LIMNOLOGY and OCEANOGRAPHY LETTERS

ASLO

Open Access

Limnology and Oceanography Letters 11, 2026, e70113

doi: 10.1002/lol2.70113

LETTER

Temporal dynamics of mesopelagic fishes within a mesoscale eddy: A Lagrangian perspective

Mei Sato [1]* **Zachary K. Erickson** [2] **Laetitia Drago** [3,4] **Amy E. Maas** [5] **Helena McMonagle** [6] **Deborah K. Steinberg** [7]

[1]Biology Department, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, USA; [2]NOAA Pacific Marine Environmental Laboratory, Seattle, Washington, USA; [3]MNHN, CNRS, IRD, Laboratoire d'Océanographie et du Climat: Expérimentations et Approches Numériques, LOCEAN, Sorbonne Université, Paris, France; [4]Laboratoire d'Océanographie de Villefranche-sur-mer, Sorbonne Université, Villefranche-sur-mer, France; [5]Bermuda Institute of Ocean Sciences, Arizona State University, St. George's, Bermuda; [6]School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington, USA; [7]Coastal and Ocean Processes Section, Virginia Institute of Marine Science, William & Mary, Gloucester Point, Virginia, USA

Scientific Significance Statement

Mesoscale eddies, large swirling currents in the ocean on the order of tens to hundreds of kilometers in diameter, create dynamic habitats that support diverse marine life. While their physical variability is well studied, much less is known about how mid-trophic organisms such as mesopelagic fishes respond as conditions change within eddies over time. By following a single eddy for nearly a month, our study shows that fish rapidly reorganize their distributions in response to shifting prey, demonstrating that eddies are dynamic ecosystems where trophic interactions and species' vertical distributions evolve on weekly to monthly timescales.

Abstract

Mesoscale eddies are physically dynamic environments, yet biological responses within them are often treated as static, with eddy polarity (anticyclones vs. cyclones) serving as the dominant conceptual framework. Temporal dynamics of animals within eddies—particularly at mid-trophic levels—remain largely unresolved. We tracked a long-lived anticyclonic eddy in the Northeast Atlantic for nearly a month using a Lagrangian framework, generating one of the few continuous time series of mesopelagic fish distribution within an eddy. Coupled physical–biological observations revealed marked vertical changes following a major wind storm: compact fish aggregations dispersed as phytoplankton distributions expanded and zooplankton deepened, despite comparable integrated fish biomass before and after. These results show that aggregation dynamics of mesopelagic fishes are modulated by bottom-up variability on weekly to monthly timescales. By moving beyond static snapshots, our study demonstrates that eddies function as dynamic ecosystems whose ecological roles in pelagic food webs evolve through time.

*Correspondence: msato@whoi.edu

Associate editor: Raphael Kudela

Biological–physical interactions shape ocean variability across space and time, structuring populations and trophic dynamics (Haury et al. 1978; Bakun 1996). Mesoscale eddies—long-lived, energetic vortices spanning tens to hundreds of kilometers—are ubiquitous throughout much of the global ocean (Chelton et al. 2007, 2011; Early et al. 2011) and define the environment for planktonic and nektonic communities. As they evolve, eddies modify nutrient fluxes (McGillicuddy 2016), transport zooplankton and ichthyoplankton (Craddock et al. 1992; Mackas and Galbraith 2002), and attract predators ranging from large pelagic fishes to seabirds (Seki et al. 2002; Weimerskirch et al. 2004; Braun et al. 2019; Arostegui et al. 2022). While cyclonic eddies ("cold-core rings") are often associated with enhanced primary production relative to anticyclonic eddies ("warm-core rings") (McGillicuddy 2016), biological responses at mid-trophic levels remain ambiguous, with studies reporting contrasting patterns (Drazen et al. 2011; Potier et al. 2014; Della Penna and Gaube 2020; Wang et al. 2023; Receveur et al. 2024).

Eddies are inherently time-varying habitats. Their polarity (cyclonic vs. anticyclonic) and life stage drive temporal shifts in isopycnal displacement, nutrient supply, and primary production (McGillicuddy and Robinson 1997; McGillicuddy 2016). Such variability is typically driven by wind-driven Ekman pumping and eddy–eddy interactions (Gaube et al. 2015), mediating the timing and intensity of phytoplankton blooms, with blooms in cyclones often preceding those in anticyclones by weeks (e.g., Maúre et al. 2017). Capturing this temporal evolution is essential for understanding ecosystem functioning.

Biological observations in mesoscale eddies, especially for mid-trophic organisms that link phytoplankton to top predators, remain scarce relative to physical measurements. Most biological sampling lacks the temporal and spatial resolution needed to assess the role of eddies in structuring pelagic communities. While satellite and optical sensors capture temporal variability in primary productivity (McGillicuddy et al. 2007; Mahadevan et al. 2012; Gaube et al. 2013), traditional net tows for zooplankton and ichthyoplankton integrate over large spatial and temporal scales (Davis and Wiebe 1985; Craddock et al. 1992; Mackas and Galbraith 2002; Goldthwait and Steinberg 2008), obscuring fine-scale patterns. Active acoustics offer higher-resolution views of zooplankton and fish in dynamic environments (Kaartvedt et al. 2012a; Benoit-Bird et al. 2019; Sato and Benoit-Bird 2024), but previous studies in eddies have largely been snapshots (Godø et al. 2012; Della Penna and Gaube 2020; Wang et al. 2023; Receveur et al. 2024). This reflects the difficulty of continuously sampling moving eddies and disentangling temporal variability in animal distributions from diel vertical migration. Consequently, biological responses have often been treated as static, with eddy polarity serving as the dominant conceptual framework, leaving temporal dynamics largely unexplored.

Here, we address this gap using multidisciplinary observations collected within an eddy tracked for nearly a month in a Lagrangian framework. By following the eddy, we move beyond the snapshot paradigm to reveal a time series of biological properties at mid-trophic levels. These observations reveal pronounced temporal dynamics in mesopelagic fish distributions linked to shifts in lower-trophic prey, highlighting the importance of predator–prey interactions and their potential implications for top predators.

Materials and methods

Study design and environmental context

This study was conducted within an anticyclonic mode-water eddy during the 2021 EXport Processes in the Ocean from RemoTe Sensing (EXPORTS) field campaign in the Northeast Atlantic (May 3–30). A detailed description of the eddy's physical properties is provided in Johnson et al. (2024). Several wind storms drove surface-water exchange via Ekman transport and intermittently interrupted ship-based sampling. Wind velocity was measured at 1 Hz at 19.4 m above sea level using an anemometer (Gill WindSonic) on the RRS *James Cook*. Sampling followed a Lagrangian framework, leveraging the eddy's retentive core ($\sim$ 15 km within an effective radius of $\sim$ 25 km) to co-locate multidisciplinary measurements from autonomous and ship-based platforms (Erickson et al. 2023; Johnson et al. 2024). This approach enabled concurrent observations of phytoplankton, zooplankton, and mesopelagic fishes. Eddy center positions were tracked using satellite and in situ observations (Erickson et al. 2022; Johnson et al. 2024). Analyses were restricted, when possible, to data collected within 15 km of the eddy center (the eddy core), where horizontal advection is minimized, allowing focus on biological variability intrinsic to the eddy. The associated data are available in Sato et al. (2025).

Phytoplankton

Temporal variability in chlorophyll concentrations was examined using in situ Seaglider profiles within the eddy core. The glider profiled from the surface to $\sim$ 1000 m every 6 h, measuring chlorophyll fluorescence every 5 m. For each profile, peak chlorophyll concentrations were identified and aggregated into 24-h bins (medians $\pm$ interquartile ranges). Vertical distributional changes were characterized using the dispersion index (Woillez et al. 2007) to quantify population spread relative to the center of mass, also summarized as daily medians.

Zooplankton

Zooplankton abundance and distribution were quantified using complementary net sampling and optical imaging. Analyses focused on nighttime observations, when mesopelagic fishes migrate to the surface to forage and overlap with their zooplankton prey. Acoustic methods were not applied here because zooplankton and fishes co-occur near the surface at night, producing overlapping backscatter that prevents reliable separation of their signals.

Net samples—Depth-stratified oblique tows were conducted with a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS; Wiebe et al. 1985) aboard the RRS *James Cook*. A 9-net system (200 μm mesh, 1 m^2 mouth opening) was towed at $\sim$ 2 knots (1 m s^{-1}). Three paired day–night tows (May 6–7, 17–18, and 26–27, 2021) sampled 50 m strata in the upper 200 m, 100 m strata from 200 to 500 m, and 250 m strata from 500 to 1000 m. Each sample was split at sea: half was fractionated into five size classes, with data merged to create three for our analysis (0.2–2.0, 2.0–5.0, and > 5.0 mm) for dry weight; a portion of the remainder was preserved in formalin. Subsamples were processed using the ZooSCAN–Zooprocess–Ecotaxa pipeline (Gorsky et al. 2010; Vandromme et al. 2012), following Maas et al. (2021). Analyses focused on the upper 200 m. Tow trajectories intersected different positions relative to the eddy center: 8.1–12.9 km (May 6–7), 17.0–21.6 km (May 17–18), and 18.4–22.0 km (May 26–27). Day–night differences were assessed by comparing integrated biomass in the upper 200 m across size classes.

Optical imaging—Zooplankton were imaged using three inter-calibrated Underwater Vision Profiler 5 (UVP5) units (Picheral et al. 2010) deployed on CTD rosettes aboard the RRS *James Cook*, RRS *Discovery*, and R/V *Sarmiento de Gamboa*. The UVP5 detects particles $\geq$ 100 μm equivalent spherical diameter (ESD) and images zooplankton and aggregates $\geq$ 600 μm ESD. Images were processed with Zooprocess and Morphocluster (Schröder et al. 2020), followed by manual validation in Ecotaxa (Picheral et al. 2017). Detailed processing is described in Drago (2023). Across vessels, 6–9 UVP profiles were typically obtained per day within the eddy core, except during storms (Siegel et al. 2023). Due to high spatial variability and low detection rates, zooplankton densities were averaged into 20 m depth bins. Only metazoan zooplankton were included, excluding Rhizaria (unicellular eukaryotes), since mesopelagic fish diets are dominated by crustaceans (Hopkins et al. 1996; Drazen and Sutton 2017) and gelatinous taxa (Eduardo et al. 2020; Bucklin et al. 2024). We focused on nighttime profiles (typically 1–3 per day) within the eddy core. When multiple profiles were available for a given night, densities were averaged to obtain a nightly mean.

Fish

Fine-scale distributions of mesopelagic fishes were examined using shipboard multifrequency echosounders and net samples for species composition within the eddy core. Analyses focused on nighttime periods (1.5 h after sunset to 1.5 h before sunrise), when vertically migrating mesopelagic fishes ascend to the upper water column to feed under reduced predation risk.

Acoustic observations—Acoustic data were collected from the RRS *James Cook* and *Discovery* using multifrequency echosounders (Simrad EK60s). Both vessels operated continuously at 18, 38, 70, 120, and 200 kHz, recording every 2 s with a pulse duration of 1024 μs and a vertical resolution of 20 cm. Data from the *Discovery*'s 38-kHz echosounder were excluded due to malfunction. The *James Cook* echosounders were calibrated using the standard sphere method (Demer et al. 2015) and used to intercalibrate instruments on the *Discovery*. Analyses focused on 18- and 70-kHz data to ensure consistency and sensitivity to fish targets.

Data were processed in Echoview (v.13.1). To minimize near-field effects and surface bubble interference, data shallower than 15 m were excluded. Due to increasing noise with depth, particularly at 70 kHz, analyses were restricted to the upper 460 m. Data were averaged over 30 pings $\times$ 5 bins ($\sim$ 70 s $\times$ 1 m) to reduce stochastic variability (Simmonds and MacLennan 2005). A 3-point running median filter was applied in both time and depth to enhance feature continuity while preserving edges. Scattering layers were identified using the difference in volume backscattering strength (ΔS_v) between frequencies (Kang et al. 2002; Sato et al. 2015), calculated as $\Delta S_{v,i-j} = S_{v,\mathrm{i}} - S_{v,j}$, where i and j denote frequency (kHz). Analyses focused on surface scattering layers, typically located within the upper 200 m at night and composed of both migratory and non-migratory components. Surface scattering layers were isolated by retaining regions where -3.5 dB re 1 $m^{-1} < \Delta S_{v,18\text{-}70\mathrm{kHz}} \leq 5.3$ dB re 1 m^{-1}. Only data with S_v stronger than -85 dB re 1 m^{-1} at both frequencies were included.

Temporal variability was quantified using the dispersion index and Nautical Area Scattering Coefficient (NASC; m^2 nmi^{-2}), a linear measure of integrated backscatter (MacLennan et al. 2002). Daily averaging was not applied because sampling within the eddy core was uneven, often limited to a few nighttime hours as the ship transited in and out of the core. To better capture short-term variability and reduce sampling bias associated with the patchy distribution of mesopelagic fishes, acoustic data from multiple days were aggregated into 15-min time-of-day intervals, excluding those with fewer than 50 samples. Two analysis periods were defined to contrast conditions before and after the strong storm event—May 3–19 and May 21–29, 2021—when scattering layer structure changed markedly (Fig. 3). Differences in dispersion index and NASC between periods were tested using Mann–Whitney U tests, and day–night differences were assessed from NASC values over the full record.

Net samples—To link acoustic observations with species identity, mesopelagic fishes were collected using a 5-net MOCNESS system (333 μm mesh, 10 m^2 mouth opening) deployed on the R/V *Sarmiento de Gamboa*. A single nighttime tow targeted the surface scattering layer (0–100 m) within the eddy core on May 6 (3.3–3.6 km from the eddy center). Specimens were flash-frozen in liquid nitrogen (-80°C) or preserved in 95% ethanol, identified to the lowest possible taxonomic level using morphological and genetic methods, and measured for standard length (SL). Additional methodological details, including the animal collection protocol, are provided in McMonagle et al. (2024). While MOCNESS

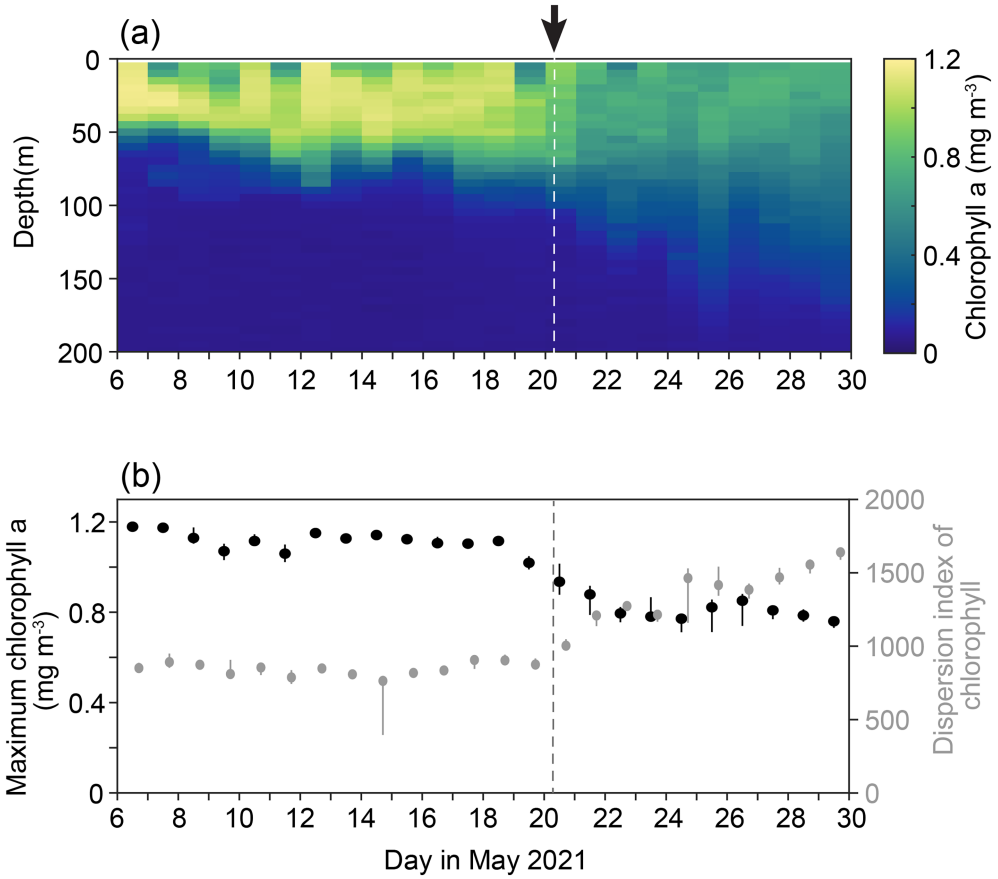

Fig. 1. Temporal variability of (**a**) chlorophyll *a* concentrations measured within the eddy core (< 15 km from the eddy center), and (**b**) maximum chlorophyll *a* concentrations (black) and their dispersion index (gray). In (b), circles indicate medians and error bars represent one interquartile range, and the two data sets are offset for clarity in visualization. The dotted lines with an arrow on May 20 indicate the timing of the strongest storm during the field campaign, corresponding with the changes in concentrations and distributions of phytoplankton.

catches underestimate abundance due to net avoidance (Wiebe et al. 1982; Kaartvedt et al. 2012b) and efficiency issues (Davison 2011; Hernández-León et al. 2019), they provided key information on the species composition and size structure of dominant acoustic scatterers.

Results

Vertical distributions of phytoplankton were strongly influenced by storm activity during the eddy occupation. The most intense storm event occurred on May 20, with wind speeds reaching 46.4 knots. This disturbance coincided with a marked redistribution of phytoplankton: prior to the storm, chlorophyll *a* was concentrated within the upper 50–80 m, whereas afterward, vertical distributions broadened (Fig. 1a), the dispersion index increased, and peak concentrations declined by ~ 30% (Fig. 1b).

Zooplankton distributions at night mirrored this pattern. Net tows on May 27 showed deeper occurrences across size classes relative to May 7 and 18 (Fig. 2a–c), consistent with a downward shift following the phytoplankton redistribution. At night, copepods dominated the zooplankton community, comprising 75.7–85.9% of individuals in the 0.2–5.0 mm range. In the > 5.0 mm fraction, amphipods (10.5–73.6%), euphausiids (2.2–48.9%), and copepods (0–61.0%) were dominant, depending on sampling date. Comparisons between day and night tows revealed higher integrated biomass in the upper 200 m at night for all size classes (Supporting Information Fig. S1), suggesting dominance of diel vertical migrators. Similarly, optical imaging observations of zooplankton densities (dominated by Crustacea) at night showed broader vertical distributions toward late May (Fig. 2d). An overall increase in zooplankton biomass later in the field campaign was evident in both the MOCNESS tows and UVP profiles, but the magnitude and timing varied among size classes and sampling periods. UVP data showed increased densities in the upper 200 m following the May 20 storm (Fig. 2d). In contrast, MOCNESS-derived biomass increased primarily on May 17–18 (Supporting Information Fig. S1), prior to the storm. A distinct post-storm increase in the MOCNESS data was observed only

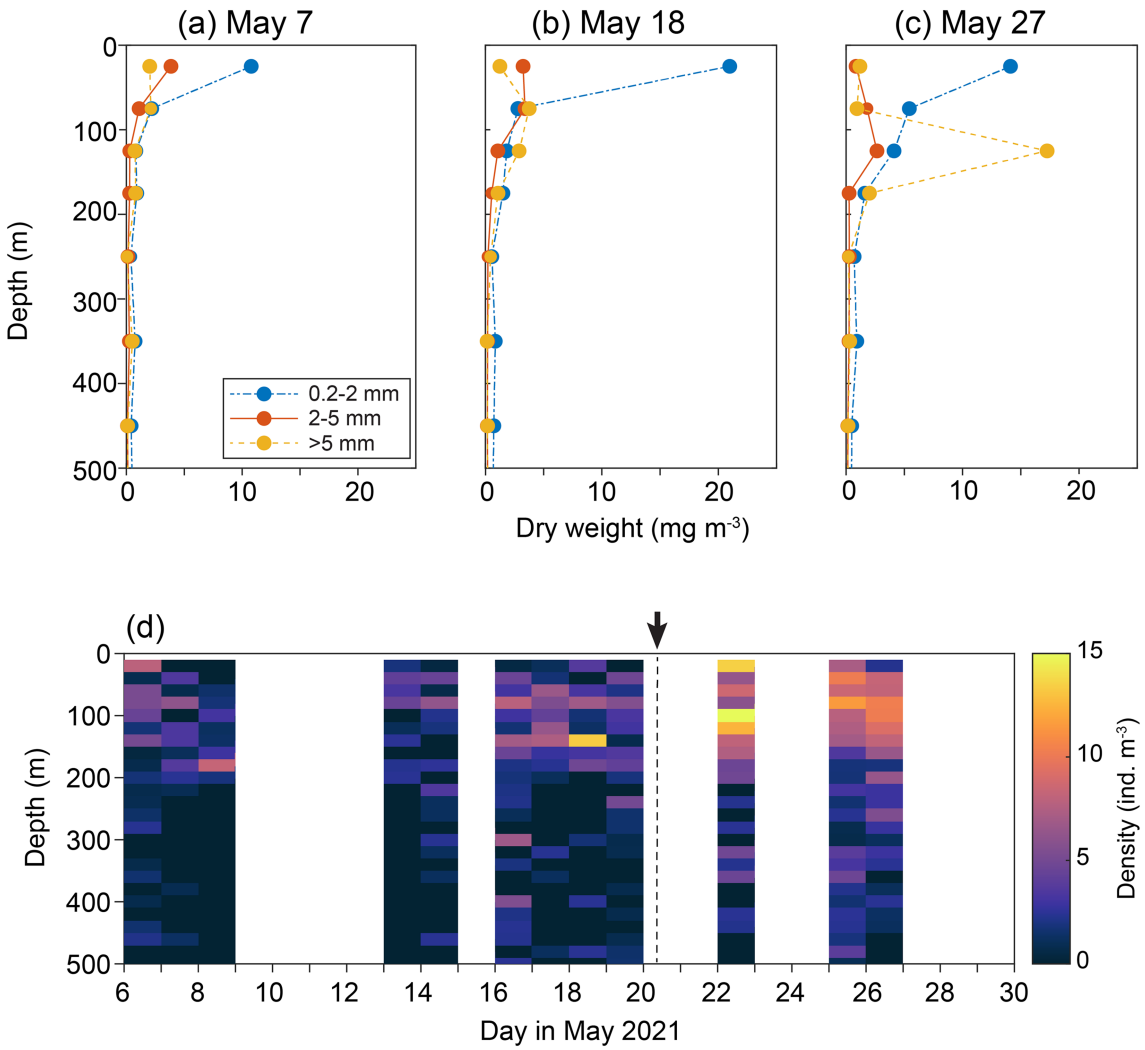

Fig. 2. Temporal variability in (**a**–**c**) dry weight of three zooplankton size classes from nighttime MOCNESS tows and (**d**) mean zooplankton density from nighttime UVP profiles. UVP data represent measurements within the eddy core (< 15 km from the center), while MOCNESS samples were collected across the eddy at 8.1–20.5 km from the center. The dotted lines with an arrow on May 20 in (**d**) mark the strongest storm event during the field campaign.

for the > 5.0 mm size class during nighttime sampling on May 27, characterized by a pronounced biomass peak at ~ 150 m depth (Fig. 2c) associated with large amphipods.

Mesopelagic fish within the eddy core exhibited parallel changes. Acoustic biomass of surface scattering layers was 2.1 times higher during nighttime than in the day, suggesting the increase of biomass due to diel vertical migrators (Fig. 3a,c). Prior to May 20, these layers formed compact aggregations (Fig. 3b), whereas afterward they broadened (Fig. 3d) and at times extended below 200 m. These structural changes were reflected in hourly patterns of the dispersion index, which remained low during May 3–19 but increased markedly during May 21–29 (Fig. 4a; $p < 0.001$ for all datasets). Nautical Area Scattering Coefficient values were comparable between periods during the first half of the night (22:00–01:00; $p < 0.05$ for only 33.3% of the data), but diverged during the latter half, being higher and more variable during May 3–19 and consistently low during May 21–29 (01:00–04:00; Fig. 4b; $p < 0.05$ for all data). Net catches from 0 to 100 m provided taxonomic context for surface scattering layers early in the campaign. These samples were dominated by a single species of myctophids, *Benthosema glaciale* (SL = 26.5 ± 6.8 mm [mean ± standard deviation]), comprising 100% of the catch on May 6.

Discussion

Using a Lagrangian framework, we tracked a single mesoscale eddy for nearly a month, yielding a rare continuous time series of mid-trophic level organisms within mesoscale eddies (e.g., Joyce et al. 1984; Davis and Wiebe 1985; Cowles et al. 1987). This sustained tracking minimized advective

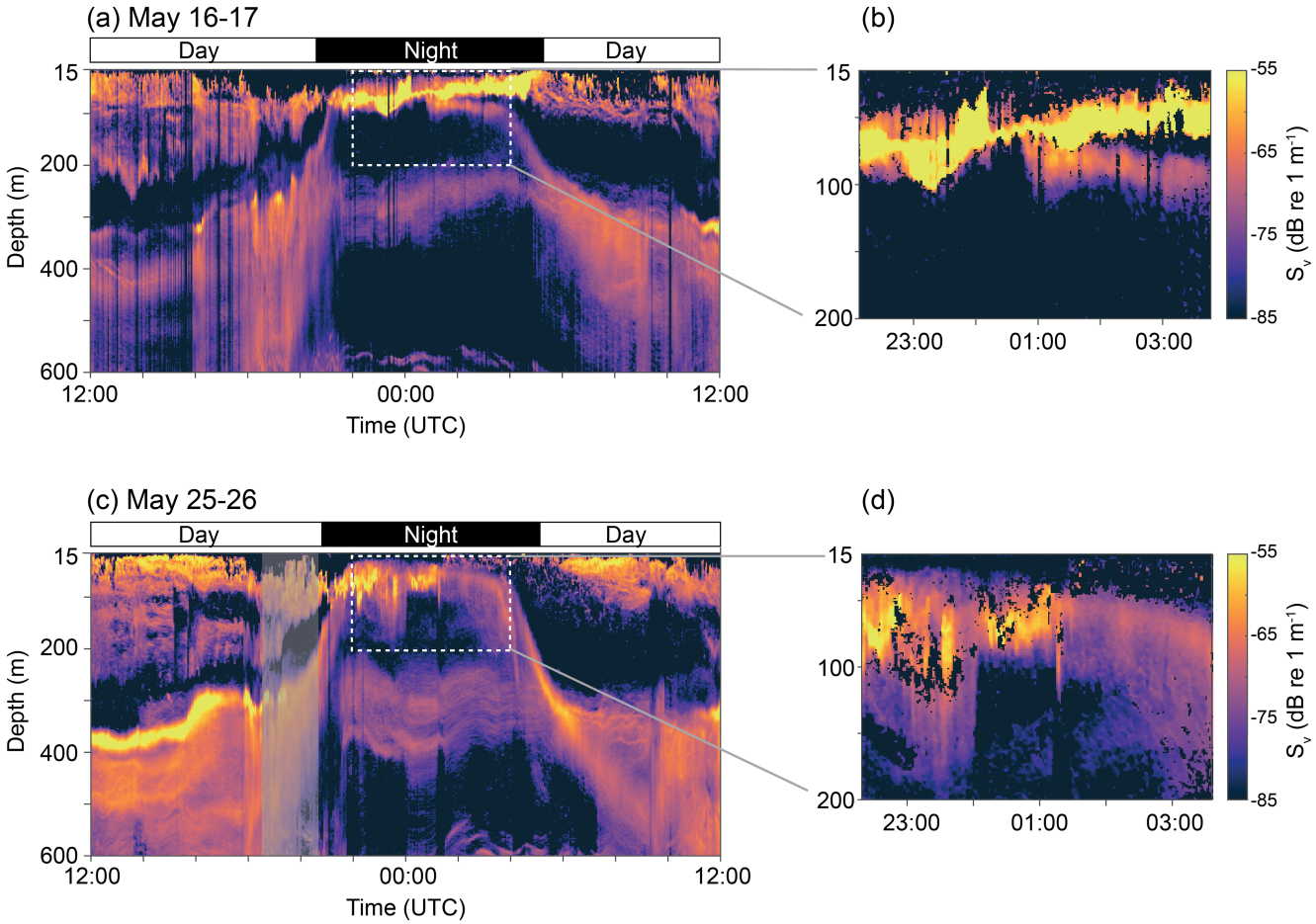

Fig. 3. Example echograms of scattering layers at 18 kHz on (**a**) 16–17 May and (**c**) 25–26 May 2021 observed within the eddy core (< 15 km from the eddy center). The gray box in (c) indicates the region outside the eddy core. Panels (**b**, **d**) show nighttime scattering layers from the upper 200 m, defined by -3.5 dB re 1 m^{-1} < $S_{v,18-70kHz} \leq 5.3$ dB re 1 m^{-1}, highlighting changes in scattering layer structure.

effects that typically obscure open-ocean behavioral patterns. Mesopelagic fish distributions shifted rapidly with changes in chlorophyll *a* and zooplankton distributions, transitioning from tight aggregations to more diffuse vertical structures, likely mediated by prey availability. In contrast to snapshot-based studies that classify eddy productivity at mid-trophic levels solely by polarity (Godø et al. 2012; Della Penna and Gaube 2020; Receveur et al. 2024), our results demonstrate that temporal variability is a critical dimension for understanding the ecological roles of mesoscale eddies.

The field campaign coincided with the decline phase of the North Atlantic spring bloom, one of the most productive phytoplankton blooms in the global open ocean (Siegel et al. 2002). After May 20, chlorophyll *a* concentrations decreased while their vertical extent increased (Fig. 1), consistent with a community shift from diatoms to haptophytes and dinoflagellates (Meyer et al. 2024) and relatively stable nitrate and silicate concentrations (Siegel et al. 2025). During this period, zooplankton distributions deepened across size classes and sampling methods, likely reflecting changes in phytoplankton availability and vertical structure. Although four storm events exchanged surface waters via Ekman transport (Johnson et al. 2024), their effects on vertically migrating taxa—typically residing below the mixed layer during the day and during periods of enhanced surface turbulence—were likely minimal (Mackas et al. 1993; Incze et al. 2001; Tsurumi et al. 2005). Net tows extended beyond the eddy core, where zooplankton species composition can differ between core and edge communities (Wiebe et al. 1992); however, the consistent dominance of diel vertical migrators across samples suggests a coherent behavioral response to food availability rather than sampling artifacts. In addition to these structural changes, temporal increases in zooplankton biomass within the upper 200 m likely resulted from enhanced accessibility to phytoplankton dispersed deeper into the water column following the storm event. This mechanism provides a plausible explanation for the post-storm biomass increase observed in the UVP data, which more clearly resolves temporal variability within the eddy core than MOCNESS samples that integrate broader spatial scales. Increased prey availability across a wider

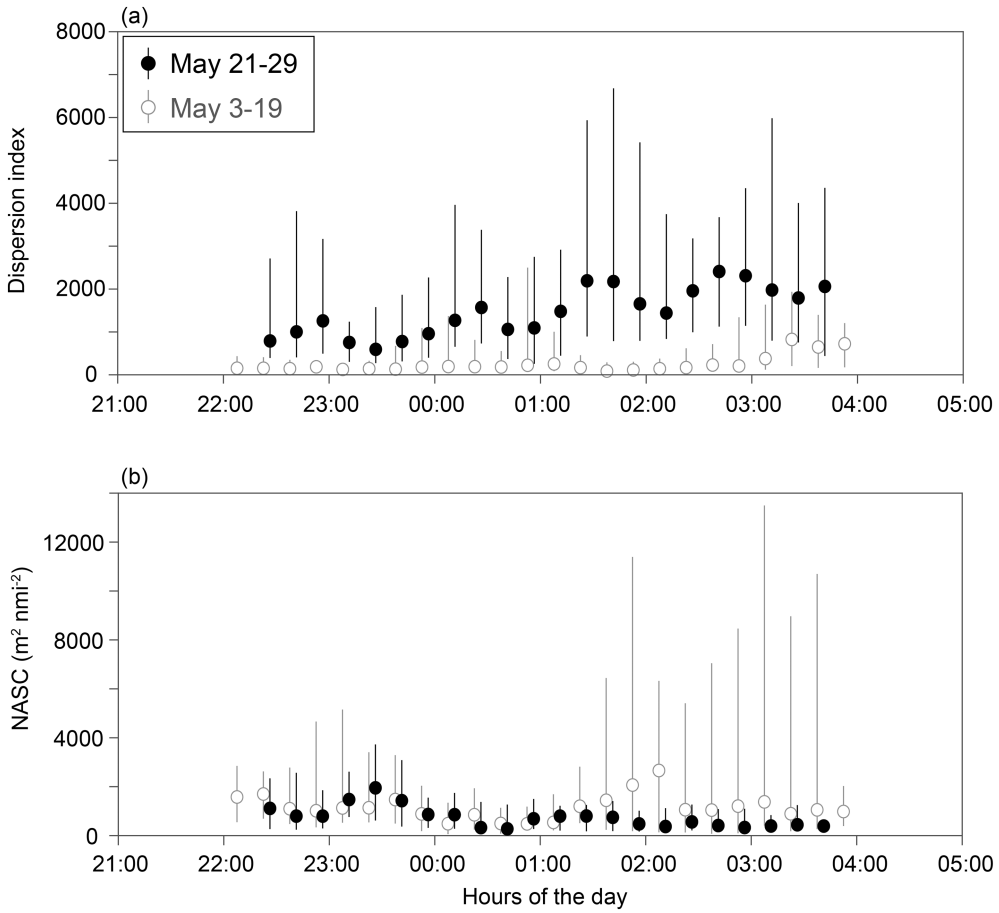

Fig. 4. (**a**) Dispersion index and (**b**) Nautical Area Scattering Coefficient (NASC) values of scattering layers at night within the eddy core. Circles indicate medians and error bars represent one interquartile range. The two data sets are offset for clarity in visualization.

depth range may, in turn, have promoted more diffuse distributions of mesopelagic fishes. Consistent with this interpretation, acoustic scattering layers became more vertically diffuse later in the campaign (May 21–29) relative to earlier (May 3–19) (Fig. 3b,d). Given that myctophids forage on zooplankton near the surface at night (Merrett and Roe 1974; Hudson et al. 2014), these changes in prey distribution likely mediated the observed shifts in fish aggregation.

We hypothesize that temporal variability in phytoplankton patchiness structured zooplankton distributions and abundance, which in turn broadened mesopelagic fish aggregations within the eddy. While bottom-up control is a well-established mechanism shaping marine food webs (Heath et al. 2014; Lynam et al. 2017), our results extend previous work focused on eddy polarity (Godø et al. 2012; Della Penna and Gaube 2020; Receveur et al. 2024) by demonstrating that even among eddies of the same polarity, fine-scale spatial heterogeneity can vary markedly over time, driven by additional physical and biological processes (e.g., Cowles et al. 1987). Patchiness—rather than total biomass—is increasingly recognized as a key driver of predator–prey interactions in pelagic ecosystems, as heterogeneous prey fields can sustain predators across trophic levels (Benoit-Bird and McManus 2012; Benoit-Bird et al. 2013; Benoit-Bird 2024). Accordingly, the temporal shifts we observed toward more diffuse prey fields near the sea surface may have cascaded upward, influencing the nighttime foraging success of top predators such as tuna, blue shark, and swordfish, which overlap with surface scattering layers at night (Josse et al. 1998; Dagorn et al. 2000; Braun et al. 2023). Foraging may therefore have been more favorable earlier in the campaign (May 3–19), when mesopelagic fishes were tightly aggregated, even though total biomass remained similar throughout. These findings suggest that the role of eddies as foraging grounds for higher trophic levels is dynamic, varying on weekly to monthly timescales in response to shifts in lower-trophic spatial structure.

Our findings demonstrate that bottom-up effects within mesoscale eddies can shape mesopelagic fish aggregation patterns over short timescales. This perspective helps explain the mixed evidence for prey enhancement across eddy types: some studies report elevated mesopelagic biomass in anticyclones (Godø et al. 2012; Fennell and Rose 2015; Della Penna

and Gaube 2020; Devine et al. 2021; Wang et al. 2023), others in cyclones (Drazen et al. 2011; Annasawmy et al. 2020), and still others weak or polarity-independent responses (Potier et al. 2014; Receveur et al. 2024). Rather than focusing on polarity or biomass alone, a shift toward understanding how trophic interactions and aggregation dynamics shape ecosystem function is essential for assessing the biological significance of eddies (see also Sato et al. 2026). Ultimately, mesoscale eddies should be viewed not as static features defined by polarity, but as dynamic ecosystems whose roles within pelagic food webs evolve through time.

Author Contributions

Mei Sato and Zachary K. Erickson developed the study concept. All authors contributed to data collection and analysis. Mei Sato led the manuscript writing with input from all coauthors.

Acknowledgments

We thank the crews of the RRS *James Cook*, RRS *Discovery*, and R/V *Sarmiento de Gamboa*, as well as all participants in the EXPORTS project in the Northeast Atlantic, for their efforts in collecting interdisciplinary field data. We are grateful to D. Siegel for leadership and coordination of this multidisciplinary project, and to J. Llopiz for leading fish and zooplankton collections aboard the *Sarmiento de Gamboa* and overseeing subsequent sample processing. We thank A. Moore for coordinating multifrequency echosounder data collection from the *James Cook* and *Discovery*. M. Ferguson assisted with acoustic data preprocessing, and J. Cope and H. Gossner assisted with MOCNESS zooplankton analyses. We also thank L. Stemmann and R. Kiko for valuable input on UVP data treatment, S.-M. Schröder for assistance with the Morphocluster software, and L. Karp-Boss for UVP data collection. We further thank R. Kiko, two anonymous reviewers, and the associate editor for constructive feedback on the manuscript. The EXPORTS project was supported by the NASA Ocean Biology and Biogeochemistry program with contributions from the National Science Foundation. This work was also supported by the Woods Hole Oceanographic Institution's Ocean Twilight Zone Project, funded as part of The Audacious Project at TED. Mei Sato received funding from the Innovation Month Program at the Woods Hole Oceanographic Institution. This is NOAA Pacific Marine Environmental Laboratory (PMEL) contribution 5818. Funding for Amy E. Maas and Deborah K. Steinberg was provided by NASA grants 80NSSC17K0654 and 80NSSC24K0514. Laetitia Drago was supported by the European Union project TRIATLAS (Horizon 2020; grant 817578), Sorbonne Université through the École Doctorale 129, and Horizon Europe RIA project NECCTON (grant 101081273). Helena McMonagle was supported by the National Science Foundation's Graduate Research Fellowship Program. Generative artificial intelligence (AI) tools were used to correct grammatical errors and improve the clarity of the text.

Conflicts of Interest

None declared.

Data Availability Statement

The data supporting the findings of this study are publicly available on Zenodo at https://doi.org/10.5281/zenodo.18064035.

References

Annasawmy, P., J.-F. Ternon, A. Lebourges-Dhaussy, et al. 2020. "Micronekton Distribution as Influenced by Mesoscale Eddies, Madagascar Shelf and Shallow Seamounts in the South-Western Indian Ocean: An Acoustic Approach." *Deep Sea Research Part II: Topical Studies in Oceanography* 176: 104812. https://doi.org/10.1016/j.dsr2.2020.104812.

Arostegui, M. C., P. Gaube, P. A. Woodworth-Jefcoats, D. R. Kobayashi, and C. D. Braun. 2022. "Anticyclonic Eddies Aggregate Pelagic Predators in a Subtropical Gyre." *Nature* 609: 535–540. https://doi.org/10.1038/s41586-022-05162-6.

Bakun, A. 1996. *Patterns in the Ocean: Ocean Processes and Marine Population Dynamics*. La Paz, Mexico: California Sea Grant, in cooperation with Centro de Investigaciones Biologicas del Noroeste.

Benoit-Bird, K. J. 2024. "Resource Patchiness as a Resolution to the Food Paradox in the Sea." *The American Naturalist* 203: 1–13. https://doi.org/10.1086/727473.

Benoit-Bird, K. J., B. C. Battaile, S. A. Heppell, et al. 2013. "Prey Patch Patterns Predict Habitat Use by Top Marine Predators with Diverse Foraging Strategies." *PLoS One* 8: e53348. https://doi.org/10.1371/journal.pone.0053348.

Benoit-Bird, K. J., and M. A. McManus. 2012. "Bottom-Up Regulation of a Pelagic Community Through Spatial Aggregations." *Biology Letters* 8: 813–816. https://doi.org/10.1098/rsbl.2012.0232.

Benoit-Bird, K. J., C. M. Waluk, and J. P. Ryan. 2019. "Forage Species Swarm in Response to Coastal Upwelling." *Geophysical Research Letters* 46: 1537–1546. https://doi.org/10.1029/2018GL081603.

Braun, C. D., P. Gaube, T. H. Sinclair-Taylor, G. B. Skomal, and S. R. Thorrold. 2019. "Mesoscale Eddies Release Pelagic Sharks From Thermal Constraints to Foraging in the Ocean Twilight Zone." *Proceedings of the National Academy of Sciences* 116: 17187–17192. https://doi.org/10.1073/pnas.1903067116.

Braun, C. D., A. D. Penna, M. C. Arostegui, et al. 2023. "Linking Vertical Movements of Large Pelagic Predators with Distribution Patterns of Biomass in the Open Ocean."

Proceedings of the National Academy of Sciences 120, no. 47: e2306357120. https://doi.org/10.1073/pnas.2306357120.

Bucklin, A., P. G. Batta-Lona, J. M. Questel, et al. 2024. "Metabarcoding and Morphological Analysis of Diets of Mesopelagic Fishes in the NW Atlantic Slope Water." *Frontiers in Marine Science* 11: 1411996. https://doi.org/10.3389/fmars.2024.1411996.

Chelton, D. B., M. G. Schlax, and R. M. Samelson. 2011. "Global Observations of Nonlinear Mesoscale Eddies." *Progress in Oceanography* 91: 167–216. https://doi.org/10.1016/j.pocean.2011.01.002.

Chelton, D. B., M. G. Schlax, R. M. Samelson, and R. A. de Szoeke. 2007. "Global Observations of Large Oceanic Eddies." *Geophysical Research Letters* 34: L15606. https://doi.org/10.1029/2007GL030812.

Cowles, T. J., M. R. Roman, A. L. Gauzens, and N. J. Copley. 1987. "Short-Term Changes in the Biology of a Warm-Core Ring: Zooplankton Biomass and Grazing." *Limnology and Oceanography* 32: 653–664. https://doi.org/10.4319/lo.1987.32.3.0653.

Craddock, J. E., R. H. Backus, and M. A. Daher. 1992. "Vertical Distribution and Species Composition of Midwater Fishes in Warm-Core Gulf Stream Meander/Ring 82-H." *Deep-Sea Research Part A, Oceanographic Research Papers* 39: S203–S218. https://doi.org/10.1016/s0198-0149(11)80012-9.

Dagorn, L., P. Bach, and E. Josse. 2000. "Movement Patterns of Large Bigeye Tuna (Thunnus Obesus) in the Open Ocean, Determined Using Ultrasonic Telemetry." *Marine Biology* 136, no. 2: 361–371.

Davis, C. S., and P. H. Wiebe. 1985. "Macrozooplankton Biomass in a Warm-Core Gulf Stream Ring: Time Series Changes in Size Structure, Taxonomic Composition, and Vertical Distribution." *Journal of Geophysical Research: Oceans* 90: 8871–8884. https://doi.org/10.1029/JC090iC05p08871.

Davison, P. C. 2011. "*The Export of Carbon Mediated by Mesopelagic Fishes in the Northeast Pacific Ocean*." PhD thesis, University of California, San Diego.

Della Penna, A., and P. Gaube. 2020. "Mesoscale Eddies Structure Mesopelagic Communities." *Frontiers in Marine Science* 7: 454. https://doi.org/10.3389/fmars.2020.00454.

Demer, D. A., L. Berger, M. Bernasconi, et al. 2015. "Calibration of Acoustic Instruments." *ICES Cooperative Research Report* 326: 1–133. https://doi.org/10.17895/ices.pub.5494.

Devine, B., S. Fennell, D. Themelis, and J. A. Fisher. 2021. "Influence of Anticyclonic, Warm-Core Eddies on Mesopelagic Fish Assemblages in the Northwest Atlantic Ocean." *Deep-Sea Research Part I, Oceanographic Research Papers* 173: 103555. https://doi.org/10.1016/j.dsr.2021.103555.

Drago, L. 2023. "Analyse globale de la pompe à carbone biologique à partir de données en imagerie quantitative." PhD thesis, Sorbonne Université https://theses.hal.science/tel-04483392.

Drazen, J. C., G. Lisa, and R. Domokos. 2011. "Micronekton Abundance and Biomass in Hawaiian Waters as Influenced by Seamounts, Eddies, and the Moon." *Deep Sea Research, Part I* 58: 557–566. https://doi.org/10.1016/j.dsr.2011.03.002.

Drazen, J. C., and T. T. Sutton. 2017. "Dining in the Deep: The Feeding Ecology of Deep-Sea Fishes." *Annual Review of Marine Science* 9: 337–366. https://doi.org/10.1146/annurev-marine-010816-060543.

Early, J. J., R. M. Samelson, and D. B. Chelton. 2011. "The Evolution and Propagation of Quasigeostrophic Ocean Eddies." *Journal of Physical Oceanography* 41: 1535–1555. https://doi.org/10.1175/2011JPO4601.1.

Eduardo, L. N., A. Bertrand, M. M. Mincarone, et al. 2020. "Hatchetfishes (Stomiiformes: Sternoptychidae) Biodiversity, Trophic Ecology, Vertical Niche Partitioning and Functional Roles in the Western Tropical Atlantic." *Progress in Oceanography* 187: 102389. https://doi.org/10.1016/j.pocean.2020.102389.

Erickson, Z. K., et al. 2022. "*EXPORTS North Atlantic Eddy Tracking*." NASA/TM-20220009705.

Erickson, Z. K., E. Fields, L. Johnson, et al. 2023. "Eddy Tracking From In Situ and Satellite Observations." *Journal of Geophysical Research: Oceans* 128: e2023JC019701. https://doi.org/10.1029/2023JC019701.

Fennell, S., and G. Rose. 2015. "Oceanographic Influences on Deep Scattering Layers across the North Atlantic." *Deep Sea Research, Part I: Oceanographic Research Papers* 105: 132–141. https://doi.org/10.1016/j.dsr.2015.09.002.

Gaube, P., D. B. Chelton, R. M. Samelson, M. G. Schlax, and L. W. O'Neill. 2015. "Satellite Observations of Mesoscale Eddy-Induced Ekman Pumping." *Journal of Physical Oceanography* 45, no. 1: 104–132. https://doi.org/10.1175/JPO-D-14-0032.1.

Gaube, P., D. B. Chelton, P. G. Strutton, and M. J. Behrenfeld. 2013. "Satellite Observations of Chlorophyll, Phytoplankton Biomass, and Ekman Pumping in Nonlinear Mesoscale Eddies." *JGR Oceans* 118: 6349–6370. https://doi.org/10.1002/2013JC009027.

Godø, O. R., A. Samuelsen, G. J. Macaulay, et al. 2012. "Mesoscale Eddies Are Oases for Higher Trophic Marine Life." *PLoS One* 7: e30161. https://doi.org/10.1371/journal.pone.0030161.

Goldthwait, S. A., and D. K. Steinberg. 2008. "Elevated Biomass of Mesozooplankton and Enhanced Fecal Pellet Flux in Cyclonic and Mode-Water Eddies in the Sargasso Sea." *Deep Sea Research Part II: Topical Studies in Oceanography* 55: 1360–1377. https://doi.org/10.1016/j.dsr2.2008.01.003.

Gorsky, G., M. D. Ohman, M. Picheral, et al. 2010. "Digital Zooplankton Image Analysis Using the ZooScan Integrated System." *Journal of Plankton Research* 32, no. 3: 285–303. https://doi.org/10.1093/plankt/fbp124.

Haury, L. R., J. A. McGowan, and P. H. Wiebe. 1978. "Patterns and Processes in the Time-Space Scales of Plankton

Distributions." In *Spatial Pattern in Plankton Communities*, edited by J. H. Steele, 277–327. Springer US.

Heath, M. R., D. C. Speirs, and J. H. Steele. 2014. "Understanding Patterns and Processes in Models of Trophic Cascades K. Lafferty [Ed.]." *Ecology Letters* 17: 101–114. https://doi.org/10.1111/ele.12200.

Hernández-León, S., M. P. Olivar, M. L. de Fernánz Puelles, et al. 2019. "Zooplankton and Micronekton Active Flux Across the Tropical and Subtropical Atlantic Ocean." *Frontiers in Marine Science* 6: 535. https://doi.org/10.3389/fmars.2019.00535.

Hopkins, T. L., T. T. Sutton, and T. M. Lancraft. 1996. "The Trophic Structure and Predation Impact of a Low Latitude Midwater Fish Assemblage." *Progress in Oceanography* 38: 205–239. https://doi.org/10.1016/S0079-6611(97)00003-7.

Hudson, J. M., D. K. Steinberg, T. T. Sutton, J. E. Graves, and R. J. Latour. 2014. "Myctophid Feeding Ecology and Carbon Transport Along the Northern Mid-Atlantic Ridge." *Deep Sea Research, Part I: Oceanographic Research Papers* 93: 104–116. https://doi.org/10.1016/j.dsr.2014.07.002.

Incze, L. S., D. Hebert, N. Wolff, N. Oakey, and D. Dye. 2001. "Changes in Copepod Distributions Associated With Increased Turbulence From Wind Stress." *Marine Ecology Progress Series* 213: 229–240. https://doi.org/10.3354/meps213229.

Johnson, L., D. A. Siegel, A. F. Thompson, et al. 2024. "Assessment of Oceanographic Conditions During the North Atlantic EXport Processes in the Ocean from RemoTe Sensing (EXPORTS) Field Campaign." *Progress in Oceanography* 220: 103170. https://doi.org/10.1016/j.pocean.2023.103170.

Josse, E., P. Bach, and L. Dagorn. 1998. "Simultaneous Observations of Tuna Movements and their Prey by Sonic Tracking and Acoustic Surveys." *Hydrobiologia* 371: 61–69. https://doi.org/10.1023/A:1017065709190.

Joyce, T., R. Backus, K. Baker, et al. 1984. "Rapid Evolution of a Gulf Stream Warm-Core Ring." *Nature* 308: 837–840. https://doi.org/10.1038/308837a0.

Kaartvedt, S., T. A. Klevjer, and D. L. Aksnes. 2012*a*. "Internal Wave-Mediated Shading Causes Frequent Vertical Migrations in Fishes." *Marine Ecology Progress Series* 452: 1–10. https://doi.org/10.3354/meps09688.

Kaartvedt, S., A. Staby, and D. L. Aksnes. 2012*b*. "Efficient Trawl Avoidance by Mesopelagic Fishes Causes Large Underestimation of Their Biomass." *Marine Ecology Progress Series* 456: 1–6. https://doi.org/10.3354/meps09785.

Kang, M., M. Furusawa, and K. Miyashita. 2002. "Effective and Accurate Use of Difference in Mean Volume Backscattering Strength to Identify Fish and Plankton." *ICES Journal of Marine Science* 59: 794–804. https://doi.org/10.1006/jmsc.2002.1229.

Lynam, C. P., M. Llope, C. Möllmann, P. Helaouët, G. A. Bayliss-Brown, and N. C. Stenseth. 2017. "Interaction Between Top-Down and Bottom-Up Control in Marine Food Webs." *Proceedings. National Academy of Sciences. United States of America* 114: 1952–1957. https://doi.org/10.1073/pnas.1621037114.

Maas, A. E., H. Gossner, M. J. Smith, and L. Blanco-Bercial. 2021. "Use of Optical Imaging Datasets to Assess Biogeochemical Contributions of the Mesozooplankton." *Journal of Plankton Research* 43, no. 3: 475–491. https://doi.org/10.1093/plankt/fbab037.

Mackas, D. L., and M. D. Galbraith. 2002. "Zooplankton Distribution and Dynamics in a North Pacific Eddy of Coastal Origin: I. Transport and Loss of Continental Margin Species." *Journal of Oceanography* 58: 725–738. https://doi.org/10.1023/A:1022802625242.

Mackas, D. L., H. Sefton, C. B. Miller, and A. Raich. 1993. "Vertical Habitat Partitioning by Large Calanoid Copepods in the Oceanic Subarctic Pacific During Spring." *Progress in Oceanography* 32: 259–294. https://doi.org/10.1016/0079-6611(93)90017-8.

MacLennan, D. N., P. G. Fernandes, and J. Dalen. 2002. "A Consistent Approach to Definitions and Symbols in Fisheries Acoustics." *ICES Journal of Marine Science* 59: 365–369. https://doi.org/10.1006/jmsc.2001.1158.

Mahadevan, A., E. D'Asaro, C. Lee, and M. J. Perry. 2012. "Eddy-Driven Stratification Initiates North Atlantic Spring Phytoplankton Blooms." *Science* 337: 54–58. https://doi.org/10.1126/science.1218740.

Maúre, E. R., J. Ishizaka, C. Sukigara, et al. 2017. "Mesoscale Eddies Control the Timing of Spring Phytoplankton Blooms: A Case Study in the Japan Sea." *Geophysical Research Letters* 44: 11115–11124. https://doi.org/10.1002/2017GL074359.

McGillicuddy, D. J. 2016. "Mechanisms of Physical–Biological–Biogeochemical Interaction at the Oceanic Mesoscale." *Annual Review of Marine Science* 8: 125–159. https://doi.org/10.1146/annurev-marine-010814-015606.

McGillicuddy, D. J., L. A. Anderson, N. R. Bates, et al. 2007. "Eddy/Wind Interactions Stimulate Extraordinary Mid-Ocean Plankton Blooms." *Science* 316: 1021–1026. https://doi.org/10.1126/science.1136256.

McGillicuddy, D. J., and A. R. Robinson. 1997. "Eddy-Induced Nutrient Supply and New Production in the Sargasso Sea." *Deep Sea Research. Part I, Oceanographic Research Papers* 44: 1427–1450. https://doi.org/10.1016/S0967-0637(97)00024-1.

McMonagle, H., J. K. Llopiz, A. E. Maas, D. K. Steinberg, A. F. Govindarajan, and T. E. Essington. 2024. "Quantifying Uncertainty in the Contribution of Mesopelagic Fishes to the Biological Carbon Pump in the Northeast Atlantic Ocean." *ICES Journal of Marine Science* 81: 2037–2051. https://doi.org/10.1093/icesjms/fsae149.

Merrett, N. R., and H. S. J. Roe. 1974. "Patterns and Selectivity in the Feeding of Certain Mesopelagic Fishes." *Marine Biology* 28: 115–126. https://doi.org/10.1007/BF00396302.

Meyer, M. G., M. A. Brzezinski, M. R. Cohn, et al. 2024. "Size-Fractionated Primary Production Dynamics During the Decline Phase of the North Atlantic Spring Bloom." *Global Biogeochemical Cycles* 38: e2023GB008019. https://doi.org/10.1029/2023GB008019.

Picheral, M., S. Colin, and J.-O. Irisson. 2017. *EcoTaxa, A Tool for the Taxonomic Classification of Images*. https://ecotaxa.obs-vlfr.fr/.

Picheral, M., L. Guidi, L. Stemmann, D. M. Karl, G. Iddaoud, and G. Gorsky. 2010. "The Underwater Vision Profiler 5: An Advanced Instrument for High Spatial Resolution Studies of Particle Size Spectra and Zooplankton." *Limnology and Oceanography: Methods* 8: 462–473. https://doi.org/10.4319/lom.2010.8.462.

Potier, M., P. Bach, F. Ménard, and F. Marsac. 2014. "Influence of Mesoscale Features on Micronekton and Large Pelagic Fish Communities in the Mozambique Channel." *Deep Sea Research. Part II, Topical Studies in Oceanography* 100: 184–199. https://doi.org/10.1016/j.dsr2.2013.10.026.

Receveur, A., C. Menkes, M. Lengaigne, et al. 2024. "A Rare Oasis Effect for Forage Fauna in Oceanic Eddies at the Global Scale." *Nature Communications* 15: 4834. https://doi.org/10.1038/s41467-024-49113-3.

Sato, M., and K. J. Benoit-Bird. 2024. "Diel Vertical Migrators Respond to Short-Term Upwelling Events." *Geophysical Research Letters* 51: e2023GL105387. https://doi.org/10.1029/2023GL105387.

Sato, M., Z. Erickson, L. Drago, A. E. Maas, H. McMonagle, and D. K. Steinberg. 2025. Temporal Dynamics of Mesopelagic Fishes Within a Mesoscale Eddy: A Lagrangian Perspective—Source data (Version 1) [Data set]. *Zenodo*. https://doi.org/10.5281/zenodo.18064035.

Sato, M., Z. K. Erickson, H. McMonagle, and J. K. Llopiz. 2026. "Mesoscale Eddy Structure Drives Spatial Variability in Mesopelagic Fishes." *Limnology and Oceanography*: e70346. https://doi.org/10.1002/lno.70346.

Sato, M., J. K. Horne, S. L. Parker-Stetter, and J. E. Keister. 2015. "Acoustic Classification of Coexisting Taxa in a Coastal Ecosystem." *Fisheries Research* 172: 130–136. https://doi.org/10.1016/j.fishres.2015.06.019.

Schröder, S.-M., R. Kiko, and R. Koch. 2020. "MorphoCluster: Efficient Annotation of Plankton Images by Clustering." *Sensors* 20: 3060. https://doi.org/10.3390/s20113060.

Seki, M. P., R. Lumpkin, and P. Flament. 2002. "Hawaii Cyclonic Eddies and Blue Marlin Catches: The Case Study of the 1995 Hawaiian International Billfish Tournament." *Journal of Oceanography* 58: 739–745. https://doi.org/10.1023/A:1022854609312.

Siegel, D., A. B. Burd, M. L. Estapa, et al. 2025. "Assessing Marine Snow Dynamics During the Demise of the North Atlantic Spring Bloom Using In Situ Particle Imagery." *Global Biogeochemical Cycles* 39: e2025GB008676. https://doi.org/10.1029/2025GB008676.

Siegel, D. A., I. Cetinić, A. F. Thompson, et al. 2023. "EXport Processes in the Ocean From RemoTe Sensing (EXPORTS) North Atlantic Sensor Calibration and Intercalibration Documents." October 11. https://doi.org/10.1575/1912/66998.

Siegel, D. A., S. C. Doney, and J. A. Yoder. 2002. "The North Atlantic Spring Phytoplankton Bloom and Sverdrup's Critical Depth Hypothesis." *Science* 296: 730–733. https://doi.org/10.1126/science.1069174.

Simmonds, J., and D. N. MacLennan. 2005. *Fisheries Acoustics: Theory and Practice*. 2nd ed. Blackwell Scientific.

Tsurumi, M., D. L. Mackas, F. A. Whitney, C. DiBacco, M. D. Galbraith, and C. S. Wong. 2005. "Pteropods, Eddies, Carbon Flux, and Climate Variability in the Alaska Gyre." *Deep Sea Research Part II: Topical Studies in Oceanography* 52: 1037–1053. https://doi.org/10.1016/j.dsr2.2005.02.005.

Vandromme, P., L. Stemmann, C. Garcìa-Comas, L. Berline, X. Sun, and G. Gorsky. 2012. "Assessing Biases in Computing Size Spectra of Automatically Classified Zooplankton from Imaging Systems: A Case Study with the ZooScan Integrated System." *Methods in Oceanography* 1: 3–21. https://doi.org/10.1016/j.mio.2012.06.001.

Wang, Y., J. Zhang, J. Yu, Q. Wu, and D. Sun. 2023. "Anticyclonic Mesoscale Eddy Induced Mesopelagic Biomass Hotspot in the Oligotrophic Ocean." *Journal of Marine Systems* 237: 103831. https://doi.org/10.1016/j.jmarsys.2022.103831.

Weimerskirch, H., M. Le Corre, S. Jaquemet, M. Potier, and F. Marsac. 2004. "Foraging Strategy of a Top Predator in Tropical Waters: Great Frigatebirds in the Mozambique Channel." *Marine Ecology Progress Series* 275: 297–308. https://doi.org/10.3354/meps275297.

Wiebe, P. H., S. H. Boyd, B. M. Davis, and J. L. Cox. 1982. "Avoidance of Towed Nets by the Euphausiid *Nematoscelis megalops*." *Fishery Bulletin* 80: 75–91.

Wiebe, P. H., N. J. Copley, and S. H. Boyd. 1992. "Coarse-Scale Horizontal Patchiness and Vertical Migration of Zooplankton in Gulf Stream Warm-Core Ring 82-H." *Deep-Sea Research Part A, Oceanographic Research Papers* 39: S247–S278. https://doi.org/10.1016/s0198-0149(11)80015-4.

Wiebe, P. H., A. W. Morton, A. M. Bradley, et al. 1985. "New Development in the MOCNESS, an Apparatus for Sampling Zooplankton and Micronekton." *Marine Biology* 87: 313–323.

Woillez, M., J.-C. Poulard, J. Rivoirard, P. Petitgas, and N. Bez. 2007. "Indices for Capturing Spatial Patterns and Their Evolution in Time, With Application to European Hake (Merluccius Merluccius) in the Bay of Biscay." *ICES Journal of Marine Science* 64, no. 3: 537–550. https://doi.org/10.1093/icesjms/fsm025.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Submitted 14 November 2025
Revised 10 January 2026
Accepted 23 February 2026