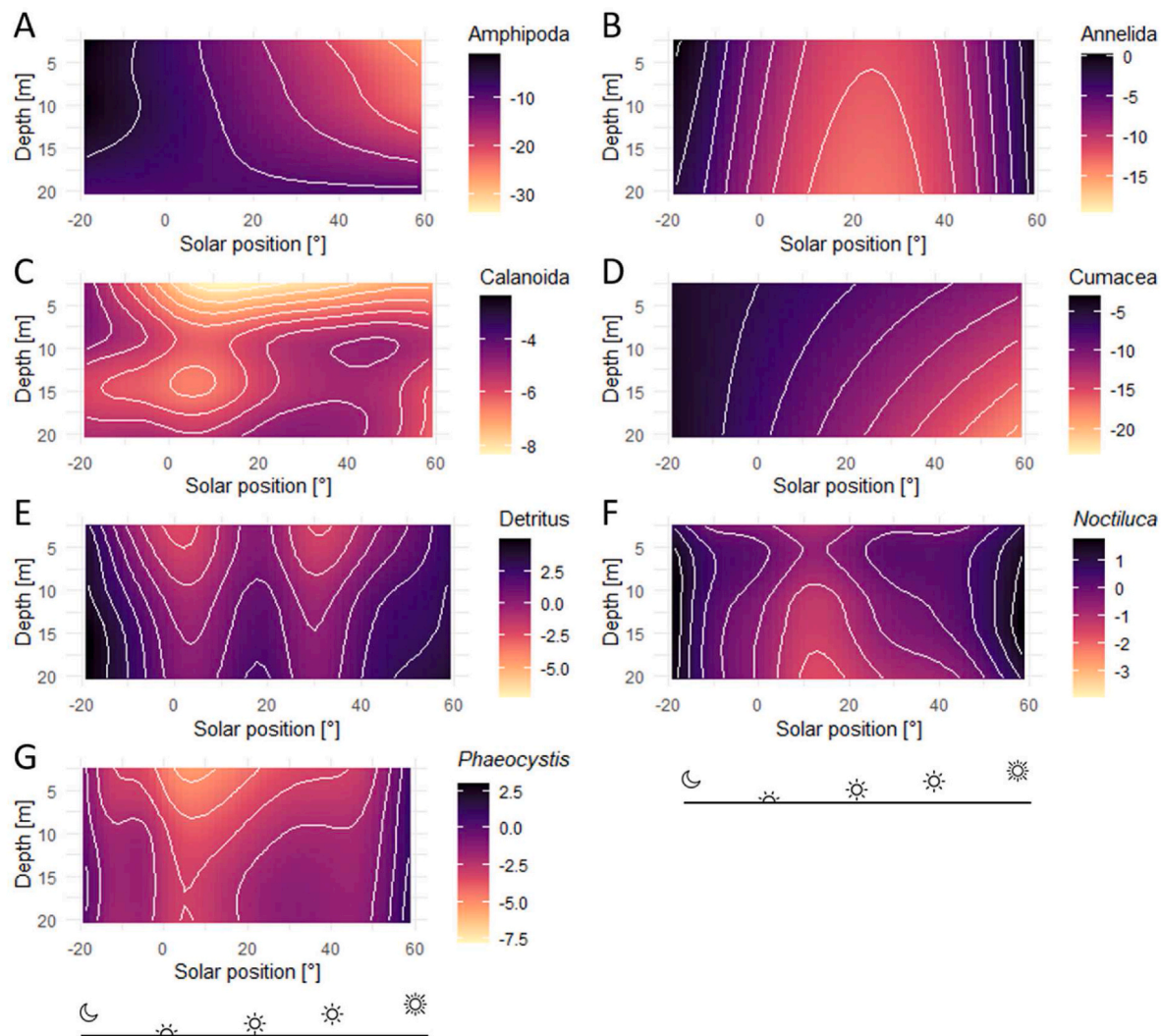


Fig. 5. Visualisation of the predicted distribution of Amphipoda, Annelida, Calanoida, Cumacea, detritus, *Noctiluca*, and *Phaeocystis* across different depths [m] and times of day based on the fitted GAM. Predicted abundances are shown using a colour gradient (yellow: low abundance; purple: high abundance). The x-axis represents the angle of the sun [°] respective to the horizon as a proxy for a diel variable (Values from -20 till 0 represent night. Higher values correspond to a higher solar position and are closer to noon.). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

linked with the ocean carbon cycling as organisms engaged in these migrations aid in transporting energy and nutrients across different ocean depths (Steinberg and Landry, 2017). Regarding sampling methodologies, the timing of plankton sampling emerges as a pivotal consideration that can shape the observed composition and abundance of plankton communities. Focusing solely on samples taken during daylight hours can lead to the oversight of crucial components, particularly the (meroplanktonic larvae of) hyperbenthic organisms, which contribute substantially to the pelagic biomass at night. This discrepancy could lead to underestimations in biomass and the representation of specific marine constituents and is a component that is often overlooked in coastal food web models (Carloti and Poggiale, 2010). Our results thus further emphasise the significance of including these overlooked entities in the overall ecological picture. Moreover, the impact of tidal cycles on plankton densities adds another layer of complexity to the sampling process. Densities can significantly differ depending on the timing of the tidal cycle (and the location of the plankton patch at that moment), as our findings suggest that tidal currents can significantly alter plankton abundances within hours. These findings bear significant implications for samples collected through stationary observations, as opposed to Lagrangian observations, and introduce a challenge that necessitates careful consideration or appropriate correction methods.

However, they also unveil a crucial explanatory factor accounting for a substantial portion of the variance in plankton densities, distinct from the more commonly acknowledged influences like phenological or seasonal shifts.

The occurrence of vertical migration and small-scale patchiness among zooplankton is widely acknowledged but rarely quantified, particularly in our study region where little knowledge on the influence of the physical environment on plankton distribution and DVM behaviour is available (Daro, 1985; Fransz et al., 1998). Our research demonstrates the suitability of the VPR as a tool for studying zooplankton DVM and collecting distribution data with high spatio-temporal resolution, offering logistical advantages over net samples at depth intervals. However, the VPR methodology presents inherent limitations, notably the exclusion of the top and bottom 3 m due to safety considerations (Ollevier et al., 2022). To address this limitation, we included complementary data from a vertical WP2 net. Although the WP2 net may not provide precise depth-specific plankton data, it does yield valuable insights into plankton densities across a substantial portion of the water column, including the upper layer. The WP2 findings have revealed comparable patterns throughout the entire water column, albeit with differences in magnitude compared to the VPR. A systematic assessment of this difference is currently under investigation. In spite of the VPR's

missing surface-layer data, its efficacy in capturing similar patterns and providing accurate insights into plankton migration and small-scale patchiness remains evident, corroborated by the observations from the WP2 net. This convergence of findings from both methodologies bolsters the reliability of the research approach and highlights the VPR's capacity to unveil intricate behaviours like DVM and patchiness, while also acknowledging the ongoing need for methodological refinement and thoughtful consideration of complementary data sources.

5. Conclusion

This study investigated how the abundances and distribution patterns of plankton taxa relate over 24-h periods, covering tidal and diel cycles, in the southern North Sea. The VPR allowed fine-scale tracking of individual planktonic taxa through a diel cycle, leading to the observation of their daily migration patterns. Next to the migration behaviour at night towards the surface layers of pelagic taxa such as Calanoida, this study is the first to describe the migration of Amphipoda and Cumacea from the sea bottom to high up into the water column at night in the southern North Sea. In addition, samples of the same location taken just a few hours apart showed significant differences regarding plankton densities over time. The density peak patterns mirrored a tidal cycle's trend, albeit with some time lag, suggesting plankton's transportation with tidal currents and emphasising its small-scale patchy distribution in the water column. This study documents the wide variability in plankton distribution patterns and highlights that tidal currents can affect plankton densities over time which has important consequences for samples from stationary observations.

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CRedit authorship contribution statement

Anouk Ollevier: Writing – review & editing, Writing – original draft, Formal analysis, Data curation. **Jonas Mortelmans:** Writing – review & editing, Supervision, Data curation. **Klaas Deneudt:** Writing – review & editing, Supervision. **Pascal I. Hablützel:** Writing – review & editing, Supervision, Formal analysis, Data curation. **Marleen De Troch:** Writing – review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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References

- Anger, K., Valentin, C., 1976. In-situ-Untersuchungen zum täglichen Aktivitätsrhythmus von *Diastylis rathkei* (Cumacea, Crustacea) und ihre Bedeutung für das „Hyperbenthos. *Helgoländer Wissenschaftliche Meeresuntersuchungen* 28 (2), 138–144. <https://doi.org/10.1007/bf01610349>.
- Average Current Direction TimeSeries - Belgian Coastal Zone - COHERENS UKMO. (n.d.). [Data set]. Koninklijk Belgisch Instituut voor Natuurwetenschappen (KBIN), Operationele Directie Natuurlijk Milieu (OD Natuur), Ecosystems data processing and modelling (ECODAM). Retrieved December 20, 2023, from http://data.europa.eu/88u/dataset/avrcurdir_ts.
- Average Current Speed TimeSeries - Belgian Coastal Zone - COHERENS UKMO. (n.d.). [Data set]. Koninklijk Belgisch Instituut voor Natuurwetenschappen (KBIN), Operationele Directie Natuurlijk Milieu (OD Natuur), Ecosystems data processing and modelling (ECODAM). Retrieved December 20, 2023, from http://data.europa.eu/88u/dataset/avrcurdir_ts.
- Bandara, K., Varpe, Ø., Wijewardene, L., Tverberg, V., Eiane, K., 2021. Two hundred years of zooplankton vertical migration research. *Biol. Rev.* 96 (4), 1547–1589. <https://doi.org/10.1111/brv.12715>. Portico.
- Bartels-Hardege, H.D., Zeeck, E., 1990. Reproductive behaviour of *nereis diversicolor* (Annelida: polychaeta). *Mar. Biol.* 106 (3), 409–412. <https://doi.org/10.1007/bf01344320>.
- Benoit-Bird, K.J., Battaile, B.C., Heppell, S.A., Hoover, B., Irons, D., Jones, N., Kuletz, K. J., Nordstrom, C.A., Paredes, R., Suryan, R.M., Waluk, C.M., Trites, A.W., 2013. Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies. *PLoS One* 8 (1), e53348. <https://doi.org/10.1371/journal.pone.0053348>.
- Bollens, S.M., Frost, B.W., 1991. Diel vertical migration in zooplankton: rapid individual response to predators. *J. Plankton Res.* 13 (6), 1359–1365. <https://doi.org/10.1093/plankt/13.6.1359>.
- Borcard, D., Gillet, F., Legendre, P., 2011. Numerical Ecology with R. <https://doi.org/10.1007/978-1-4419-7976-6>.
- Brunel, P., 1979. Seasonal changes of daily vertical migrations in a suprabenthic coldlayer shelf community over mud in the gulf of St. Lawrence. *Cyclic Phenomena in Marine Plants and Animals* 383–390. <https://doi.org/10.1016/b978-0-08-023217-1.50056-4>.
- Carlotti, F., Poggiale, J.C., 2010. Towards methodological approaches to implement the zooplankton component in “end to end” food-web models. *Prog. Oceanogr.* 84 (1–2), 20–38. <https://doi.org/10.1016/j.pocan.2009.09.003>.
- Cohen, J.H., Forward Jr., R.B., 2016. Zooplankton diel vertical migration — a review of proximate control. *Oceanogr. Mar. Biol.* 89–122. <https://doi.org/10.1201/9781420094220-5>.
- Daro, M.H., 1974. Etude des migrations nycthemerales du zooplancton dans un milieu marin peu profond. *Hydrobiologia* 44, 149–160.
- Daro, M.H., 1985. Feeding rhythms and vertical distribution of marine copepods. *Bull. Mar. Sci.* 37 (2), 487–497.
- Dauvin, J.-C., Zouhiri, S., 1996. Suprabenthic crustacean fauna of a dense Ampeliscacommunity from the English Channel. *J. Mar. Biol. Assoc. U. K.* 76 (4), 909–929. <https://doi.org/10.1017/s0025315400040881>.
- Davis, C.S., Gallagher, S.M., Berman, M.S., Haury, L.R., Strickler, J.R., 1992. The video plankton recorder (VPR): design and initial results. *Arch. Hydrobiol. Beih.* 36, 67–81.
- Ducklow, H., Steinberg, D., Buesseler, K., 2001. Upper Ocean carbon export and the biological pump. *Oceanography* 14 (4), 50–58. <https://doi.org/10.5670/oceanog.2001.06>.
- Fettweis, M.P., Nechad, B., 2010. Evaluation of in situ and remote sensing sampling methods for SPM concentrations, Belgian continental shelf (southern North Sea). *Ocean Dynam.* 61 (2–3), 157–171. <https://doi.org/10.1007/s10236-010-0310-6>.
- Franz, H., Gonzalez, S., Steeneken, S., 1998. Metazoan plankton and the structure of the plankton community in the stratified North Sea. *Mar. Ecol. Prog. Ser.* 175, 191–200. <https://doi.org/10.3354/meps175191>.
- Gerbersdorf, S.U., Schubert, H., 2011. Vertical migration of phytoplankton in coastal waters with different UVR transparency. *Environ. Sci. Eur.* 23 (1) <https://doi.org/10.1186/2190-4715-23-36>.
- Gerken, S., Meland, K., Glenner, H., 2022. First multigene phylogeny of Cumacea (crustacea: peracarida). *Zool. Scripta* 51 (4), 460–477. <https://doi.org/10.1111/zsc.12542>. Portico.
- Gorsky, G., Ohman, M.D., Picheral, M., Gasparini, S., Stemmann, L., Romagnan, J.-B., Cawood, A., Pesant, S., Garcia-Comas, C., Prejger, F., 2010. Digital zooplankton image analysis using the ZooScan integrated system. *J. Plankton Res.* 32 (3), 285–303. <https://doi.org/10.1093/plankt/fbp124>.
- Grosjean, P., 2004. Enumeration, measurement, and identification of net zooplankton samples using the ZOO SCAN digital imaging system. *ICES (Int. Council. Explor. Sea) J. Mar. Sci.* [https://doi.org/10.1016/s1054-3139\(04\)00040-2](https://doi.org/10.1016/s1054-3139(04)00040-2).
- Guthrie, D.M., 1986. Role of vision in fish behaviour. *The Behaviour of Teleost Fishes* 75–113. https://doi.org/10.1007/978-1-4684-8261-4_4.
- Haupt, F., Stockenreiter, M., Baumgartner, M., Boersma, M., Stibor, H., 2009. Daphnia diel vertical migration: implications beyond zooplankton. *J. Plankton Res.* 31 (5), 515–524. <https://doi.org/10.1093/plankt/fbp003>.

- Hough, A., Naylor, E., 1991. Field studies on retention of the planktonic copepod *Eurytemora affinis* in a mixed estuary. *Mar. Ecol. Prog. Ser.* 76, 115–122. <https://doi.org/10.3354/meps076115>.
- Hough, A.R., Naylor, E., 1992. Endogenous rhythms of circatidal swimming activity in the estuarine copepod *Eurytemora affinis* (Poppe). *J. Exp. Mar. Biol. Ecol.* 161 (1), 27–32. [https://doi.org/10.1016/0022-0981\(92\)90187-f](https://doi.org/10.1016/0022-0981(92)90187-f).
- Hutchinson, G.E., 1957. A treatise on limnology. *Geogr. Phys. Chem.* 1015.
- Jacobsen, H., Norrbin, M., 2009. Fine-scale layer of hydromedusae is revealed by video plankton recorder (VPR) in a semi-enclosed bay in northern Norway. *Mar. Ecol. Prog. Ser.* 380, 129–135. <https://doi.org/10.3354/meps07954>.
- Kaartvedt, S., Klevjer, T., Aksnes, D., 2012. Internal wave-mediated shading causes frequent vertical migrations in fishes. *Mar. Ecol. Prog. Ser.* 452, 1–10. <https://doi.org/10.3354/meps09688>.
- Kelley, D., Richards, C., 2022. *Oce: Analysis of Oceanographic Data*. R package version 1.7-2. <https://CRAN.R-project.org/package=oce>.
- Keskinen, E., Leu, E., Nygård, H., Røstad, A., Thormar, J., 2004. New Findings of Diel Vertical Migration in High Arctic Ecosystems. University Centre Publication Series (UNIS), Svalbard, Norway. *Report AB320*.
- Legrand, S., Allen-Perkins, S., Ayensa, G., Lepers, L., Montero, P., Orsi, S., 2023. D5.3 - MANIFESTS DSS - User Guides. Royal Belgian Institute of Natural Sciences. MANIFESTS project report(D5.3).
- Loose, C.J., Dawidowicz, P., 1994. Trade-offs in diel vertical migration by zooplankton: the costs of predator avoidance. *Ecology* 75 (8), 2255. <https://doi.org/10.2307/1940881>.
- Luo, J., Ortner, P.B., Forcucci, D., Cummings, S.R., 2000. Diel vertical migration of zooplankton and mesopelagic fish in the Arabian Sea. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 47 (7–8), 1451–1473. [https://doi.org/10.1016/S0967-0645\(99\)00150-2](https://doi.org/10.1016/S0967-0645(99)00150-2).
- Möller, K., St John, M., Temming, A., Floeter, J., Sell, A., Herrmann, J., Möllmann, C., 2012. Marine snow, zooplankton and thin layers: indications of a trophic link from small-scale sampling with the Video Plankton Recorder. *Mar. Ecol. Prog. Ser.* 468, 57–69. <https://doi.org/10.3354/meps09984>.
- Mortelmans, J., Goossens, J., Amadei Martínez, L., Deneudt, K., Cattrijsse, A., Hernandez, F., 2019b. LifeWatch observatory data: zooplankton observations in the Belgian part of the North Sea. *Geosci. Data J.* 6, 76–84. <https://doi.org/10.1002/gdj3.68>.
- Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., Weedon, J., 2022. *Vegan: Community Ecology Package*. R package version 2.6-2. <https://CRAN.R-project.org/package=vegan>.
- Ollevier, A., Mortelmans, J., Vandegehuchte, M.B., Develter, R., De Troch, M., Deneudt, K., 2022. A Video Plankton Recorder user guide: lessons learned from in situ plankton imaging in shallow and turbid coastal waters in the Belgian part of the North Sea. *J. Sea Res.* 188, 102257. <https://doi.org/10.1016/j.seares.2022.102257>.
- Otto, L., Zimmerman, J.T.F., Furnes, G.K., Mork, M., Saetre, R., Becker, G., 1990. Review of the physical oceanography of the North Sea. *Neth. J. Sea Res.* 26 (2–4), 161–238. [https://doi.org/10.1016/0077-7579\(90\)90091-t](https://doi.org/10.1016/0077-7579(90)90091-t).
- Pearre, S., 2003. Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. *Biol. Rev. Camb. Phil. Soc.* 78 (1), 1–79. <https://doi.org/10.1017/S146479310200595x>.
- Pinel-Alloul, P., 1995. Spatial heterogeneity as a multiscale characteristic of zooplankton community. *Hydrobiologia* 300–301 (1), 17–42. <https://doi.org/10.1007/bf00024445>.
- R Core Team, 2020. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. URL: <https://www.R-project.org/>.
- Reichwaldt, E.S., Stibor, H., 2005. The impact of diel vertical migration of *Daphnia* on phytoplankton dynamics. *Oecologia* 146, 50–56. <https://doi.org/10.1007/s00442-005-0176-3>.
- Ringelberg, J., 2010. Diel Vertical Migration of Zooplankton in Lakes and Oceans. <https://doi.org/10.1007/978-90-481-3093-1>.
- Robinson, K.L., Sponaugle, S., Luo, J.Y., Gleiber, M.R., Cowen, R.K., 2021. Big or small, patchy all: resolution of marine plankton patch structure at micro- to submesoscales for 36 taxa. *Sci. Adv.* 7 (47) <https://doi.org/10.1126/sciadv.abk2904>.
- Royal Belgian Institute of Natural Sciences. (n.d.). ERDDAP - Data Access Protocol. ERDDAP. <https://erddap.naturalsciences.be/erddap/index.html>.
- Solberg, I., Kaartvedt, S., 2017. The diel vertical migration patterns and individual swimming behavior of overwintering sprat *Sprattus sprattus*. *Prog. Oceanogr.* 151, 49–61. <https://doi.org/10.1016/j.pocean.2016.11.003>.
- Steinberg, D.K., Landry, M.R., 2017. Zooplankton and the ocean carbon cycle. *Ann. Rev. Mar. Sci.* 9 (1), 413–444. <https://doi.org/10.1146/annurev-marine-010814-015924>.
- Ullberg, J., Ólafsson, E., 2003. Effects of biological disturbance by *Monoporeia affinis* (Amphipoda) on small-scale migration of marine nematodes in low-energy soft sediments. *Mar. Biol.* 143 (5), 867–874. <https://doi.org/10.1007/s00227-003-1139-z>.
- van Leeuwen, S., Tett, P., Mills, D., van der Molen, J., 2015. Stratified and nonstratified areas in the North Sea: long-term variability and biological and policy implications. *J. Geophys. Res.: Oceans* 120 (7), 4670–4686. <https://doi.org/10.1002/2014jc010485>. Portico.
- Verfaillie, E., 2008. *Ontwikkeling en validering van een ruimtelijke verspreidingsmodellen van mariene habitats, ter ondersteuning van het ecologisch waarden van de zeebodem = Development and validation of spatial distribution models of marine habitats, in support of the ecological valuation of the seabed*. PhD Thesis Instituut voor de Aanmoediging van Innovatie door Wetenschap en Technologie in Vlaanderen/RCMG/Universiteit Gent: Brussel 207.
- Vernet, M., 2000. Effects of UV radiation on the physiology and ecology of marine phytoplankton. *The Effects of UV Radiation in the Marine Environment* 237–278. <https://doi.org/10.1017/cbo9780511535444.010>.
- Wang, Z., Dauvin, J.C., 1994. The suprabenthic crustacean fauna of the infralittoral fine sand community from the Bay of Seine (Eastern English Channel): composition, swimming activity and diurnal variation. *Cah. Biol. Mar.* 35 (2), 135–156.
- Wirtz, K., Smith, S.L., 2020. Vertical migration by bulk phytoplankton sustains biodiversity and nutrient input to the surface ocean. *Sci. Rep.* 10 (1) <https://doi.org/10.1038/s41598-020-57890-2>.
- Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. Roy. Stat. Soc.* 73 (1), 3–36.
- Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. *Mixed effects models and extensions in ecology with R*. In: *Statistics for Biology and Health*. Springer, New York. <https://doi.org/10.1007/978-0-387-87458-6>.