Temporal and Spatial Influences of Environmental Factors on the Distribution of Mesopelagic organism in the North Atlantic Ocean

Jie Yang[1,2,*], Jian Hui Li[1,2,*], and Ge Chen[1,2]

[1]Department of Marine Technology, Ocean University of China, Qingdao, China
[2]Laoshan Laboratory, Qingdao, China
[*]These authors contributed equally to this work.

Correspondence: Ge Chen (gechen@ouc.edu.cn)

Abstract. Mesopelagic organisms play a critical role in marine ecosystems and the global carbon cycle, acting as key intermediaries between trophic levels through diel (DVM) and seasonal vertical migrations (SVM). However, the seasonal vertical migration patterns of these organisms, and the environmental drivers influencing them, remain insufficiently understood. Here, we analyzed 83,603 backscattering coefficient (b_{bp}) profiles obtained from 720 BGC-Argo floats deployed in the North Atlantic

5   Ocean from 2010 to 2021. This extensive dataset enabled the identification of spiking layer signals, allowing us to investigate the diurnal and seasonal vertical distributions of mesopelagic organisms, as indicated by these b_{bp} spikes. Additionally, we examined the horizontal heterogeneity in these distributions and their correlations with key environmental variables. Our findings reveal distinct diurnal migrations, characterized by multilayered aggregations predominantly in the mid-ocean during daylight, with prominent signals at depths around 150 m, 330 m, 650 m, and 780 m. At night, a strong scattering layer forms in the upper

10   ocean, with signals concentrated at depths shallower than 350 m, particularly in the top 100 m. Seasonal analyses shows that in spring and winter, the average b_{bp} spike intensity is lower in the upper ocean than in the mid-ocean, although the frequency of b_{bp} spikes is higher in the upper ocean. In contrast, summer and autumn—especially summer—exhibit both higher mean b_{bp} spike intensity and frequency near the surface. Spatially, mesopelagic organisms migrate deeper in the northeast and remain shallower in the southwest, correlating with higher temperatures and shallower distributions. Random forest analysis identified

15   temperature as the most influential environmental factor affecting the distribution of mesopelagic organisms year-round, with the temperature gradient being particularly critical. Other critical factors include seawater salinity, dissolved oxygen, surface chlorophyll concentration, and latitude, with relative importance of 29.44%, 15.49%, 14.85%, 13.46%, and 12.35%, respectively. This study enhances our understanding of the mechanisms driving carbon transfer to the deep ocean and the energy and material cycles within marine ecosystems, providing a basis for future fisheries management in mesopelagic environments.

20   ## 1   Introduction

The mesopelagic organisms, comprising species such as zooplankton, shrimp, squid, fish, and jellyfish, are estimated to harbor around one billion tonnes of biomass, representing a significant fraction of global fish biomass(Irigoien et al., 2014). This biome is a crucial component of marine ecosystems, serving as a vital link between primary producers and higher trophic levels. It plays a fundamental role in the ocean's energy transfer and nutrient cycling(Klevjer et al., 2016; Kruse et al., 2010).

25 A prominent behavioral adaptation in the mesopelagic zone is diel vertical migration (DVM), wherein organisms undertake extensive vertical movements to optimize survival and foraging efficiency. During daylight, they inhabit depths of several hundred meters in the mesopelagic zone to minimize predation risk, while at night, they migrate to the epipelagic zone to exploit food resources. This migration is recognized as one of the largest-scale migrations on Earth(Kapelonis et al., 2023; Hays, 2003; Petrusevich et al., 2020). Additionally, mesopelagic organisms undergo seasonal vertical migration (SVM), adjusting

30 their vertical distribution in response to environmental fluctuations. Both DVM and SVM drive the active export of organic and inorganic materials—through excretion, defecation, respiration, and mortality—into deeper ocean layers(Lourenço and Jany, 2021). These processes are not only ecologically important but also play a significant role in biogeochemical cycling, carbon sequestration, and mitigating global climate change(Govindarajan et al., 2023; Hazen, 2022; Gjoesaeter et al., 1980; Hays, 2003; Ramirez-Llodra et al., 2010; Robinson et al., 2010; Bailey, 2021).

35 Traditional approaches to study mesopelagic organisms have largely relied on trawl and acoustic sampling methods. Although trawl sampling is more frequently used, it suffers from limitations in spatial and temporal resolution, as well as biases related to evasion and selectivity, which impede accurate estimates of migration timing, rate, and extent(Sutton, 2013; Underwood et al., 2020; Luo et al., 2000). Acoustic sampling offers greater precision but is restricted by the spatial and temporal coverage due to platform constraints, such as vessels. The resolution of acoustic sensors often fails to detect small, dispersed,

40 and weakly scattering species at depth, and the high costs associated with traditional ADCP-based methods further limit extensive in situ observations(Haëntjens et al., 2020; Chai et al., 2020; Underwood et al., 2020; Nakao et al., 2021). Recently, the increased deployment of BGC-Argo floats has enhanced accuracy and broadened the scope of applications in various studies, including inter-annual analyses of phytoplankton communities, quantification of carbon export from the ocean interior, and observations of mesocosm flux decay due to fragmentation processes(Rembauville et al., 2017; Xing et al., 2020; Wang

45 and Fennel, 2022; Galí et al., 2022; Briggs et al., 2020; Boyd et al., 2019). Bio-optical sensors mounted on these floats have proven effective in detecting a range of bio-optical properties, renderiimportanceerful tools for large-scale spatial detection of mesopelagic organisms(Claustre et al., 2019; Haëntjens et al., 2020).

Recent advancements have demonstrated that backscattering coefficient (b_{bp}) spike signals from BGC-Argo floats can effectively infer mesopelagic biological information, showing high concordance with acoustic trawl observations(Haëntjens et al.,

50 2020). These b_{bp} spike signals are primarily generated by larger particles, which are closely associated with biological aggregations(Briggs et al., 2011). Notably, the extensive diatom blooms in the North Atlantic each spring result in substantial pulses of particulate matter, comprising fresh phytoplankton aggregates that rapidly descend to the seafloor(Lampitt, 1985; Honjo and Manganini, 1993). Occasionally, large peaks in optical profiles are interpreted as aggregates or zooplankton(Bishop et al., 1999; Gardner et al., 2000; Bishop and Wood, 2008). The b_{bp} signal captures the entire particle assemblage, including zooplankton,

55 detritus, bacteria, and mineral particles. Significant increases in b_{bp} are observed when small zooplankton dominate the mixed layer community(Rembauville et al., 2017; Petit, 2023). Furthermore, satellite-based lidar inversion of b_{bp} signals has shown that zooplankton activity leads to pronounced b_{bp} spikes, particularly at night, with these spikes most evident in the surface ocean layers, revealing the global distribution characteristics and evolutionary patterns of diel vertical migration(Behrenfeld

et al., 2019). Collectively, these studies indicate that b_{bp} spike signals not only reflect the presence of large particulate matter

60 and tiny zooplankton but also capture the diel vertical migration of zooplankton.

However, substantial challenges remain in the large-scale detection of mesopelagic organisms, resulting in significant uncertainties in biomass estimates, which range widely from billions to hundreds of tonnes(Gjoesaeter et al., 1980; Sarant, 2014). Moreover, the patterns of DVM and SVM, their adaptive mechanisms, and the multifactorial influences on these behaviors remain poorly understood(Bandara et al., 2021).

65 In this study, we extracted b_{bp} spike signals from BGC-Argo floats in the mid- and high-latitude regions of the North Atlantic Ocean to statistically infer the aggregation patterns of mesopelagic organisms. We then investigated diurnal and seasonal vertical migration patterns, analyzed the horizontal spatial distribution characteristics, and evaluated the environmental drivers influencing vertical distribution using Random Forest modeling.

2 Material and methods

70 ### 2.1 Study area

The North Atlantic plays a critical role in global carbon sequestration, where pelagic fish are key to marine ecosystem dynamics and represent a largely untapped resource for fisheries(Gruber et al., 2002). The high-latitude overturning circulation, combined with the subduction processes of the Subtropical Circulation (STC), drives the transport of dissolved organic carbon (DOC) to the deep ocean, functioning as a core mechanism of the biological pump and contributing significantly to the global carbon

75 cycle(Hansell et al., 2002). Recent studies have reported notable shifts in species composition and dominance within fish assemblages in the subarctic Northwest Atlantic, especially around the shallow Reykjanes Ridge(Sutton et al., 2008). These changes highlight the potential for profound impacts on marine ecosystem management and the sustainable use of fishery resources. Thus, the North Atlantic is central to addressing global climate change, preserving biodiversity, and guiding the sustainable use of marine resources. This study examines the North Atlantic Ocean, spanning latitudes from 35° to 75°N and

80 longitudes from 0 to 70°W. Figure 1 illustrates the spatial distribution of the backscattering coefficient (b_{bp}) profiles collected by BGC-Argo floats across the study area, based on 1°×1°grid statistics.
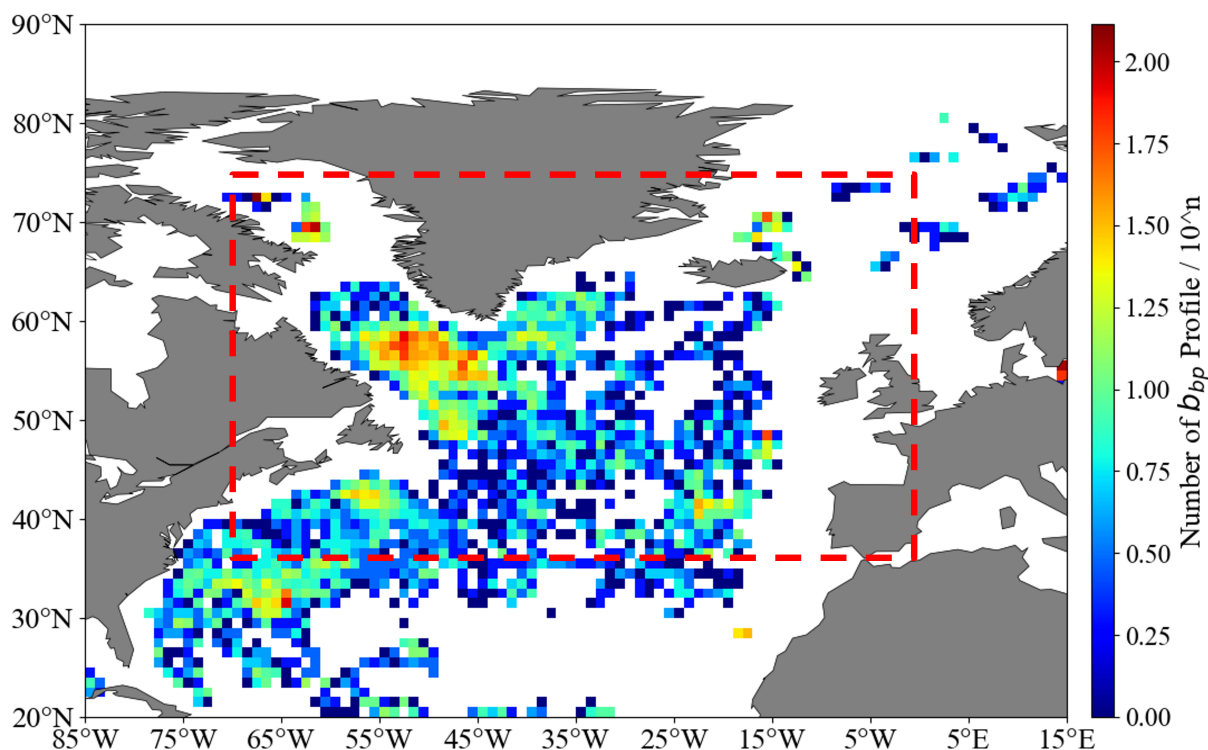
Figure 1. Total BGC-Argo Profile Count with b_{bp} Layer at 1°×1°Grid Resolution; Study Area Highlighted in Red.dotted frame

2.2 Data

The dataset used in this study includes BGC-Argo profiles and remote sensing data collected from 2010 to 2021. The BGC-Argo dataset consists of profiles from 720 floats, capturing key parameters such as Chlorophyll-a, dissolved oxygen, salinity, temperature, and particle backscattering at 700 nanometers (b_{bp}700). A total of 83,603 valid profiles were selected based on the detection of b_{bp}700 spikes. Remote sensing data comprises sea surface temperature (SST) and chlorophyll-a (Chl). SST data, obtained from the National Oceanic and Atmospheric Administration (NOAA), consists of optimally interpolated fields with a spatial resolution of 0.25°, derived from a fusion of Advanced Very High-Resolution Radiometer (AVHRR) observations from multiple platforms, providing high accuracy and broad spatial coverage. The Chl data, sourced from GlobColour, is a Level 3 ocean color product with a 0.25° resolution, combining outputs from multiple chlorophyll sensors to ensure data continuity, enhance spatial and temporal coverage, and reduce noise.

2.3 Methods

2.3.1 BGC-Argo spike layer observations method

To investigate the aggregation patterns of mesopelagic organisms, we utilized a previously established spike layer detection
95 algorithm(Haëntjens et al., 2020)to extract b_{bp} spike signals. The extraction process involved several key steps: Initially, we
screened b_{bp} profiles, selecting those with more than 30 sampling points and a maximum depth greater than 50 meters. The
raw b_{bp} signal of each profile was smoothed using a 15-point Hampel filter, establishing a baseline signal. Next, we computed
the difference between the original b_{bp} signal and the baseline. Signals exhibiting differences exceeding twice the smad were
identified as spike signals.(see Eq. (1) for smad calculation, where smad represents the minimum threshold of the profile and
100 b_{bp}(n) represents all b_{bp} signals in the profile). These detected spike signals were subsequently clustered hierarchically using a
depth parameter of 50 meters, and the results were categorized based on distinct features. Spike signals with identical features
across two profiles were aggregated into a spike layer. For each layer, we quantified the intensity, depth, and spike count, which
were then recorded for further analysis. The spike layer extraction workflow is illustrated in Figure 2.

$$smad = -\frac{1}{\sqrt{2} \cdot erfcinv(\frac{3}{2})} \cdot median(\mid b_{bp}(i) - median(b_{bp}(n)) \mid) \tag{1}$$

105 where $smad$ represents the minimum threshold of the profile, $b_{bp}(i)$ represents the median value of all signals in the profile,
and $b_{bp}(n)$ represents all b_{bp} values throughout the profile.

We first removed outliers from the environmental profiles and interpolated missing data points. Subsequently, a 25-point
median filter followed by a mean filter was applied to the environmental data to minimize the influence of outliers and missing
values on the analysis accuracy. After preprocessing, we calculated the temperature gradients for each profile, along with the
110 mean dissolved oxygen and salinity values over depth intervals of 0–200 m, 200–500 m, and 500–800 m. Given the higher
variability in chlorophyll and temperature in the upper and middle layers, we averaged these parameters over depth ranges
of 0–50 m, 50–200 m, and 200–500 m. These averaged values served as environmental inputs for the Random Forest model.
Additionally, sea surface chlorophyll and sea surface temperature data, with a spatial resolution of 0.25 degrees and a temporal
resolution of one day, were integrated with the BGC-Argo profile data to enhance the analysis.
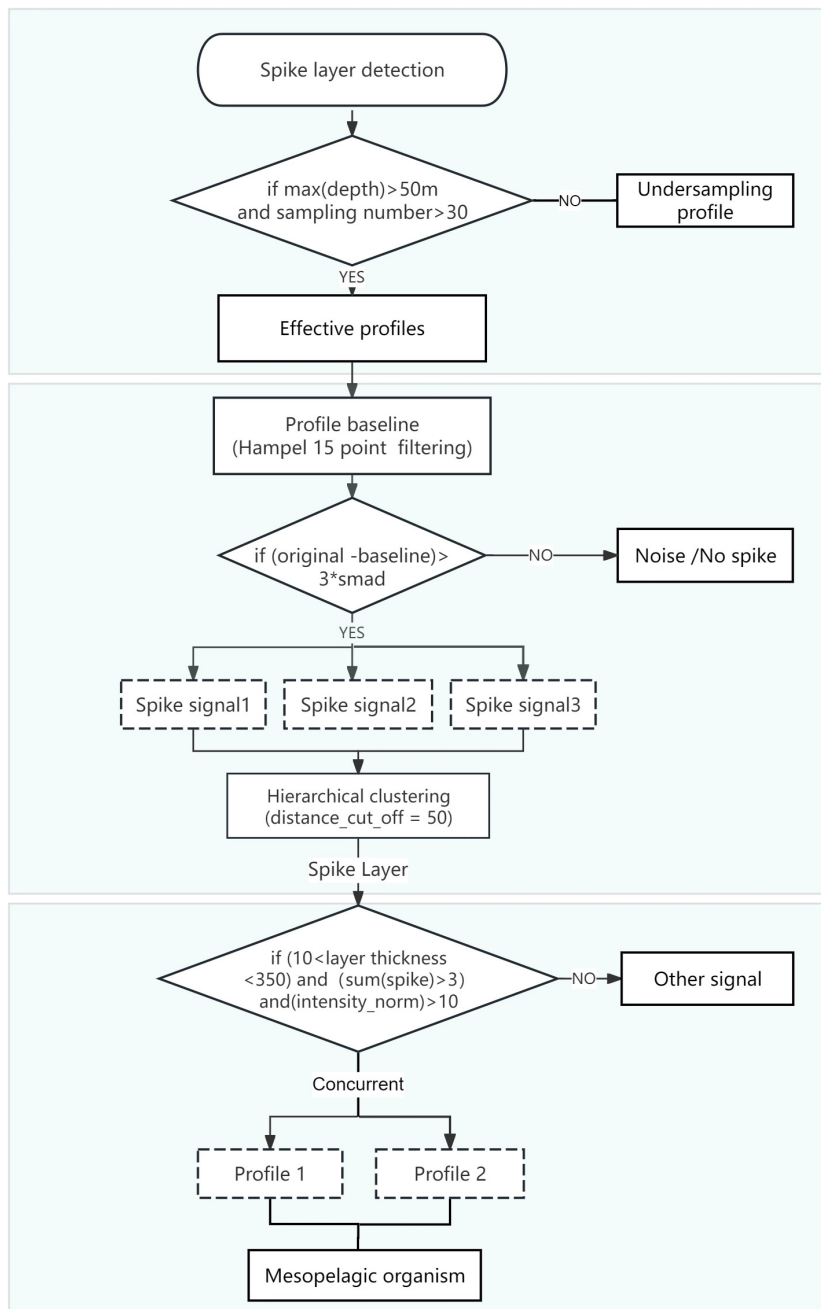
Figure 2. Extraction process of spike layer signal.

2.3.2   Statistical Method

To elucidate the diurnal vertical migration patterns of mesopelagic organisms, the water column was divided into 10-meter depth bins. Within each bin, spiking signals were normalized by calculating the proportion of spiking points relative to the total number of detected spiking points. Environmental factors were then averaged within each bin. Profiles were further categorized into daytime and nighttime based on local solar time.

For the seasonal analysis, profiles containing spiking layers were categorized, and those with comprehensive environmental data were selected, yielding 1,045 profiles for spring, 1,722 for summer, 1,739 for autumn, and 801 for winter. Following established literature and conventional definitions of depth ranges for the upper (0–200 m) and middle (200–800 m) oceanic zones, the intensity and frequency of spiking signals were quantified for each season. To account for seasonal variations in the number of profiles, frequency distributions were normalized. Frequency, defined as the number of pinnacles per unit depth, represents the likelihood of aggregation for specific taxa. Intensity, measured as the median number of b_{bp} signals within each pinnacle layer, serves as a proxy for species composition (size) or abundance within the mesopelagic zone. For spatial distribution analysis, a grid with a 1° resolution was employed to statistically average the depth distribution of mesopelagic organisms across the study area.

To capture the complex, nonlinear relationships influencing the distribution of mesopelagic organisms, we utilized a Random Forest model, building on methodologies from prior studies(De Forest and Drazen, 2009; Scales et al., 2016; Cuttitta et al., 2018; Villafaña and Rivadeneira, 2018; Song et al., 2022; Alexander et al., 2023). Initially, Spearman correlation analysis was conducted to explore the associations between the depth and intensity of spiking signals within the pinnacle layer and environmental variables. Subsequently, we applied the Random Forest model to elucidate the regression relationships between mesopelagic organism densities and environmental factors, thereby providing a nuanced understanding of their interactions.

3   Results

3.1   Diurnal Vertical Migration

Our findings reveal a distinct diurnal migration pattern with a multilayered structure in mesopelagic organisms. Normalized data indicate prominent intensity bands within the b_{bp} cusp layer at depths of approximately 150 m, 330 m, 650 m, and 780 m during daylight hours. In contrast, nighttime observations show a strong scattering layer at a shallower depth of around 350 m. Notably, the mean intensity of the b_{bp} spike layer at depths shallower than 380 m is 1.24 times higher at night compared to daytime, increasing to 1.28 times at depths shallower than 100 m. Conversely, at a depth of approximately 380 m, the average daytime intensity is 1.17 times higher than nighttime values (Fig. 3a, b).

These observations are consistent with the acoustic findings by(Klevjer et al., 2020a) across four regions, indicating a substantial overlap in mesopelagic distribution patterns detected by both methods. Our results suggest that spike layer signals predominantly concentrate in mid-ocean layers during the day, with a significant portion migrating to upper ocean layers at night.
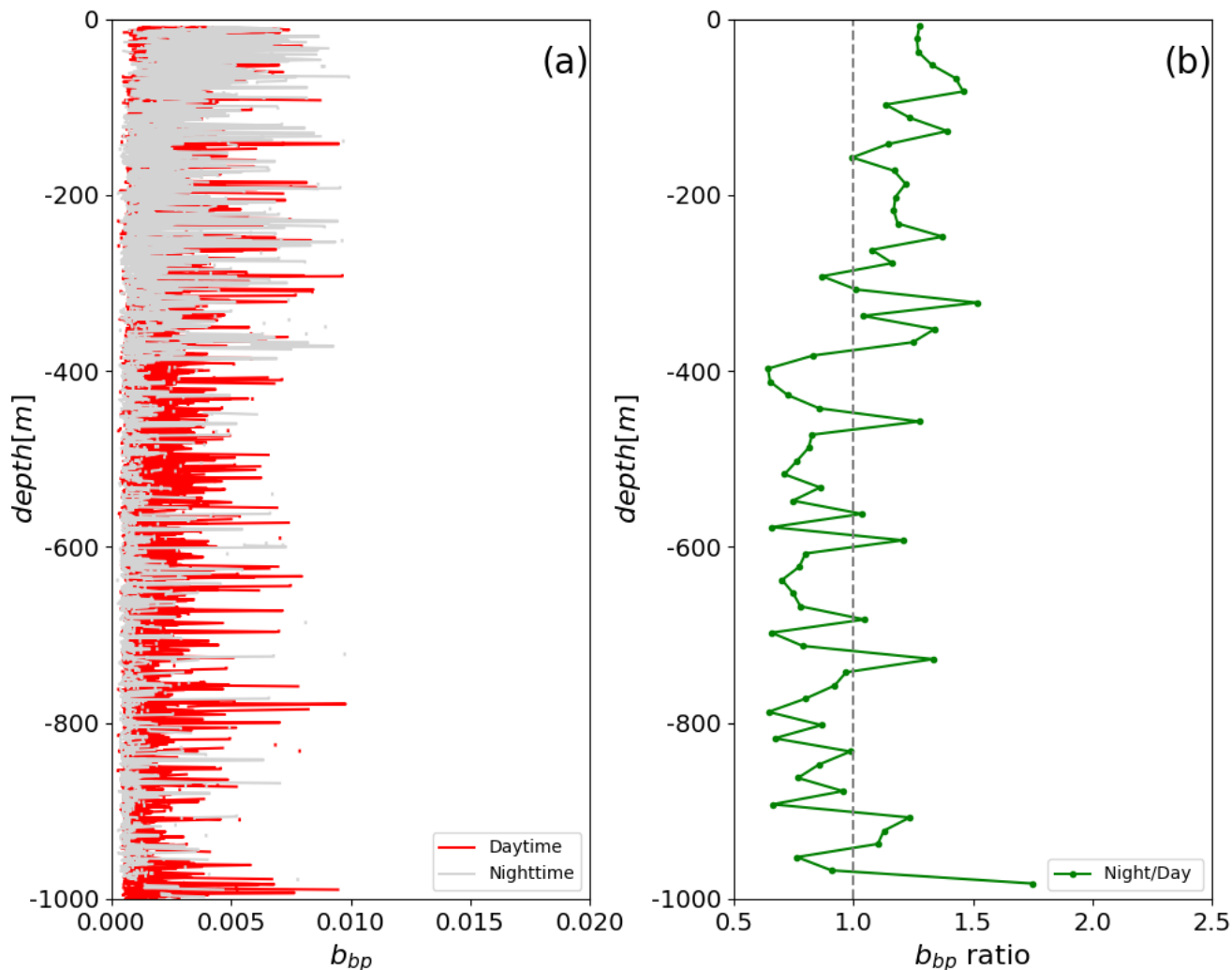
Figure 3. This figure illustrates the diurnal distribution of b_{bp} signals and environmental factors, with colored lines indicating daytime and grey lines representing nighttime. Specifically, figure a depicts b_{bp} signals, figure b shows chlorophyll levels.

3.2 Seasonal Vertical Migration

Seasonal analysis reveals notable variability in the intensity of b_{bp} spike layer signals across different ocean layers. The average intensity between the upper and middle layers exhibits minor differences in spring and autumn (below 10%), whereas more substantial disparities are observed in summer and winter (over 50%). In spring and winter, b_{bp} spike intensity in the upper ocean is generally lower than in the middle layer, with the opposite pattern in summer and autumn. The upper ocean reaches

peak intensity in summer (0.002290 m^{-1}) and minimum intensity in winter (0.001635 m^{-1}). In the middle layer, peak intensity occurs in winter (0.005748 m^{-1}), with the lowest in autumn (0.001502 m^{-1}) (Table 1).

Table 1. Seasonal average intensity of Mesopelagic organism aggregation in the upper and middle layers of the ocean; The peak intensity denotes the highest intensity recorded for a particular layer, with the depth indicating the precise location .

season	layer(depth)	intensity(m^{-1})	peak intensity m^{-1}(depth)
spring	upper layer(0-200m)	0.001699	
	middle layer(200-800m)	0.001760	0.003369(510m)
summer	upper layer(0-200m)	0.002290	0.003225(20m)
	middle layer(200-800m)	0.001647	
autumn	upper layer(0-200m)	0.001665	
	middle layer(200-800m)	0.001502	0.002064(440m)
winter	upper layer(0-200m)	0.001635	
	middle layer(200-800m)	0.002582	0.005748(600m)

The distribution of extreme values in the b_{bp} cusp layer intensity exhibits clear seasonal patterns. In spring, extreme signals
155 appear around 350 m, 510 m, and 700 m, with a peak intensity at 510 m (0.003369 m^{-1}). During summer, the highest intensity shifts to the near-surface layer, around 20 m (0.003225 m^{-1}). In autumn, intensity is primarily concentrated between 300 m and 600 m, with a peak around 440 m (0.002064 m^{-1}). Winter signals concentrate between 200 m and 700 m, with maximum intensity at 600 m (0.005748 m^{-1}) (Fig. 4). These findings suggest that the maximum intensity of the b_{bp} cusp layer predominantly occurs in the middle ocean layer during spring and winter, reflecting a multilayer aggregation pattern, while in
160 summer, the highest intensity is near the surface. In autumn, the difference between upper and middle layers is less pronounced, consistent with the findings of (Loisel et al., 2002)for the same region. Additionally, the depth of the strongest b_{bp} spike signal demonstrates a distinct seasonal dynamic: it is deepest in winter (around 600 m), ascends in spring (approximately 510 m), rises further to near-surface levels in summer (around 100 m), and descends in autumn (about 440 m).
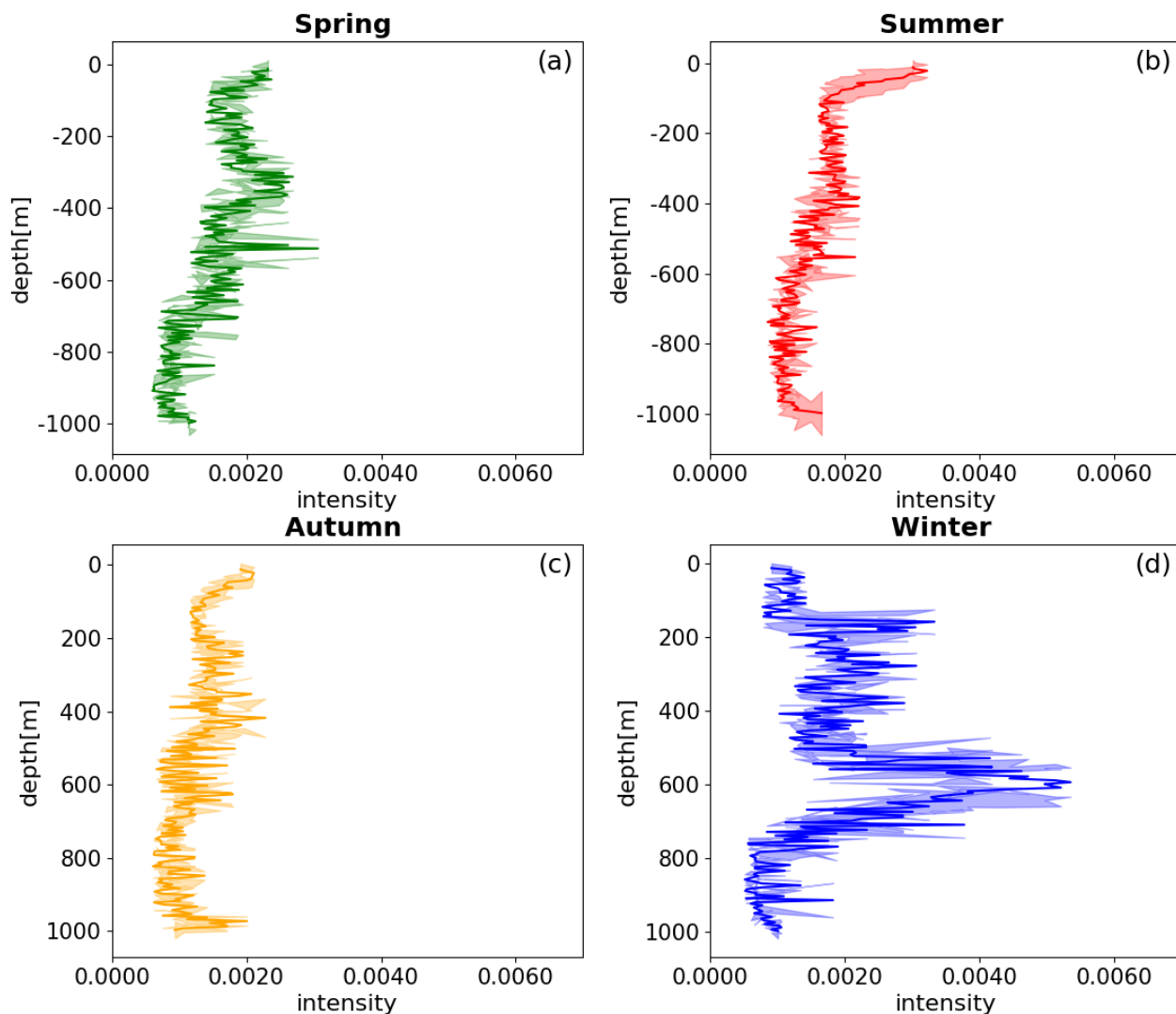
Figure 4. The diagram depicts the density distribution of mesopelagic organisms in different seasons. The four seasons are represented by a, b, c, and d, corresponding to spring, summer, autumn, and winter, respectively. The shaded areas correspond to the spike layer, while the error bars indicate the standard deviation of the depth range.

The normalized frequency distribution of the b_{bp} spike layer across different seasons (Fig. 5) reveals a consistent trend of

165 relatively high-frequency aggregation of mesopelagic organisms at depths shallower than approximately 350 m. In spring and winter, the average frequency of b_{bp} spike signals within the upper 350 m is elevated by factors of 1.28 and 1.33, respectively, compared to deeper waters. Additionally, there is a significant increase in the proportion of organisms migrating to the upper 200 m during spring, rising from 1.17 in winter to 1.58, indicating a notable shift toward shallower depths. In summer and

autumn, the mean frequency of b_{bp} spike signals at depths shallower than 350 m is 1.85 and 4.15 times higher, respectively,
170 than at greater depths. Notably, there is a pronounced aggregation of high-frequency signals in the near-surface layer, shallower than 50 m. These observations suggest that in spring and winter, despite lower average b_{bp} spike intensity in the upper ocean compared to the mid-layer—with peak values primarily in the mid-layer—mesopelagic organisms aggregate at specific mid-layer depths while foraging in the upper ocean. In contrast, in summer and autumn, especially summer, both the average intensity and frequency of b_{bp} spikes are significantly higher in the upper layer than in the mid-layer, with a marked concen-
175 tration in the near-surface zone. This shift indicates a seasonal change in mesopelagic behavior, with a heightened preference for upper-layer habitats and foraging during warmer months.
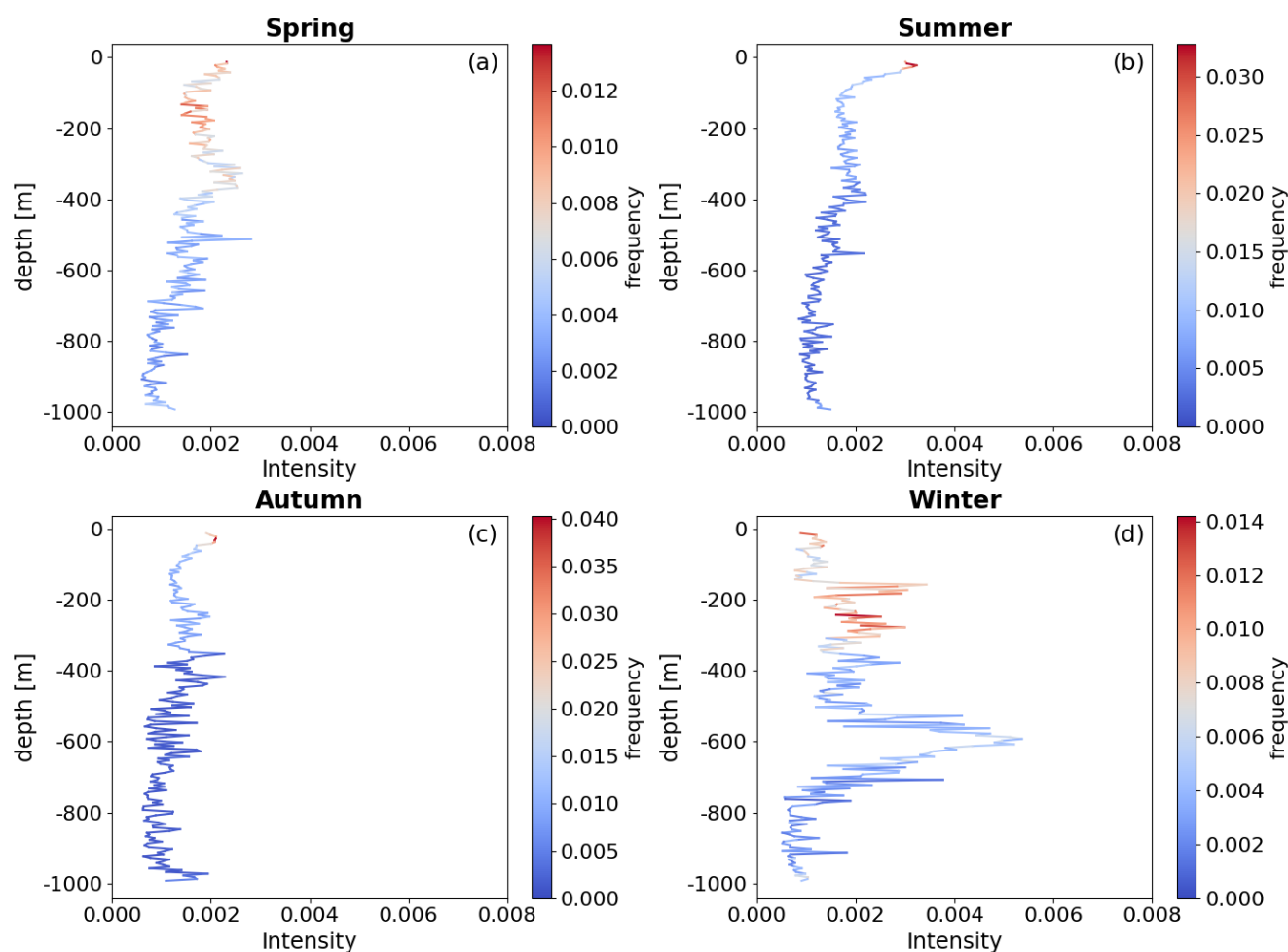

Figure 5. This figure illustrates the intensity and density of mesopelagic organisms vertical distribution, with red areas indicating multiple occurrences of these organisms throughout the mesopelagic zone. The color bar represents the proportion of occurrences of mesopelagic organisms within each 5m bin relative to the total seasonal frequency.

3.3 Horizontal Spatial Distribution

The horizontal spatial distribution of mesopelagic organisms was analyzed by calculating the mean depths of all b_{bp} cusp layers within a $1° \times 1°$ grid across mid- and high-latitude regions of the North Atlantic (Fig. 6). The results indicate a predominantly shallow distribution in the northwestern North Atlantic and the Mediterranean Sea, with mean depths around 200 m. In contrast, the Labrador Sea shows a deeper average b_{bp} cusp layer depth of approximately 400 m, while the Irminger Sea averages around 300 m. In the eastern Iceland Sea, organisms are found at substantially greater depths, averaging around 800 m. Prominent frontal zones, including the Greenland-Icelandic-Norwegian Fronts, Eastern Greenland Fronts, La Nerado Fronts, and North Atlantic Drift Fronts, show b_{bp} cusp layers at depths ranging from several tens to a few hundred meters.
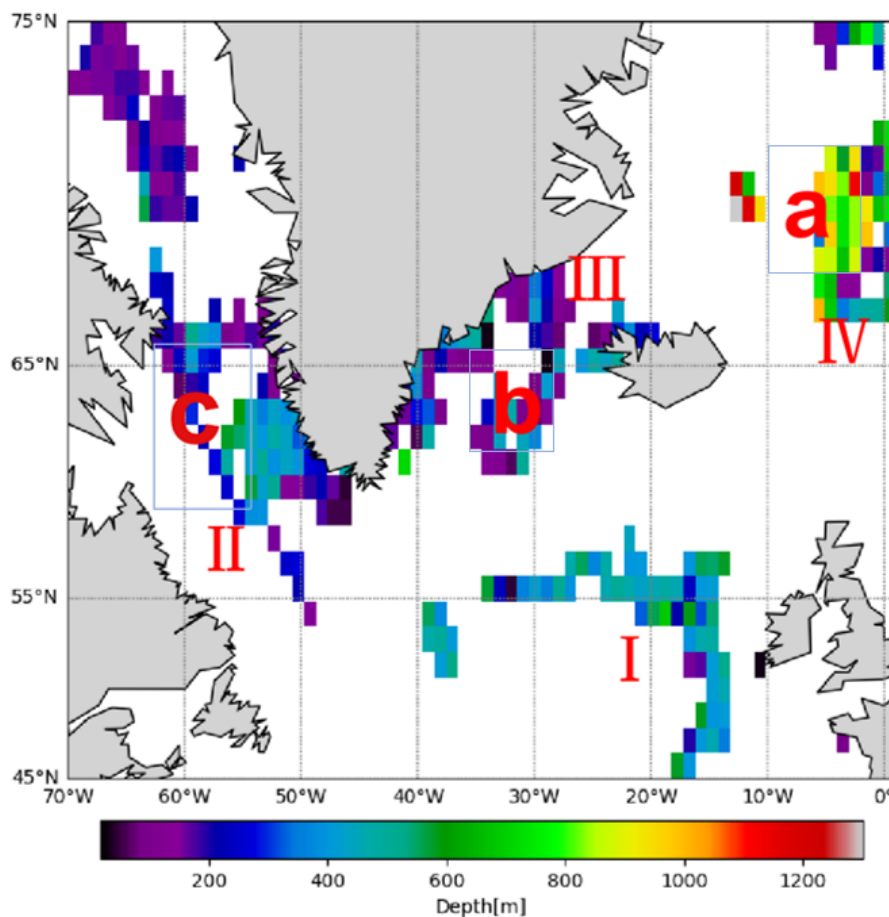

Figure 6. The figure shows the spatial differences in the depth distribution of mesopelagic organisms, with a spatial resolution of $1° \times 1°$. The map shows the Iceland Sea (a), Irminger Sea (b), and Labrador Sea (c). The North Atlantic Drift Front (I), Laredo Front (II), East Greenland Front (III), and Greenland-Iceland-Norway Front (IV) are indicated.

3.4 Environmental driving factors

Spearman correlation analysis revealed that the vertical distribution of mesopelagic organisms is influenced by several environmental factors, despite the low contribution rates of individual variables. Subsequent analysis using the Random Forest model identified the temperature gradient as the most significant factor, explaining 29.44% of the variance. Other influential factors include seawater salinity in the 500-800 m layer (15.49%), dissolved oxygen in the 500-800 m layer (14.85%), mean sea surface temperature (SST) (14.41%), and sea surface chlorophyll concentration (SSC) (13.46%). Latitude accounted for 12.35% of the variance. The model's overall goodness of fit was represented by an R^2 value of 0.58. Among these factors, the temperature gradient exerted the most substantial influence on the seasonal and spatial distribution of mesopelagic organisms. Throughout the year, light conditions (solar altitude angle) were notably influential in spring, while summer distributions were predominantly driven by sea surface chlorophyll concentration. Dissolved oxygen was the most significant factor in autumn and winter. Latitude, as a critical geographic factor, also influenced distribution patterns, with mesopelagic organisms typically found at shallower depths at higher latitudes. Model response curves further elucidated the relationship between environmental factors and mesopelagic aggregation depth. An increase in temperature gradients within a specific range was associated with shallower depths of mesopelagic organism aggregation. This observation partly explains the alignment between the spatial distribution of mesopelagic organisms and temperature heterogeneity. Conversely, when considering the intensity of biotic aggregation as the response variable, signals from mesopelagic organisms at shallower depths were generally more intense.
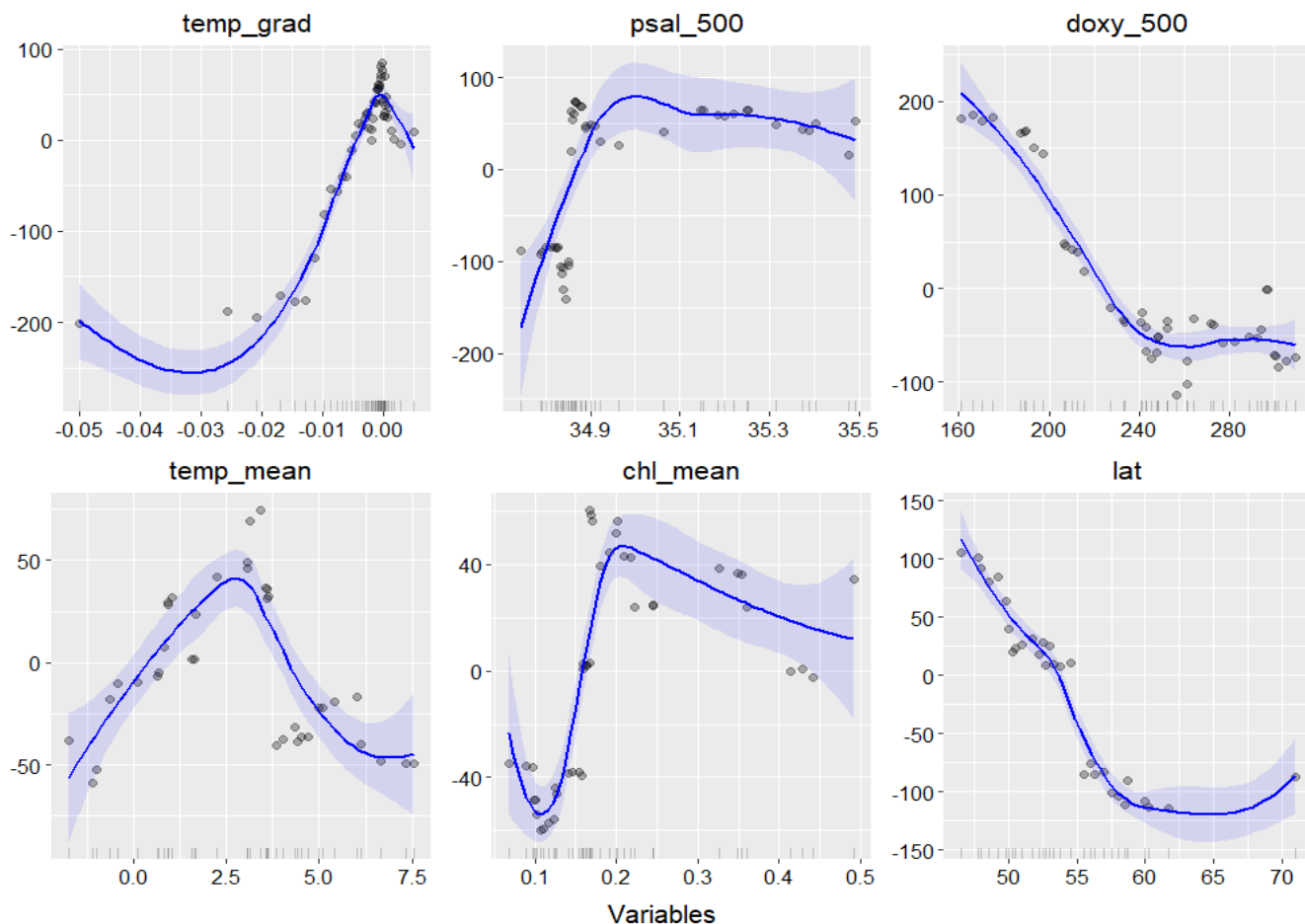
Figure 7. Response curves from the random forest model, with the blue line indicating the influence of various factors. The small black line on the horizontal axis denotes data distribution density, while the gray points represent individual data points.

4 Discussion

Recent research underscores the complex factors influencing the aggregation and vertical migration of mesopelagic organisms, driven by a myriad of environmental variables such as food availability, light conditions, oceanographic features, and hypoxia. Short-term transient influences, including variations in cloud cover, ocean currents, and lunar phases, further modulate these processes(Lampert et al., 1989; Ramos-Jiliberto et al., 2002; Parra et al., 2019; Klevjer et al., 2020b; Hauss et al., 2016).

During the day time, mesopelagic organisms predominantly reside within the mesopelagic zone (150–800 m), forming distinct signal bands. Conversely, nocturnal migrations lead these organisms to occupy shallower pelagic strata, particularly those below 380 m. Despite these observations, the environmental dynamics within these shallower strata remain insufficiently

defined. Comparative analyses indicate that elevated chlorophyll concentrations, more favorable thermal conditions, and re-
210 duced nocturnal illumination in the upper pelagic layers collectively reduce predation risk and avoid hypoxic conditions. These
factors create a more favorable environment for mesopelagic organisms, thereby enhancing their nocturnal migrations and in-
tensifying the b_{bp} signal in the upper pelagic layers, consistent with satellite-based lidar observations(Behrenfeld et al., 2019).
Additionally, the interaction between diurnal b_{bp} spiking layer characteristics and environmental factors such as chlorophyll
and temperature emphasizes the importance of thermal and salinity gradients. Enhanced spiking signals are observed above
215 these gradients, driven by increased food availability and physiological predispositions favoring aggregation in regions of
chlorophyll maxima and thermal gradients(Sameoto, 1986). These findings align with Random Forest model results, which
demonstrate that pronounced temperature gradients correlate with shallower mesopelagic distributions.

Seasonal variations in the b_{bp} spike layer intensity are influenced by multiple environmental factors, including water temper-
ature, ocean currents, dissolved oxygen levels, light availability, and food sources(Bianchi et al., 2013; Klevjer et al., 2016). The
220 impact of these factors varies significantly across different regions and seasons(Klevjer et al., 2020a), leading to fluctuations in
mean intensity, intensity maxima distribution, and the frequency of b_{bp} spike layer signals within the mesocosm. During spring
and winter, the mean intensity of the b_{bp} spike layer in the upper mesopelagic zone decreases, while its frequency increases
relative to the middle mesopelagic layer. This shift likely results from mesopelagic organisms' preference for specific depths
influenced by lower temperatures, deeper mixed layers, limited light availability, and reduced phytoplankton concentrations
225 in the upper layers during these seasons. In contrast, as temperatures and light levels rise in spring, and with the mixed layer
becoming shallower and phytoplankton blooms increasing, mesopelagic organisms migrate to the upper layers for improved
foraging opportunities. This behavior results in higher-frequency aggregations and a relative decrease in mean intensity of
the mesopelagic acropora signal(Allan et al., 2021; Henson et al., 2012; Lutz et al., 2007; Woodd-Walker et al., 2002; Briggs
et al., 2011; Vedenin et al., 2022). Furthermore, in cooler spring and winter months, strong downwelling increases surface
230 density, while salinity differences and stratification in high latitudes and the Atlantic Ocean facilitate the transfer of dissolved
oxygen to deeper waters. Consequently, mesopelagic organisms migrate to greater depths in search of suitable habitats and
food resources, avoiding elevated predation pressure in surface waters(Freeman, 2006; Garcia-Soto et al., 2021; Yin et al.,
2024). This results in a higher concentration of organisms in the middle layer, leading to multilayer aggregation phenomena.
The correlation between dissolved oxygen in the 200–500 m layer and the negative correlation in the 500–800 m range indi-
235 cates a distinct oxygen minimum zone around 500–600 m, delineating the emergence of a prominent mesopelagic signal layer
at approximately 600 m depth. Larger mesopelagic organisms, resistant to currents, migrate deeper, while smaller organisms
remain in the upper layers. These observations align with Random Forest analyses and previous studies showing that smaller
species dominate in surface waters, while larger species are more prevalent in deeper layers(Lin and Costello, 2023; Sorochan
et al., 2023). During spring and winter, the North Atlantic's deeper mixed layer and unstable water column, along with transient
240 stratification events often disrupted by storms, favor the accumulation of organic matter in the deeper mixed layer, resulting in
increased biotic aggregation frequencies in the mid-ocean(Dall'Olmo et al., 2016).In contrast, during summer, a stable shallow
mixed layer isolates the surface from deeper waters, concentrating mesopelagic organisms in the upper-middle layer. High-
intensity and high-frequency signal layers emerge in the ocean's surface during summer and autumn. In autumn, these strong

signals are frequently associated with chlorophyll maxima around 200 m depth. Increased solar radiation enhances phyto-
245   plankton photosynthesis, significantly boosting primary productivity and providing abundant food resources for larger marine
organisms(Flombaum et al., 2013). Warmer sea surface temperatures also create favorable conditions for species thriving in
warmer waters, promoting the survival, reproduction, and growth of larger marine organisms(Chen et al., 2019; Bova et al.,
2021). Additionally, ocean circulation and upwelling transport nutrient-rich deep waters to the surface, attracting larger marine
species to feed during the day. The mesopelagic layer at 400–500 m, typically inhabited by non-swimming species or crus-
250   taceans, is shaped by vertical fluxes of organic carbon and particulate matter(Marohn et al., 2021; Liu, 2011; Sikder et al.,
2019; Henson et al., 2012; Lutz et al., 2007). These factors collectively contribute to the aggregation of mesopelagic organisms
at the sea surface during summer and autumn. Similar patterns are observed in the Gulf of Mexico, where high stratification in
summer and autumn leads to high signal abundance and frequency in the surface layer, whereas spring and winter show deeper
mixed layers and predominantly deeper distributions(Contreras-Catala et al., 2016), reflecting high mesopelagic activity in the
255   upper ocean layer and strong aggregation during these seasons.

The spatial distribution of mesopelagic organisms reveals a pattern of shallower depths in warmer regions, gradually deep-
ening with increasing latitude. This latitudinal shift is primarily attributed to variations in light conditions, consistent with prior
acoustic studies that report a positive linear correlation between deep scattering layer (DSL) backscattering and temperature
at corresponding depths(Proud et al., 2017, $p = 0.0001$). In the Iceland Sea, carbon flux to the upper ocean is more than eight
260   times lower than in lower-latitude regions, leading to a general mid-ocean distribution of mesopelagic organisms(Klevjer et al.,
2020a). However, latitude alone does not fully explain the spatial distribution differences observed. For example, despite sim-
ilar latitudes, the western side of Greenland's Iceland Sea hosts shallower mesopelagic populations compared to the eastern
side, with the reasons for this disparity remaining unexplored. Given the North Atlantic's complexity, factors such as sea ice
cover, the North Atlantic Oscillation, and diverse current systems likely influence mesopelagic distributions(Gu et al., 2024;
265   Puerta et al., 2020; Lynch-Stieglitz et al., 2024). Environmental differences show that the eastern coast of Greenland, influ-
enced by the North Atlantic Warm Current, experiences higher temperatures and increased chlorophyll concentrations, creating
more favorable conditions for mesopelagic organisms, predominantly found in mid-ocean layers. In contrast, the western coast,
shaped by the Greenland Cold Current, features lower temperatures and reduced nutrient availability. The colder sea surface
on the west may decrease large predator activity, providing a relatively safer habitat with suitable nutritional conditions for
270   mesopelagic organisms(Chawarski et al., 2022).

Mesopelagic organisms also exhibit significant aggregation behaviors in frontal zones, where alternating downwelling and
upwelling currents induce vertical displacements with substantial ecological impacts. These regions are characterized by steep
environmental gradients, including variations in sea surface temperature, chlorophyll concentration, sea surface height, and dis-
solved oxygen, which significantly influence fish distribution(Owen, 1981; Woodd-Walker et al., 2002). Frontal zones, marked
275   by distinct thermal gradients resulting from the convergence of different water masses, serve as biodiversity and productivity
hotspots(Longhurst, 2007). In the study area, an average of three to four water masses interact, with polar fronts demarcating the
boundary between Atlantic and polar water masses. The interaction between colder northern waters and terrestrial runoff cre-
ates gradients of declining temperature and salinity, forming distinct physiographic environments that influence mesopelagic

distribution(Sutton et al., 2017; Astthorsson et al., 2007). Notably, the Greenland-Iceland-Norway front, characterized by a
280 significant temperature-salinity gradient, corresponds to deeper mesopelagic aggregations, driven by the separation of colder
Arctic and warmer Atlantic waters and the resulting temperature-salinity gradient, which critically impacts marine productivity
and spatial distribution. Moreover, vertical mixing within frontal zones enhances nutrient upwelling, supporting higher primary
productivity and providing abundant food resources for mesopelagic organisms(Ljungström et al., 2021). Previous studies have
similarly highlighted the role of water masses and frontal zones in influencing mesopelagic distributions(Yin et al., 2024).

285 5 Conclusions

Comparative analysis using acoustic trawl and satellite lidar detection confirms that b_{bp} from BGC-Argo effectively capture the
biological signal of mesopelagic organisms. During the day, mesopelagic organisms predominantly inhabit the middle layers,
exhibiting multi-layered aggregation patterns. At night, reduced light levels lower predation risks, driving a general upward
migration into the upper layers, where pronounced diel vertical migration (DVM) is observed.

290 Seasonally, the mean intensity of b_{bp} spikes in the upper layers remains lower than in the middle layers during spring and
winter, although the frequency of these spikes in the upper layers is higher. In contrast, summer and autumn show an increase
in both intensity and frequency of b_{bp} signals in the upper layers, particularly near the surface. This seasonal shift reflects a
change in habitat utilization, with mesopelagic organisms becoming more active in the upper layers for foraging. The depth
of the strongest b_{bp} signal exhibits a periodic pattern, shallowing from winter through spring and summer, and deepening in
295 autumn, which corresponds to seasonal fluctuations in mixed layer concentration.

Horizontally, the study area reveals deeper distributions in the northeast and shallower distributions in the southwest. In
the northwestern North Atlantic, mesopelagic organisms typically reside at an average depth of 200 meters, while in the
eastern Iceland Sea, they are found at greater depths, around 800 meters. The Labrador Sea features an average signal layer
depth of 400 meters, whereas the Irminger Sea has it at approximately 300 meters. Oceanic fronts, such as the Greenland-
300 Iceland-Norway Front, East Greenland Front, Labrador Front, and North Atlantic Drift Front, present pronounced temperature
gradients, favorable light conditions, and nutrient-rich waters, attracting significant concentrations of mesopelagic organisms
and leading to substantial biological aggregations.

Spatiotemporal distribution patterns highlight that mesopelagic depth distribution is influenced by multiple environmental
factors. Correlation and random forest analyses underscore temperature as a primary determinant year-round, with temperature
305 gradients emerging as the most significant factor affecting mesopelagic distribution in peak layers. Seawater salinity, dissolved
oxygen, sea surface chlorophyll concentration, and latitude also play important roles.

BGC-Argo data provide valuable insights into the spatial distribution and seasonal variability of mesopelagic organisms,
promoting our understanding of organic carbon transfer to the deep sea, ecosystem energy and material cycling, and fisheries
management. Future research should incorporate additional environmental factors such as eddies, currents, and oceanic fronts
310 to further elucidate the complex dynamics influencing mesopelagic organisms. Despite the extensive vertical profile data pro-

vided by BGC-Argo, clustering effects and limited sampling of certain environmental parameters suggest that advancements in lidar technology could substantially improve mesopelagic organism detection capabilities.

References

Alexander, H., Hu, S. K., Krinos, A. I., Pachiadaki, M., Tully, B. J., Neely, C. J., and Reiter, T.: Eukaryotic genomes from a global metagenomic data set illuminate trophic modes and biogeography of ocean plankton, mBio, 14, e01 676–23, https://doi.org/10.1128/mbio.01676-23, 2023.

330

Allan, E. A., DiBenedetto, M. H., Lavery, A. C., Govindarajan, A. F., and Zhang, W. G.: Modeling characterization of the vertical and temporal variability of environmental DNA in the mesopelagic ocean, Scientific Reports, 11, 21 273, https://doi.org/s41598-021-00288-5, 2021.

Astthorsson, O. S., Gislason, A., and Jonsson, S.: Climate variability and the Icelandic marine ecosystem, Deep Sea Research Part II: Topical

335   Studies in Oceanography, 54, 2456–2477, https://doi.org/10.1016/j.dsr2.2007.07.030, 2007.

Bailey, R.: Life in the Mesopelagic Zone of the Ocean, https://www.thoughtco.com/mesopelagic-zone-4685646, 2021.

Bandara, K., Varpe, Ø., Wijewardene, L., Tverberg, V., and Eiane, K.: Two hundred years of zooplankton vertical migration research, Biological Reviews, 96, 1547–1589, https://doi.org/10.1111/brv.12715, 2021.

Behrenfeld, M. J., Gaube, P., Della Penna, A., O'malley, R. T., Burt, W. J., Hu, Y., Bontempi, P. S., Steinberg, D. K., Boss, E. S., Siegel,

340   D. A., et al.: Global satellite-observed daily vertical migrations of ocean animals, Nature, 576, 257–261, https://doi.org/10.1038/s41586-019-1796-9, 2019.

Bianchi, D., Galbraith, E. D., Carozza, D. A., Mislan, K., and Stock, C. A.: Intensification of open-ocean oxygen depletion by vertically migrating animals, Nature Geoscience, 6, 545–548, https://doi.org/10.1038/NGEO1837, 2013.

Bishop, J. K. and Wood, T.: Particulate matter chemistry and dynamics in the twilight zone at VERTIGO ALOHA and K2 sites, Deep Sea

345   Research Part I: Oceanographic Research Papers, 55, 1684–1706, https://doi.org/10.1016/j.dsr.2008.07.012, 2008.

Bishop, J. K., Calvert, S. E., and Soon, M. Y.: Spatial and temporal variability of POC in the northeast Subarctic Pacific, Deep Sea Research Part II: Topical Studies in Oceanography, 46, 2699–2733, https://doi.org/10.1016/S0967-0645(99)00081-8, 1999.

Bova, S., Rosenthal, Y., Liu, Z., Godad, S. P., and Yan, M.: Seasonal origin of the thermal maxima at the Holocene and the last interglacial, Nature, 589, 548–553, https://doi.org/10.1038/s41586-020-03155-x, 2021.

350   Boyd, P. W., Claustre, H., Levy, M., Siegel, D. A., and Weber, T.: Multi-faceted particle pumps drive carbon sequestration in the ocean, Nature, 568, 327–335, https://doi.org/10.1038/s41586-019-1098-2, 2019.

Briggs, N., Perry, M. J., Cetinić, I., Lee, C., D'Asaro, E., Gray, A. M., and Rehm, E.: High-resolution observations of aggregate flux during a sub-polar North Atlantic spring bloom, Deep Sea Research Part I: Oceanographic Research Papers, 58, 1031–1039, https://doi.org/10.1016/J.DSR.2011.07.007, 2011.

355   Briggs, N., Dall'Olmo, G., and Claustre, H.: Major role of particle fragmentation in regulating biological sequestration of CO2 by the oceans, Science, 367, 791–793, https://doi.org/10.1126/science.aay1790, 2020.

Chai, F., Johnson, K. S., Claustre, H., Xing, X., Wang, Y., Boss, E., Riser, S., Fennel, K., Schofield, O., and Sutton, A.: Monitoring ocean biogeochemistry with autonomous platforms, Nature Reviews Earth & Environment, 1, 315–326, https://doi.org/10.1038/s43017-020-0053-, 2020.

360   Chawarski, J., Klevjer, T. A., Cote, D., and Geoffroy, M.: Evidence of temperature control on mesopelagic fish and zooplankton communities at high latitudes, Frontiers in Marine Science, 9, 917 985, https://doi.org/10.3389/fmars.2022.917985, 2022.

Chen, B., Smith, S. L., and Wirtz, K. W.: Effect of phytoplankton size diversity on primary productivity in the North Pacific: trait distributions under environmental variability, Ecology Letters, pp. 56–66, https://doi.org/10.1111/ele.13167, 2019.

Claustre, H., Johnson, K. S., and Takeshita, Y.: Observing the global ocean with biogeochemical-Argo, Annual review of marine science, 12,
365   23–48, https://doi.org/10.1146/annurev-marine-010419-010956, 2019.

Contreras-Catala, F., Sánchez-Velasco, L., Beier, E., Godínez, V. M., Barton, E. D., and Santamaria-del Angel, E.: Effects of geostrophic
        kinetic energy on the distribution of mesopelagic fish larvae in the southern Gulf of California in summer/fall stratified seasons, Plos one,
        11, e0164 900, https://doi.org/10.1371/journal.pone.0164900, 2016.

Cuttitta, A., Torri, M., Zarrad, R., Zgozi, S., Jarboui, O., Quinci, E. M., Hamza, M., Abdulfatah, E., Haddoud, D., El Turki, A., et al.: Linking
370   surface hydrodynamics to planktonic ecosystem: the case study of the ichthyoplanktonic assemblages in the Central Mediterranean Sea,
        Hydrobiologia, 821, 191–214, https://doi.org/10.1007/s10750-017-3483-x, 2018.

Dall'Olmo, G., Dingle, J., Polimene, L., Brewin, R. J., and Claustre, H.: Substantial energy input to the mesopelagic ecosystem from the
        seasonal mixed-layer pump, Nature Geoscience, 9, 820–823, https://doi.org/10.1038/ngeo2818, 2016.

De Forest, L. and Drazen, J.: The influence of a Hawaiian seamount on mesopelagic micronekton, Deep Sea Research Part I: Oceanographic
375   Research Papers, 56, 232–250, https://doi.org/10.1016/j.dsr.2008.09.007, 2009.

Flombaum, P., Gallegos, J. L., Gordillo, R. A., Rincón, J., Zabala, L. L., Jiao, N., Karl, D. M., Li, W. K., Lomas, M. W., Veneziano, D., et al.:
        Present and future global distributions of the marine Cyanobacteria Prochlorococcus and Synechococcus, Proceedings of the National
        Academy of Sciences, 110, 9824–9829, https://doi.org/10.1073/pnas.1307701110, 2013.

Freeman, A.: Size-dependent trait-mediated indirect interactions among sea urchin herbivores, Behavioral Ecology, 17, 182–187,
380   https://doi.org/10.1093/beheco/17.2.182, 2006.

Galí, M., Falls, M., Claustre, H., Aumont, O., and Bernardello, R.: Bridging the gaps between particulate backscattering measurements and
        modeled particulate organic carbon in the ocean, Biogeosciences, 19, 1245–1275, https://doi.org/10.5194/bg-19-1245-2022, 2022.

Garcia-Soto, C., Cheng, L., Caesar, L., Schmidtko, S., Jewett, E. B., Cheripka, A., Rigor, I., Caballero, A., Chiba, S., Báez, J. C., et al.: An
        overview of ocean climate change indicators: Sea surface temperature, ocean heat content, ocean pH, dissolved oxygen concentration,
385   arctic sea ice extent, thickness and volume, sea level and strength of the AMOC (Atlantic Meridional Overturning Circulation), Frontiers
        in Marine Science, 8, 642 372, https://doi.org/0.3389/fmars.2021.642372, 2021.

Gardner, W. D., Richardson, M. J., and Smith Jr, W. O.: Seasonal patterns of water column particulate organic carbon and fluxes in the
        Ross Sea, Antarctica, Deep Sea Research Part II: Topical Studies in Oceanography, 47, 3423–3449, https://doi.org/10.1016/S0967-
        0645(00)00074-6, 2000.

390 Gjoesaeter, J., Kawaguchi, K., Fao, R. E. D., and FIR: A review of the world resources of mesopelagic fish, Fao Fish Tech Rap, 93, 1980.

Govindarajan, A. F., Llopiz, J. K., Caiger, P. E., Jech, J. M., Lavery, A. C., McMonagle, H., Wiebe, P. H., and Zhang, W.: As-
        sessing mesopelagic fish diversity and diel vertical migration with environmental DNA, Frontiers in Marine Science, 10, 1219 993,
        https://doi.org/10.3389/fmars.2023.1219993, 2023.

Gruber, N., Keeling, C. D., and Bates, N. R.: Interannual variability in the North Atlantic Ocean carbon sink, Science, 298, 2374–2378,
395   https://doi.org/10.1126/science.1077077, 2002.

Gu, Q., Gervais, M., Danabasoglu, G., Kim, W. M., Castruccio, F., Maroon, E., and Xie, S.-P.: Wide range of possible trajectories of North
        Atlantic climate in a warming world, Nature communications, 15, 4221, https://doi.org/10.1038/s41467-024-48401-2, 2024.

Haëntjens, N., Della Penna, A., Briggs, N., Karp-Boss, L., Gaube, P., Claustre, H., and Boss, E.: Detecting mesopelagic organisms using
        biogeochemical-Argo floats, Geophysical Research Letters, 47, e2019GL086 088, https://doi.org/10.1029/2019GL086088, 2020.

400 Hansell, D. A., Carlson, C. A., and Suzuki, Y.: Dissolved organic carbon export with North Pacific Intermediate Water formation, Global
        Biogeochemical Cycles, 16, 7–1, https://doi.org/10.1029/2000GB001361, 2002.

Hauss, H., Christiansen, S., Schütte, F., Kiko, R., Edvam Lima, M., Rodrigues, E., Karstensen, J., Löscher, C. R., Körtzinger, A., and Fiedler, B.: Dead zone or oasis in the open ocean? Zooplankton distribution and migration in low-oxygen modewater eddies, Biogeosciences, 13, 1977–1989, https://doi.org/110.5194/bg-13-1977-2016, 2016.

405 Hays, G. C.: A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations, Hydrobiologia, 503, 163–170, https://doi.org/10.1023/B:HYDR.0000008476.23617.b0, 2003.

Hazen, E. L.: Climate change 'heard' in the ocean depths, Nature Climate Change, 12, 891–892, https://doi.org/10.1038/s41558-022-01484-5, 2022.

Henson, S. A., Sanders, R., and Madsen, E.: Global patterns in efficiency of particulate organic carbon export and transfer to the deep ocean,

410 Global Biogeochemical Cycles, 26, https://doi.org/10.1029/2011GB004099, 2012.

Honjo, S. and Manganini, S. J.: Annual biogenic particle fluxes to the interior of the North Atlantic Ocean; studied at 34 N 21 W and 48 N 21 W, Deep Sea Research Part II: Topical Studies in Oceanography, 40, 587–607, https://doi.org/10.1016/0967-0645(93)90034-K, 1993.

Irigoien, X., Klevjer, T. A., Røstad, A., Martinez, U., Boyra, G., Acuña, J. L., Bode, A., Echevarria, F., Gonzalez-Gordillo, J. I., Hernandez-Leon, S., et al.: Large mesopelagic fishes biomass and trophic efficiency in the open ocean, Nature communications, 5, 3271,

415 https://doi.org/10.1038/ncomms4271, 2014.

Kapelonis, Z., Siapatis, A., Machias, A., Somarakis, S., Markakis, K., Giannoulaki, M., Badouvas, N., and Tsagarakis, K.: Seasonal patterns in the mesopelagic fish community and associated deep scattering layers of an enclosed deep basin, Scientific Reports, 13, 17 890, https://doi.org/10.21203/rs.3.rs-2947537/v1, 2023.

Klevjer, T., Melle, W., Knutsen, T., Strand, E., Korneliussen, R., Dupont, N., Salvanes, A. G. V., and Wiebe, P. H.: Micronekton biomass

420 distribution, improved estimates across four north Atlantic basins, Deep Sea Research Part II: Topical Studies in Oceanography, 180, 104 691, https://doi.org/10.1016/j.dsr2.2019.104691, 2020a.

Klevjer, T. A., Irigoien, X., Røstad, A., Fraile-Nuez, E., Benítez-Barrios, V. M., and Kaartvedt, S.: Large scale patterns in vertical distribution and behaviour of mesopelagic scattering layers, Scientific reports, 6, 19 873, https://doi.org/10.1038/srep19873, 2016.

Klevjer, T. A., Melle, W., Knutsen, T., and Aksnes, D. L.: Vertical distribution and migration of mesopelagic scatterers in four north Atlantic

425 basins, Deep Sea Research Part II: Topical Studies in Oceanography, 180, 104 811, https://doi.org/10.1016/j.dsr2.2020.104811, 2020b.

Kruse, S., Brey, T., and Bathmann, U.: Role of midwater chaetognaths in Southern Ocean pelagic energy flow, Marine Ecology Progress Series, 416, 105–113, https://doi.org/0.3354/meps08773, 2010.

Lampert, W., Fleckner, W., Pott, E., Schober, U., and Strkel, K. U.: Herbicide effects on planktonic systems of different complexity, Hydrobiologia, 188-189, 415–424, 1989.

430 Lampitt, R.: Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension, Deep Sea Research Part A. Oceanographic Research Papers, 32, 885–897, https://doi.org/10.1016/0198-0149(85)90034-2, 1985.

Lin, H.-Y. and Costello, M. J.: Body size and trophic level increase with latitude, and decrease in the deep-sea and Antarctica, for marine fish species, PeerJ, 11, e15 880, 2023.

Liu, R.: Progress of marine biodiversity studies in China seas, Biodiversity Science, 19, 614, https://doi.org/10.17520/biods.2022526, 2011.

435 Ljungström, G., Langbehn, T. J., and Jørgensen, C.: Light and energetics at seasonal extremes limit poleward range shifts, Nature Climate Change, 11, 530–536, 2021.

Loisel, H., Nicolas, J.-M., Deschamps, P.-Y., and Frouin, R.: Seasonal and inter-annual variability of particulate organic matter in the global ocean, Geophysical Research Letters, 29, 49–1, https://doi.org/10.1029/2002GL015948, 2002.

Longhurst, A.: Ecological Geography of the Sea, Academic Press, https://doi.org/10.1016/B978-0-12-455521-1.X5000-1, 2007.

440 Lourenço, S. and Jany, M.: Zooplankton Diel Vertical Migration impact on particulate matter flux in the Atlantic, Ph.D. thesis, WASCAL, 2021.

Luo, J., Ortner, P. B., Forcucci, D., and Cummings, S. R.: Diel vertical migration of zooplankton and mesopelagic fish in the Arabian Sea, Deep Sea Research Part II: Topical Studies in Oceanography, 47, 1451–1473, https://doi.org/10.1016/S0967-0645(99)00150-2, 2000.

Lutz, M. J., Caldeira, K., Dunbar, R. B., and Behrenfeld, M. J.: Seasonal rhythms of net primary production and particulate organic
445 carbon flux to depth describe the efficiency of biological pump in the global ocean, Journal of Geophysical Research: Oceans, 112, https://doi.org/10.1029/2006JC003706, 2007.

Lynch-Stieglitz, J., Vollmer, T. D., Valley, S. G., Blackmon, E., Gu, S., and Marchitto, T. M.: A diminished North Atlantic nutrient stream during Younger Dryas climate reversal, Science, 384, 693–696, https://doi.org/10.1126/science.adi5543, 2024.

Marohn, L., Schaber, M., Freese, M., Pohlmann, J.-D., Wysujack, K., Czudaj, S., Blancke, T., and Hanel, R.: Distribution and diel verti-
450 cal migration of mesopelagic fishes in the Southern Sargasso Sea—observations through hydroacoustics and stratified catches, Marine Biodiversity, 51, 1–24, https://doi.org/10.1007/s12526-021-01216-6, 2021.

Nakao, L. T. H., Krueger, C. P., and Bleninger, T.: Benchmarking for using an acoustic Doppler current profiler for bathymetric survey, Environmental Monitoring and Assessment, 193, 356, https://doi.org/10.1007/s10661-021-09073-3, 2021.

Owen, R. W.: Fronts and eddies in the sea: mechanisms, interactions and biological effects, Analysis of marine ecosystems, 98, 3–5, 1981.

455 Parra, D., Valverde, L., Pino, F. J., and Patel, M. K.: A review on the role, cost and value of hydrogen energy systems for deep decarbonisation, Renewable and Sustainable Energy Reviews, 101, 279–294, https://doi.org/10.1016/j.rser.2018.11.010, 2019.

Petit, F.: Developement and exploitation of new approaches for observation of phytoplankton community composition from BGC-Argo floats in open ocean, Ph.D. thesis, Sorbonne Université, 2023.

Petrusevich, V. Y., Dmitrenko, I. A., Niemi, A., Kirillov, S. A., Kamula, C. M., Kuzyk, Z. Z. A., Barber, D. G., and Ehn, J. K.: Impact of tidal
460 dynamics on diel vertical migration of zooplankton in Hudson Bay, Ocean Science, 16, 337–353, 2020.

Puerta, P., Johnson, C., Carreiro-Silva, M., Henry, L.-A., Kenchington, E., Morato, T., Kazanidis, G., Rueda, J. L., Urra, J., Ross, S., et al.: Influence of water masses on the biodiversity and biogeography of deep-sea benthic ecosystems in the North Atlantic, Frontiers in Marine Science, 7, 239, https://doi.org/10.3389/fmars.2020.00239, 2020.

Ramirez-Llodra, E., Brandt, A., Danovaro, R., De Mol, B., Escobar, E., German, C. R., Levin, L. A., Martinez Arbizu, P., Menot, L.,
465 Buhl-Mortensen, P., et al.: Deep, diverse and definitely different: unique attributes of the world's largest ecosystem, Biogeosciences, 7, 2851–2899, https://doi.org/10.5194/bg-7-2851-2010, 2010.

Ramos-Jiliberto, R., González-Olivares, E., and Bozinovic, F.: Population-level consequences of antipredator behavior: A meta-physiological model based on the functional ecology of the leaf-eared mouse, Theoretical Population Biology, 62, 63–80, https://doi.org/10.1006/tpbi.2002.1581, 2002.

470 Rembauville, M., Briggs, N., Ardyna, M., Uitz, J., Catala, P., Penkerc'h, C., Poteau, A., Claustre, H., and Blain, S.: Plankton assemblage estimated with BGC-Argo floats in the Southern Ocean: Implications for seasonal successions and particle export, Journal of Geophysical Research: Oceans, 122, 8278–8292, https://doi.org/10.1002/2017jc013067, 2017.

Robinson, C., Steinberg, D. K., Anderson, T. R., Arístegui, J., Carlson, C. A., Frost, J. R., Ghiglione, J.-F., Hernández-León, S., Jackson, G. A., Koppelmann, R., et al.: Mesopelagic zone ecology and biogeochemistry–a synthesis, Deep Sea Research Part II: Topical Studies in
475 Oceanography, 57, 1504–1518, https://doi.org/10.1016/j.dsr2.2010.02.018, 2010.

Sameoto, D.: Influence of the biological and physical environment on the vertical distribution of mesozooplankton and micronekton in the eastern tropical Pacific, Marine Biology, 93, 263–279, https://doi.org/10.1016/j.dsr2.2010.02.018, 1986.

Sarant, L.: Little mesopelagic fish have big carbon capture impact, Nature Middle East, https://api.semanticscholar.org/CorpusID:87615417, 2014.

480 Scales, K. L., Miller, P. I., Ingram, S. N., Hazen, E. L., Bograd, S. J., and Phillips, R. A.: Identifying predictable foraging habitats for a wide-ranging marine predator using ensemble ecological niche models, Diversity and distributions, 22, 212–224, https://doi.org/10.1111/ddi.12389, 2016.

Sikder, M. N. A., Abdullah Al, M., Xu, G., Hu, G., and Xu, H.: Spatial variations in trophic-functional patterns of periphytic ciliates and indications to water quality in coastal waters of the Yellow Sea, Environmental Science and Pollution Research, 26, 2592–2602, 485 https://doi.org/10.1007/s11356-018-3744-x, 2019.

Song, W., Liu, J., Qin, W., Huang, J., Yu, X., Xu, M., Stahl, D., Jiao, N., Zhou, J., and Tu, Q.: Functional traits resolve mechanisms governing the assembly and distribution of nitrogen-cycling microbial communities in the global ocean, MBio, 13, e03 832–21, https://doi.org/10.1128/mbio.03832-21, 2022.

Sorochan, K., Plourde, S., and Johnson, C.: Near-bottom aggregations of Calanus spp. copepods in the southern Gulf of St. 490 Lawrence in summer: significance for North Atlantic right whale foraging, ICES Journal of Marine Science, 80, 787–802, https://doi.org/10.1093/icesjms/fsad003, 2023.

Sutton, T.: Vertical ecology of the pelagic ocean: classical patterns and new perspectives, Journal of fish biology, 83, 1508–1527, https://doi.org/10.1111/jfb.12263, 2013.

Sutton, T., Porteiro, F., Heino, M., Byrkjedal, I., Langhelle, G., Anderson, C., Horne, J., Søiland, H., Falkenhaug, T., Godø, O., et al.: Vertical 495 structure, biomass and topographic association of deep-pelagic fishes in relation to a mid-ocean ridge system, Deep Sea Research Part II: Topical Studies in Oceanography, 55, 161–184, https://doi.org/10.1016/j.dsr2.2007.09.013, 2008.

Sutton, T. T., Clark, M. R., Dunn, D. C., Halpin, P. N., Rogers, A. D., Guinotte, J., Bograd, S. J., Angel, M. V., Perez, J. A. A., Wishner, K., et al.: A global biogeographic classification of the mesopelagic zone, Deep Sea Research Part I: Oceanographic Research Papers, 126, 85–102, https://doi.org/10.1016/j.dsr.2017.05.006, 2017.

500 Underwood, M. J., García-Seoane, E., Klevjer, T. A., Macaulay, G. J., and Melle, W.: An acoustic method to observe the distribution and behaviour of mesopelagic organisms in front of a trawl, Deep Sea Research Part II: Topical Studies in Oceanography, 180, 104 873, https://doi.org/10.1016/j.dsr2.2020.104873, 2020.

Vedenin, A., Musaeva, E., and Vereshchaka, A.: Three-dimensional distribution of mesoplankton assemblages in the Central Atlantic, Global Ecology and Biogeography, 31, 1345–1365, https://doi.org/10.1111/geb.13509, 2022.

505 Villafaña, J. A. and Rivadeneira, M. M.: The modulating role of traits on the biogeographic dynamics of chondrichthyans from the Neogene to the present, Paleobiology, 44, 251–262, https://doi.org/10.1017/pab.2018.7, 2018.

Wang, B. and Fennel, K.: Biogeochemical-Argo data suggest significant contributions of small particles to the vertical carbon flux in the subpolar North Atlantic, Limnology and Oceanography, 67, 2405–2417, https://doi.org/10.1002/lno.12209, 2022.

Woodd-Walker, R. S., Ward, P., and Clarke, A.: Large-scale patterns in diversity and community structure of surface water copepods from 510 the Atlantic Ocean, Marine Ecology Progress Series, 236, 189–203, https://doi.org/10.3354/meps236189, 2002.

Xing, X., Wells, M. L., Chen, S., Lin, S., and Chai, F.: Enhanced winter carbon export observed by BGC-Argo in the Northwest Pacific Ocean, Geophysical Research Letters, 47, e2020GL089 847, https://doi.org/10.1029/2020GL089847, 2020.

Yin, Z., Zhang, X., Wang, S., and Xu, Y.: Spatiotemporal variation of dissolved oxygen concentration in the northern Gulf of Mexico during the period of 1992–2017, Marine Pollution Bulletin, 198, 115 771, https://doi.org/10.1016/j.marpolbul.2023.115771, 2024.