

Review

Biodiversity in Motion: How Marine Diversity Shapes the Ocean's Active Carbon Pump

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Abstract

The biological carbon pump plays a central role in regulating atmospheric CO₂ by transporting carbon from the surface ocean to depth. Although diel vertical migration and the Active Migrant Pump (AMP) are increasingly recognized as important components of carbon sequestration, previous reviews have focused primarily on carbon fluxes and individual migrant groups, with less attention to how taxonomic and functional biodiversity, community composition, biomass, and environmental forcing interact to shape active carbon transport. Here, we synthesize current knowledge on the biodiversity underlying the AMP and evaluate how organismal identity, functional traits, behavior, life history, and biomass influence the magnitude, pathways, and efficiency of active carbon export. We further examine major mechanisms of active carbon transport and their links to biodiversity across ocean basins, and assess how climate-driven changes in species composition, migratory behavior, and ecosystem structure may alter the AMP. The review identifies three major knowledge gaps: substantial uncertainty in the biomass of migrating organisms, insufficient taxonomic resolution of key migrant groups, and limited incorporation of biodiversity and functional traits into carbon-flux models. Active carbon transport is determined by interactions between biodiversity, biomass, organismal traits, migration behavior, and environmental factors. Explicit integration of these dimensions into biogeochemical models is therefore essential for improving estimates of the AMP and predicting its response to ocean change.

Keywords: active migrant pump; biological carbon pump; biodiversity; taxonomic diversity; functional diversity; diel vertical migration; zooplankton; mesopelagic fishes; gelatinous zooplankton; carbon sequestration; ocean carbon cycle; climate change; biological oceanography

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1. The Vertical Pulse of the Global Carbon Cycle

Marine phytoplankton form a phylogenetically and functionally diverse group of primary producers that generate organic matter and sustain marine food webs. Global net marine primary production is estimated at ~50 Gt C yr⁻¹, comparable to that of terrestrial ecosystems [1]. Although a large fraction is rapidly remineralized in surface waters, primary production underpins the oceanic Biological Carbon Pump (BCP), which transfers carbon from the euphotic zone to the deep ocean and sediments, contributing to long-term sequestration and lowering atmospheric CO₂ concentrations [2].

The ocean is therefore a major biogeochemical sink for atmospheric carbon dioxide,

including anthropogenic emissions accumulated since the industrial era [3]. This function is mediated by the BCP, a coupled set of ecological, biogeochemical, and physical processes that export carbon from surface waters and store it in the ocean interior and sediments over geological timescales [4].

BCP strength depends not only on the amount of primary production but also on the composition, abundance, biomass, and functional attributes of the organisms that process and transport organic carbon. Early sediment-trap studies estimated particulate organic carbon (POC) export at $\sim 6 \text{ Gt C yr}^{-1}$ [5]. Subsequent work has shown that export is not a single-particle flux but a combination of processes, with global estimates ranging from ~ 4 to 12 Gt C yr^{-1} , and some model-based approaches reaching $\sim 9 \times 10^{15} \text{ g C yr}^{-1}$ [2]. These revisions emphasize that carbon export efficiency depends on interacting biological and physical pathways shaped by ecosystem structure.

The BCP is now commonly described as comprising three partially decoupled but co-occurring pathways: the gravitational pump (sinking particles), the mixing pump (physical transport of dissolved and suspended material), and the active migrant pump (transport by vertically migrating organisms) [6,7]. Although mechanistically distinct, all three are ultimately constrained by surface production, trophic interactions, community composition, organismal abundance and biomass, and functional traits that determine how carbon is produced, transformed, transported, and remineralized [8].

Throughout this review, I distinguish between carbon export, transport, injection, and sequestration. Carbon export refers to the removal of carbon from the surface ocean or euphotic zone. Carbon transport denotes its subsequent movement to greater depths or between ecosystem compartments. Carbon injection specifically refers to the delivery of biologically processed carbon below a defined depth horizon. None of these processes, however, necessarily equate to long-term carbon sequestration. Sequestration requires that exported carbon remain isolated from the atmosphere over sufficiently long time-scales through transfer to the deep ocean or sediments. Ultimately, it depends on where and in what form the carbon is remineralized or stored.

The gravitational pump is the most intensively studied component. It is driven by sinking particulate organic matter, including fecal pellets, aggregates, phytoplankton cells, and detritus [6]. Particle properties, such as size, density, composition, and shape, regulate sinking velocity and degradation. Large, silicified diatoms often form fast-sinking aggregates that can bypass surface remineralization, whereas smaller flagellates tend to form fragile, slow-sinking particles that are efficiently recycled in the upper ocean [3]. Bacterial community composition further modulates aggregate breakdown and remineralization rates [9]. Thus, carbon export via sinking particles is a result of interactions among phyto-, zoo-, and bacterioplankton communities rather than purely physical settling.

The mixing pump transfers dissolved organic carbon and suspended particles from surface waters into depth through physical processes such as winter convection, mixed-layer deepening, eddy subduction, and turbulent diffusion [10]. These processes operate across seasonal to submesoscale ranges, moving surface-derived organic matter into the mesopelagic, where it is processed by microbial communities [7,9]. While physically driven, this pathway depends indirectly on biological diversity through its control on the quantity and composition of organic substrates produced in surface waters.

The active migrant pump (AMP) is driven by vertically migrating organisms and their metabolism at depth [10]. Its magnitude and efficiency depend on the taxonomic composition, abundance and biomass of migrant communities, as well as on functional traits, body size, life history, feeding strategy, and migration behavior. The AMP therefore provides a particularly useful framework for examining how variation in biological communities translates into differences in active carbon transport and injection. This bi-

odiversity–biogeochemistry interface is the primary focus of this review. The dominant mechanism considered in current AMP estimates is diel vertical migration (DVM), the largest synchronized biomass movement on Earth, involving zooplankton and micronekton that ascend to surface waters at night and descend during daylight to mesopelagic and upper bathypelagic depths to avoid visual predators [11–16]. The organisms performing these migrations differ strongly in taxonomic identity, biomass, body size, life-history strategy, feeding mode, and migration depth, potentially generating markedly different carbon fluxes even when their vertical displacement is similar. Reverse migrations occur but appear limited in magnitude and are not considered a major carbon export pathway [17].

Carbon export via the AMP results from feeding in surface waters and subsequent respiration, excretion, egestion, and mortality at depth, effectively bypassing slower gravitational transport [18–20]. Estimates suggest that the AMP may sometimes contribute roughly 15–50% of total carbon export, with higher values in oligotrophic gyres and upwelling systems where it can match or exceed particle sinking fluxes [12,21,22]. These estimates, however, remain uncertain and method-dependent.

Active vertical transport includes multiple migratory modes, not only DVM (Figure 1). Ontogenetic vertical migration, where life stages occupy different depths, is widespread but underrepresented in global budgets. Fishes are particularly relevant owing to their biomass and large-scale depth movements, making them important vectors of carbon transfer [23]. Copepods contribute notably through seasonal ontogenetic descent, especially in high latitudes, where lipid-rich individuals descend and metabolize carbon at depth, forming the so-called “lipid pump” [24]. The lipid pump flux ($3.5\text{--}6.0\text{ gC m}^{-2}\text{ yr}^{-1}$) at depths between 1000 and 3000 m is comparable to the flux of detrital organic carbon at equivalent depths [24]. Because these processes are seasonal, they represent a distinct but often under-quantified component of active export.

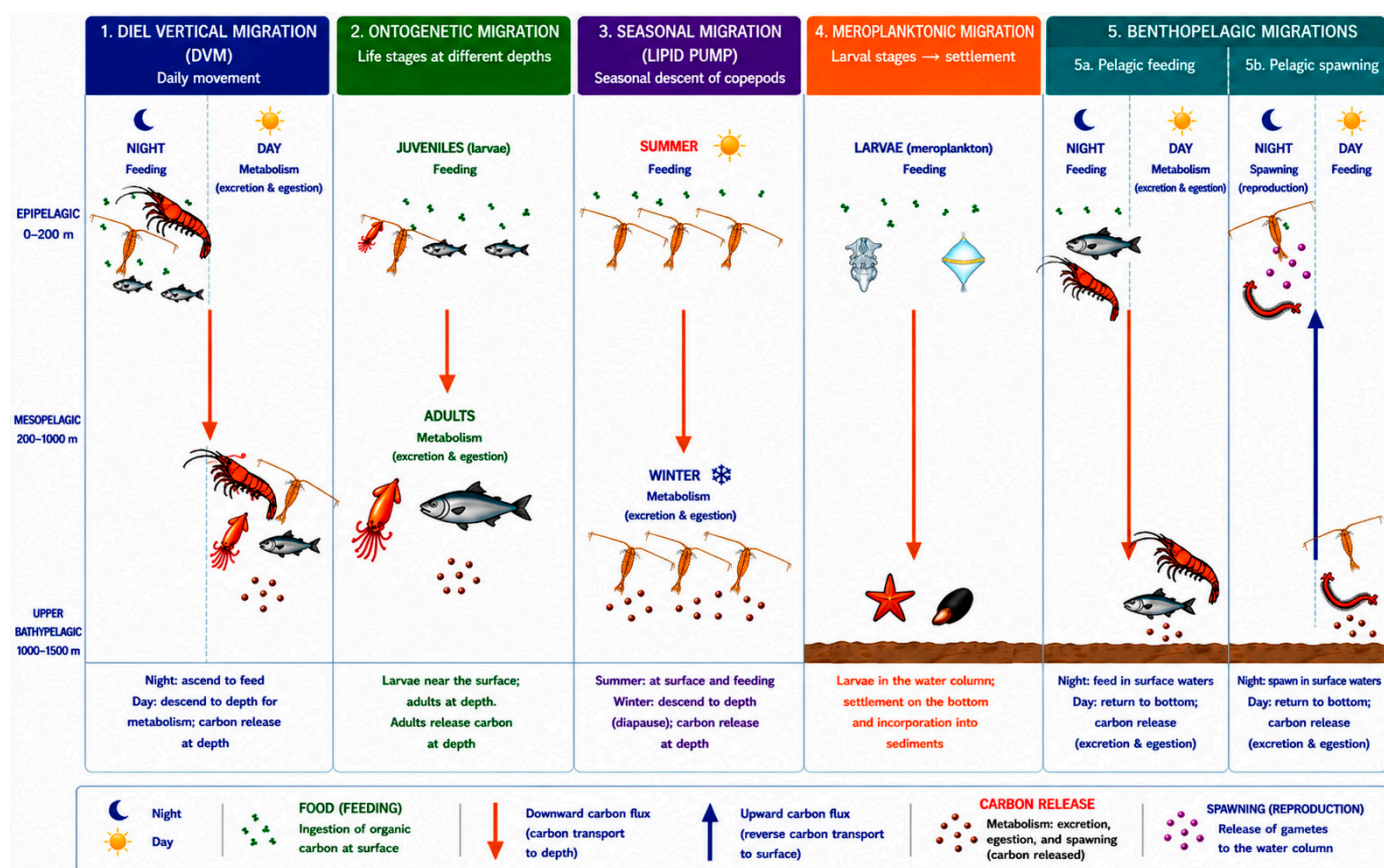


Figure 1. Basic types of vertical migrations shaping the active migrant pump (AMP).

Ontogenetic migration is also common among benthic taxa with planktonic larval stages. In coastal regions and around seamounts, meroplankton can contribute substantially to plankton biomass [25,26]. These organisms may influence carbon pathways through pelagic feeding, followed by settlement and burial, although their net contribution to basin-scale carbon export remains poorly constrained.

Benthopelagic organisms, which span benthic and pelagic habitats [27], may also contribute to vertical carbon transport. Some crustaceans (notably shrimps and lophogastrids) and fishes form aggregations above slopes and seamounts, feeding in surface waters at night and returning to depth during the day for respiration and egestion. These 200–500 m migrations [27] can facilitate efficient carbon transfer between surface and benthic systems. Despite their abundance and occasional fishery relevance [28], their contribution to the AMP has not been quantified at regional or global scales.

In some cases, net transport may occur in the opposite direction, particularly when organisms feed on benthic resources and migrate upward for reproduction. This includes harpacticoid and cumacean crustaceans [29,30] and polychaetes [31], including famous palolo worms [32], which release gametes into the water column during synchronized spawning. Although their vertical displacements are small (meters to tens of meters), their high local abundance may make them relevant for nearshore carbon redistribution.

Overall, current quantitative frameworks for the AMP are heavily biased toward pelagic DVM, while seasonal, ontogenetic, meroplanktonic, and benthopelagic pathways remain insufficiently incorporated into global carbon export estimates. More fundamentally, existing assessments rarely resolve how taxonomic diversity, community composition, biomass, and functional traits translate into differences in carbon transport among migrant assemblages. Major uncertainties therefore remain in estimating migratory biomass, resolving the taxonomic identity of migrating organisms, quantifying the contribution of less-studied migration modes, and incorporating biological diversity and functional traits into carbon-flux models.

This review addresses a gap in previous syntheses of DVM and the AMP by examining active carbon transport not simply as a consequence of vertical migration, but as a process generated by the composition, biomass, diversity, and functional traits of migrant communities. Specifically, we ask (1) which taxonomic and functional groups contribute to active carbon transport; (2) how migration mode, life history, body size, feeding strategy, and migration depth influence the magnitude and pathway of carbon transport; (3) how active transport varies among oceanic regions and ecosystem types; (4) what uncertainties in migrant biomass, taxonomic resolution, and carbon-flux estimates currently limit global assessments; and (5) how biodiversity and functional traits can be incorporated into models of active carbon transport and its potential contribution to long-term carbon sequestration. We distinguish carbon export and transport from carbon sequestration throughout, recognizing that active transport below the euphotic zone does not necessarily result in long-term atmospheric carbon removal.

2. Small Creatures, Big Commutes: The Biodiversity Underlying the AMP

Current research on the AMP largely focuses on quantifying carbon fluxes from the surface ocean to depth and sediments [33]. Yet this flux is ultimately produced by individual organisms, whose physiology and behavior determine when, where, and how carbon is transported. The AMP is therefore not only a biogeochemical pathway but also

a biological one, generated by the taxonomic and functional diversity of migrating organisms and modulated by their abundance, biomass, body size, physiology, and behavioral strategies. These dimensions of biodiversity are not interchangeable: taxonomic diversity likely shapes which organismal pathways are available, while community composition can influence which taxa dominate local transport. Furthermore, functional diversity appears to modulate the mechanisms and efficiency of carbon transfer, and abundance and biomass largely regulate the magnitude of transport generated by these traits [34–36]. Consequently, variation in the taxonomic and functional composition of migrant communities can alter the magnitude, depth, and direction of active carbon transport.

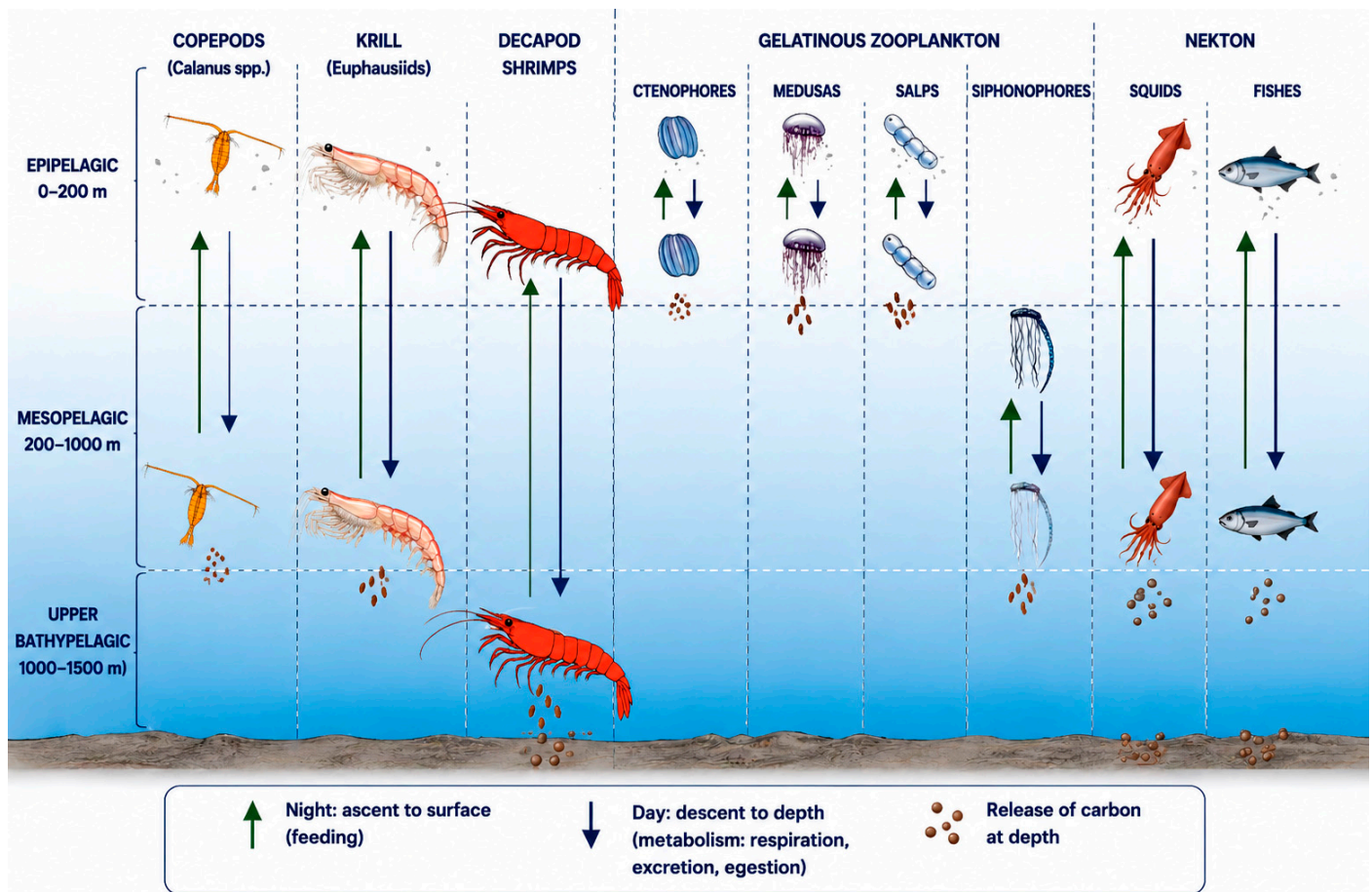


Figure 2. Major taxonomic groups participating in the active migrant pump (AMP).

Very small zooplankton (<0.2 mm, often grouped as microzooplankton [37]) do show vertical movements, but these are generally weak in amplitude and contribute little to net vertical carbon transfer [38]. Their role is more relevant to grazing and particle transformation in the upper ocean than to active export, and they are, therefore, not considered further here.

2.1. Crustacean Migrants: Abundance, Diversity, and Active Carbon Transport

Crustaceans are central to the AMP. They dominate meso- and macroplankton communities in both abundance and diversity, spanning a wide range of sizes, feeding modes, and metabolic and migratory strategies [39]. Many species undertake DVM from surface waters to depths of tens to hundreds of meters, effectively linking surface feeding with deep respiration and excretion. Crustacean contributions to the AMP differ markedly among taxa because their migration strategies, body sizes, trophic modes, and

life histories largely regulate both the amount of carbon transported and the mechanism by which it is transferred. Diel migrants primarily transport carbon through respiration, excretion, and egestion at depth, whereas seasonal and ontogenetic migrants can deliver carbon to depth over much longer timescales. Thus, high taxonomic diversity translates into multiple functionally distinct pathways of active carbon transport.

Copepods (Figure 2, Table 1) are the most abundant metazoans in the ocean and occur across all major basins. Although they are classically associated with the gravitational pump through grazing and fecal pellet production, they also contribute substantially to active transport via DVM [40]. In addition, many species undertake seasonal and ontogenetic vertical migrations. This is especially pronounced at high latitudes and in subtropical and tropical upwellings; for example, in high latitudes, *Calanus*, *Calanoides*, and *Neocalanus* spp. underpin the so-called “lipid pump” [24]. In winter, lipid-rich individuals descend to depth and enter diapause, slowly metabolizing wax esters and releasing respired carbon in the deep ocean [41]. Additional export occurs through mortality during diapause, predation, or failure to return to surface waters after reproduction [41,42]. Copepod contribution to the AMP therefore depends not simply on their exceptional abundance, but on the combination of high biomass, pronounced vertical displacement, lipid storage, and prolonged residence at depth. DVM primarily promotes active transport through respiration, excretion, and egestion, whereas ontogenetic descent additionally transfers carbon stored in body tissues to depth.

Some harpacticoid copepods are benthopelagic, feeding near the seafloor and migrating into the water column for reproduction [43,44]. These movements can reverse the typical directionality of carbon transport locally, depending on whether feeding or reproductive phases dominate. This diversity of migration modes makes copepods a functionally heterogeneous component of the AMP: closely related taxa can contribute through fundamentally different pathways, and community composition can therefore modulate which form of active transport dominates locally.

Euphausiids (krill) are another major vector of active carbon transport. Their fecal pellets and molted exoskeletons contribute strongly to particulate export [45]. Their large body size, high biomass, and extensive diel migrations allow krill to couple surface feeding with respiration and egestion at depth, while their rapid seasonal population growth can produce strong temporal pulses in active transport. They are particularly important in Polar Regions and upwelling systems, where high biomass and large body size amplify fluxes, especially during spring and summer blooms [46]. In the Southern Ocean, krill-driven sequestration has been likened, in carbon terms, to emissions associated with tens of millions of cars annually [45], underscoring their climatic relevance.

Krill also contribute directly through respiration at depth. Because they migrate daily over large vertical ranges, a significant fraction of their metabolic activity occurs in mesopelagic waters, where CO₂ is directly released [47]. Most assessments, however, focus on sinking pellets and underestimate this active component, despite its tight coupling to migration intensity [48]. Thus, krill illustrate how functional traits, such as particularly body size, biomass, feeding mode, and migration amplitude, jointly modulate the magnitude and pathway of active carbon transport.

Pelagic decapod shrimps are poorly represented in global AMP budgets. Their large migration amplitudes and substantial biomass suggest a potentially important role, but evidence for their contribution to carbon export remains indirect. Families such as Sergestidae, Acanthephyridae, and Oplophoridae migrate several hundred meters daily, connecting epipelagic feeding zones with deeper mesopelagic and upper bathypelagic layers [49]. Many are omnivorous or carnivorous, feeding on smaller zooplankton and micronekton. This feeding strategy short-circuits parts of the food web, moving carbon rapidly across trophic levels before export. Recent estimates suggest that deep-pelagic

shrimp biomass is an order of magnitude greater than previously assumed: the standing stock (wet weight) in the Atlantic is documented at 1.6×10^8 across both subtropical gyres combined and 0.8×10^8 in the intervening equatorial mesotrophic waters [15]. These observations provide evidence for substantial migrant biomass, but biomass alone does not demonstrate a quantitatively important carbon flux. Direct measurements linking shrimp migration to respiration, egestion, excretion, or mortality at depth are still lacking. If the reported biomass is representative of other oceanic regions, however, the potential contribution of decapods to active carbon transport warrants substantially greater attention.

Benthopelagic shrimps, including genera such as *Challengerosergia*, *Lucensosergia*, *Pasiphaea*, *Janicella*, and some *Acanthephyra*, form dense aggregations over slopes and seamounts. These aggregations can be locally abundant and even commercially exploited [28,50], indicating substantial local biomass. However, neither their standing stock nor their commercial importance provides direct evidence of their contribution to the AMP, and their quantitative role in regional or global carbon transport remains unquantified.

2.2. Gelatinous Migrants: Episodic Biomass and the “Gelatinous Pump”

Gelatinous zooplankton include cnidarians, ctenophores, and pelagic tunicates. Despite their ecological importance, they are often underrepresented in carbon budgets due to low carbon density, fragile bodies, and episodic occurrence. Many taxa respond rapidly to prey availability and can shift between scarcity and bloom conditions over short timescales [51,52]. Their potential contribution to the AMP is linked to a distinctive set of functional traits, including high feeding rates, rapid population responses, gelatinous body composition, and, in some taxa, substantial vertical mobility. These traits generate carbon-transfer pathways that differ from those of crustacean migrants, particularly through rapid grazing, respiration, production of sinking carcasses, and episodic bloom-associated export.

Salps and doliolids are among the most efficient pelagic filter feeders, capable of ingesting particles from bacteria to large phytoplankton [53]. During blooms, tunicates can dominate grazing and generate substantial carbon export, with estimates of 1.6–5.2 Gt C yr⁻¹ and up to ~40% of global particulate export [54]. This makes their contribution highly dependent on community composition and episodic biomass accumulation. These events are spatially patchy and temporally brief, but can strongly restructure carbon flux during bloom phases [55,56]. Thus, the AMP contribution of gelatinous taxa may be disproportionately important during short-lived biomass peaks despite their relatively small contribution to average standing biomass.

Cnidarians and ctenophores contribute primarily through sinking carcasses and aggregates (“jelly-falls”), which transfer relatively unprocessed organic matter directly to the seafloor [54]. This pathway bypasses much of the microbial degradation typical of smaller particles.

Evidence for their role in the AMP is still limited. Some taxa, including ctenophores, medusae, and tunicates, show low-amplitude vertical movements [57–60], while siphonophores may migrate several hundred meters (~350 m [61]). The available evidence therefore supports a potential AMP role for gelatinous organisms, but the contribution remains poorly quantified because observations of vertical migration are sparse and highly heterogeneous among taxa [57–61]. Their importance may be episodic rather than persistent, highlighting the need to incorporate taxon-specific behavior and bloom dynamics into AMP estimates.

2.3. Nektonic Contributors: Fishes and Cephalopods as High-Mobility Carbon Vectors

Nekton represents both a potentially major and one of the most uncertain components of the AMP. Mesopelagic fishes and cephalopods differ strongly in body size, biomass, trophic position, metabolic rate, migration amplitude, and life history, generating several distinct pathways of active carbon transport. Mesopelagic fish biomass alone spans roughly 1–15 Gt [62–64], whereas global cephalopod biomass remains poorly constrained. These uncertainties in biomass and community composition propagate directly into estimates of AMP magnitude. Their contribution to the AMP is shaped by the combination of high biomass, large migration amplitude, active feeding in surface waters, and high metabolic rates. These traits allow fish to transfer carbon through respiration and excretion at depth, while egestion and mortality provide particulate pathways.

Mesopelagic fishes, including myctophids, gonostomatids, and sternoptychids, undertake diel vertical migrations over hundreds of meters [64]. This movement couples surface feeding with deep metabolic processing, rapidly transferring both organic and inorganic carbon to depth [65]. In some regions, fish-mediated export may be comparable to zooplankton-mediated fluxes; in oligotrophic gyres it can exceed 40% of total export, while in more productive systems it is typically much lower (<10%) [65].

Multiple mechanisms contribute to fish-mediated export. Respiration at depth directly injects CO₂ into mesopelagic waters, while fecal pellets provide a fast-sinking particulate pathway, sometimes exceeding thousands of meters per day [66]. Predation further redistributes carbon across trophic levels, integrating multiple sources into deeper layers [67]. Consequently, fish-mediated transport depends not only on total biomass but also on the taxonomic composition of migrant communities, because species differ substantially in migration depth, diet, metabolic rate, and body size. Despite this, most carbon budgets still emphasize passive sinking flux and only partially incorporate active transport.

Cephalopods, particularly squids, are highly mobile predators with vertical migration ranges of hundreds of meters [68]. Their combination of large body size, high metabolic rates, predatory feeding, and rapid growth gives them the potential to transfer substantial amounts of carbon across trophic levels and depths. Biomass estimates remain uncertain due to sampling limitations [69]. Their high metabolic rates and rapid growth intensify carbon turnover at depth, while their short life cycles (~1–2 years) often end in mass mortality events that rapidly transfer biomass to the seafloor [70–72]. Compared with fishes, their faster life history may enhance episodic carbon export, although this pathway remains poorly quantified.

Across these taxonomic groups, the contribution to the AMP emerges from the interaction of biodiversity, biomass, and behavior rather than from taxonomy alone. Taxonomic diversity provides the pool of potential migrant strategies, whereas community composition, abundance, and biomass largely regulate which strategies dominate locally. Functional traits such as body size, feeding mode, metabolic rate, lipid storage, migration amplitude, and life-history strategy, then shape how carbon is transported and transformed at depth. Evidence for AMP contributions is strongest for groups with well-characterized biomass and migration behavior, whereas for several poorly sampled taxa, particularly pelagic and benthopelagic decapods and gelatinous organisms, high biomass or large migration amplitudes indicate potential rather than demonstrated carbon export. This distinction is essential when extrapolating organism-level observations to basin-scale AMP estimates.

Table 1. Major taxonomic groups contributing to the Active Migrant Pump.

Group	Dominant Migration Mode	Typical Migration Depth, m	Major Functional Traits	Principal Carbon-Transfer Pathways	Evidence for AMP Contribution
Copepods	DVM; ontogenetic;	Tens–	High abundance; lipid	Respiration, excretion,	Strong for selected

	seasonal	thousands	storage; diverse feeding modes	egestion, mortality, tissue transport (lipid pump)	taxa; globally incompletely quantified
Euphausiids	DVM, seasonal	Hundreds–thousands	High biomass; swarm formation	Respiration, excretion, egestion, mortality, tissue transport (lipid pump)	Strong for selected taxa; globally incompletely quantified
Decapods	DVM, benthopelagic	Hundreds	Large body size; high biomass; slope/seamount aggregation	Respiration, egestion, excretion, trophic relay	Potentially important; poorly quantified
Salps, doliolids	Very limited DVM	Tens	Rapid population growth; high filtration rates	Respiration, egestion, sinking carcasses/aggregates	Strong episodic contribution
Cnidarians, ctenophores	Limited DVM	Tens–hundreds	Gelatinous bodies; predation	Respiration, carcass sinking	Poorly constrained
Mesopelagic fishes	DVM; ontogenetic; benthopelagic	Hundreds	Large biomass; high metabolic rate; active predation; slope/seamount aggregation	Respiration, excretion, egestion, mortality, trophic relay	Strong but highly uncertain globally
Cephalopods	DVM; ontogenetic;	Hundreds	Large size; high metabolic rate; predation	Respiration, excretion, mortality, trophic relay	Potentially important; poorly quantified

3. Methodological Frontiers

The diversity of organisms contributing to the AMP, together with their behavioral plasticity, creates substantial challenges for quantifying active carbon transport. Migration amplitude, timing, metabolic rates, trophic interactions, and participation in migration vary among species, populations, life stages, and environmental settings [73–75]. These differences directly influence carbon transport, but no single observational method can simultaneously resolve taxonomic identity, abundance or biomass, migration behavior, and metabolic activity. Migratory communities are also patchily distributed [76], show varying degrees of net avoidance [77], and respond dynamically to environmental variability. Consequently, reliable estimates of AMP require complementary methods that resolve different components of biodiversity and organismal function at appropriate spatial and temporal scales.

Traditional sampling methods have provided the basement of our understanding of DVM, yet they offer only spatiotemporally discrete snapshots of highly dynamic communities. Progress in AMP research, therefore, increasingly depends on integrated observational frameworks capable of simultaneously resolving biodiversity, organism traits, metabolic rates, and biogeochemical processes across multiple spatial and temporal scales.

Recent methodological developments have substantially improved our ability to characterize the composition, abundance, physiology, and behavior of migratory organisms. These advances together refine estimates of carbon export and reveal how biodiversity and ecosystem functioning interact to regulate the AMP.

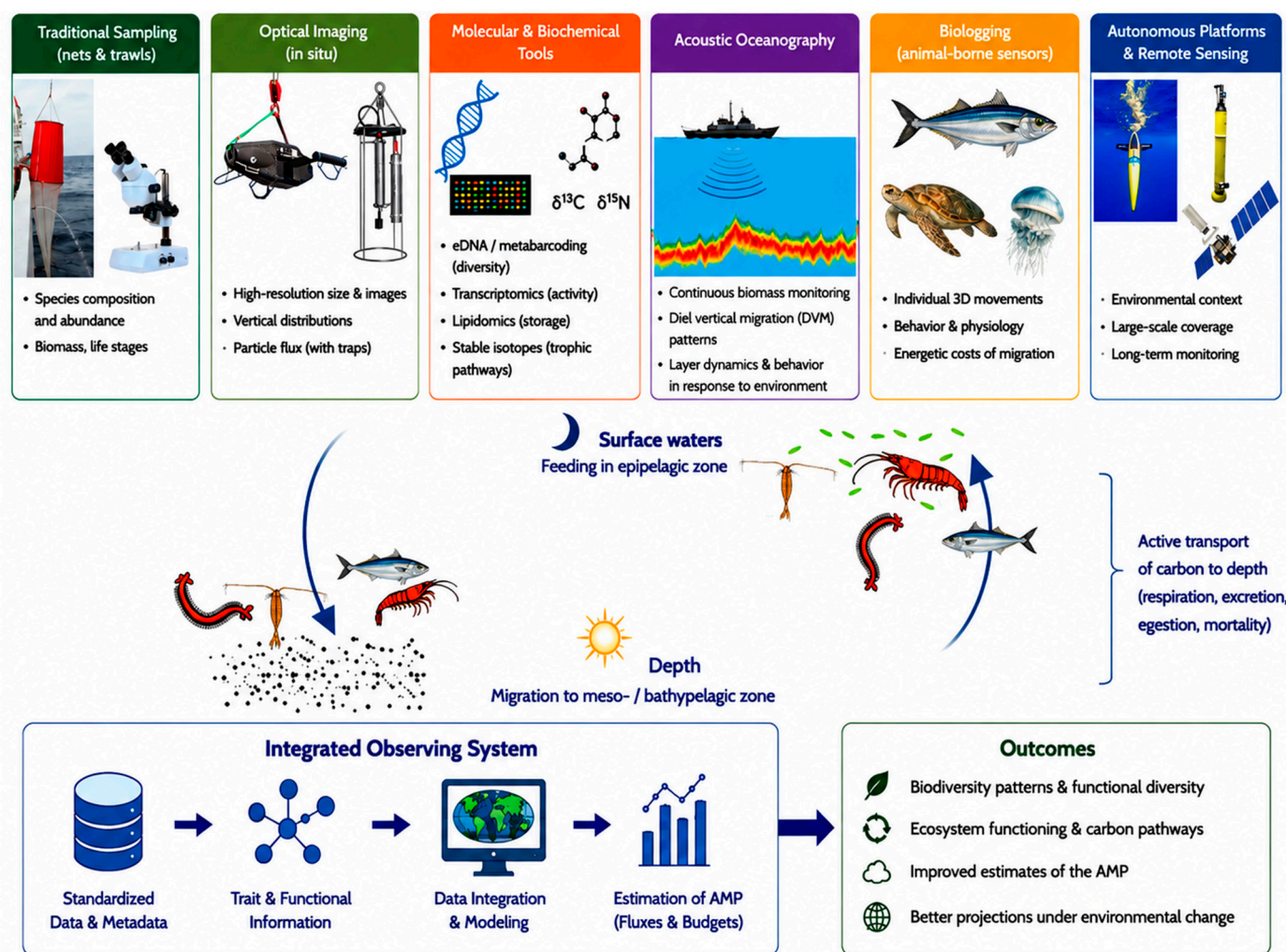


Figure 3. Observational frontiers for quantifying the active migrant pump (AMP).

3.1. From Nets to Imaging: Resolving Biodiversity in the Water Column

Traditional small [78,79] and big [80,81] nets, trawls [82,83], and multinet systems [84] have formed the backbone of zooplankton ecology and biomass assessments for more than a century (Figure 3). Their major strength is high taxonomic resolution, allowing direct identification, enumeration, measurement, and biomass estimation of collected organisms. These datasets remain essential for evaluating biodiversity, community composition, size structure, and vertical distribution across ocean basins. However, nets provide spatially and temporally discrete observations and are subject to substantial sampling biases. Fast-swimming organisms may actively avoid sampling gear, whereas fragile taxa are frequently damaged or destroyed during collection [85]. Thus, although nets remain indispensable for taxonomic and biomass calibration, they cannot alone resolve the continuous dynamics of migratory communities.

Despite these limitations, net-based observations continue to provide valuable information on the abundance and biomass of dominant zooplankton groups and remain indispensable for taxonomic validation and calibration of emerging technologies [86]. Their greatest value increasingly lies in their integration with complementary observational approaches.

Direct visual observations from manned submersibles represented an important advance by allowing in situ assessments of plankton abundance and distribution

throughout the water column while simultaneously documenting fragile gelatinous taxa that are poorly represented in net samples [87]. Because such observations are expensive and logistically demanding, they have largely been replaced by modern optical imaging systems.

Contemporary optical platforms can image and size organisms and particles continuously at high spatial and temporal resolution [88]. Their principal advantage is therefore the combination of broad temporal coverage with quantitative information on organism size and particle abundance, although taxonomic identification is generally less precise than in collected material. Instruments such as the Underwater Vision Profiler (UVP) have generated extensive datasets describing particle abundance, size spectra, and vertical distributions across diverse oceanic environments [89]. When coupled with sediment-trap systems, these observations also provide in situ estimates of particle sinking velocities and facilitate direct incorporation of particle fluxes into carbon export assessments [90].

Optical imaging has been particularly important for documenting fragile and previously underrepresented groups, including appendicularians [91], siphonophores, ctenophores, medusae, and pelagic tunicates [92]. Many of these organisms play significant roles in carbon export through the production of rapidly sinking particles (tunicates), jelly-falls (medusae) or large-scale DVM (siphonophores) but have historically been underestimated because of methodological limitations. Improved observations of these taxa have therefore expanded current understanding of biodiversity contributions to the BCP. Importantly, optical platforms like UVP detect particles and zooplankton within a size range of 100 μm to several centimeters. While these systems reliably quantify small, abundant organisms such as copepods, they suffer from a detection gap regarding larger nekton. Because of small sample volumes and avoidance behaviors by fast-swimming organisms, larger nekton are not quantitatively captured. Consequently, optical profiling must be combined with acoustic methods and net sampling to provide an unbiased overview of the entire pelagic size spectrum.

Overall, nets, trawls, visual observations, and optical imaging provide complementary rather than interchangeable information. Nets maximize taxonomic resolution and biomass calibration but provide limited spatial and temporal coverage; optical systems provide much greater coverage and preserve fragile organisms but offer more limited taxonomic resolution and incomplete detection of large nekton; direct visual observations provide valuable in situ information but remain logistically restricted. Their integration is therefore essential for linking taxonomic and functional diversity with abundance, biomass, migration behavior, and carbon transport in the AMP.

3.2. Molecular and Biochemical Tools: Revealing Hidden Diversity and Function

Traditional microscopy remains fundamental to plankton ecology but is time-consuming and often unable to distinguish cryptic or morphologically similar species. Molecular approaches have therefore become increasingly important for resolving taxonomic and genetic diversity within migratory communities. High-throughput sequencing technologies, including next-generation sequencing (NGS), metabarcoding, and environmental DNA (eDNA) analyses, enable the simultaneous detection of multiple taxa from a single environmental sample [93]. Initially developed for studies of prokaryotes and unicellular organisms [94–96], these approaches are now widely used to characterize zooplankton communities across broad spatial scales [97]. Beyond species identification, molecular markers can reveal genetic diversity, population differentiation, and cryptic evolutionary structure that cannot be assessed reliably from morphology alone [98]. Such information is particularly relevant to the AMP because geographically separated populations or genetically distinct lineages may differ in migration behavior,

phenology, body size, or metabolic characteristics despite similar morphology [99]. However, molecular approaches have important limitations for AMP applications. Taxonomic resolution depends strongly on the molecular marker and the completeness of reference databases, while primer choice can introduce taxonomic bias and PCR amplification can distort the relative representation of taxa. DNA degradation may further reduce detection probability, particularly in environmental samples. Most importantly, sequence read abundance from eDNA or metabarcoding cannot generally be converted directly into organism abundance or biomass because DNA shedding, degradation, extraction, amplification, and sequencing efficiencies differ among taxa [97]. Consequently, molecular data provide powerful information on taxonomic and genetic diversity but cannot by themselves provide the quantitative biomass estimates required to calculate carbon flux.

Molecular methods are particularly valuable for revealing hidden diversity and identifying taxa that cannot be reliably distinguished morphologically. When applied to vertically stratified samples, they provide detailed insights into changes in community composition associated with DVM, environmental gradients, and habitat partitioning [100]. Molecular approaches may therefore reveal substantially greater biodiversity than traditional microscopy-based assessments. However, this additional taxonomic resolution must be combined with quantitative observations of abundance, biomass, and migration if it is to be translated into estimates of AMP strength.

The integration of molecular methods with transcriptomics and metatranscriptomics has further expanded their ecological relevance. These approaches enable the characterization of physiological processes occurring *in situ* and can thus reveal how organisms respond to changing environmental conditions during migration. Such information improves estimates of species-specific contributions to the AMP by identifying ecological niches, optimal habitats, adaptive capacity, and phenological responses to environmental change [101]. Unlike metabarcoding, however, these approaches are primarily informative about physiological function rather than providing direct estimates of migratory biomass.

Stable isotope analyses of carbon and nitrogen provide complementary information on trophic structure and carbon transfer pathways within pelagic food webs. By identifying food sources and trophic positions of migratory organisms, isotope-based approaches help quantify the pathways through which carbon moves across trophic levels and ultimately contributes to active export [102].

Lipidomics represents another promising avenue for understanding the functional role of biodiversity in carbon sequestration. Marine organisms show remarkable diversity in lipid composition and storage strategies [103], mirroring differences in life-history traits and environmental adaptation. In particular, LC-MS-based lipidomic analyses have improved estimates of the contribution of seasonal migrants to the lipid pump by quantifying wax ester accumulation and utilization during diapause. Meanwhile, triacylglycerols (TAGs) serve as the primary lipid class and biomarker for carbon storage during this period [24,26].

Molecular and biochemical approaches thus connect biodiversity with BCP processes by linking organismal identity and genetic diversity to physiology, trophic ecology, and carbon-processing pathways. Their principal limitation for AMP quantification is that taxonomic or genetic information is not equivalent to biomass or carbon flux. Integration with net, imaging, acoustic, and biogeochemical observations is therefore required to translate molecular diversity into quantitative estimates of active carbon transport.

3.3. Acoustic Oceanography: Monitoring Biomass Dynamics

Acoustic methods provide a powerful complement to taxonomically resolved sampling approaches because they enable continuous, non-invasive observations of migratory biomass across broad spatial and temporal scales. Their principal advantage over nets and imaging is the ability to quantify the dynamics of extensive scattering layers continuously, whereas their principal limitation is that acoustic backscatter is not inherently taxonomically resolved. Unlike nets and imaging systems, which typically provide discrete observations, acoustics can resolve diel migration patterns continuously over periods ranging from days to years, revealing the timing, amplitude, and vertical structure of migratory communities with exceptional spatiotemporal resolution [104].

Because acoustic backscatter depends on the abundance, size, and physical characteristics of sound-scattering organisms, acoustic observations are particularly useful for quantifying the biomass and distribution of migratory assemblages. Advances in acoustic technology have substantially improved the ability to resolve vertical movements of zooplankton, micronekton, and fishes and to track changes in scattering layers through time [105,106]. These developments including ADCP-equipped tools have greatly expanded our understanding of how environmental variability influences migration behavior [107–109].

Acoustic observations have shown that DVM is strongly regulated by interactions occurring across multiple trophic levels. For example, phytoplankton blooms can alter migration behavior by increasing feeding opportunities in surface waters and reducing the benefits of migration [110]. Likewise, predator–prey interactions influence migration amplitude and timing, as vertically migrating zooplankton and micronekton respond to predation risk from higher trophic levels [111]. Such observations highlight the importance of biodiversity and trophic interactions in shaping active carbon transport.

Acoustics have also unveiled the sensitivity of migratory behavior to environmental gradients and stressors. Studies of oxygen minimum zones have shown that many migratory organisms adjust their vertical distribution in response to hypoxia, while certain species of krill, copepods, and fish routinely enter severely oxygen-depleted waters during daytime refuge phases [112,113]. These findings emphasize that physiological adaptations and species-specific tolerances can strongly influence migration strategies and, consequently, the efficiency of the AMP.

The principal limitation of acoustic observations is their relatively low taxonomic resolution. Acoustic signals alone cannot identify organisms that form observed scattering layers, and converting backscatter to biomass requires assumptions about organism size, morphology, orientation, and target strength. Acoustic data are therefore most informative when calibrated with optical, molecular, and net-based observations that provide taxonomic and size information.

3.4. *Biologging: Individual Perspectives on Migration*

Recent advances in animal-borne sensors have opened new opportunities for studying migration behavior at the level of individual organisms. Biologging technologies were initially developed for large marine vertebrates such as whales, turtles, and seabirds [114,115], but ongoing miniaturization now permits their application to increasingly smaller organisms, including some gelatinous zooplankton [116].

Modern biologgers can record not only movement trajectories but also environmental conditions, activity patterns, and physiological responses [117]. They therefore provide a unique individual-level perspective on migration that is largely unavailable from nets, imaging, molecular sampling, or acoustics. Such observations can reveal energetic costs, behavioral variability, and environmental drivers of migration, including differences among individuals of the same species associated with age, physiological condition, food availability, or predation risk.

Potentially, biologging directly links individual behavior with carbon transport processes and refines estimates of metabolic carbon release at depth through quantifying migration depth. Its major limitation is scale: observations are typically restricted to relatively few individuals and species and therefore cannot directly provide population- or basin-scale biomass estimates. Biologging is consequently best viewed as a mechanistic complement to population-level observations rather than a stand-alone method for estimating AMP flux.

3.5. Toward an Integrated Biodiversity Observing System

No single observational technique can adequately resolve the diversity, behavior, physiology, and ecological functions of organisms contributing to the AMP. Each method samples a different component of the system and operates at different spatial and temporal scales. Consequently, future progress depends on the development of integrated biodiversity observing systems capable of combining complementary sources of information within a unified framework.

A major challenge is incorporating biodiversity data to carbon flux models. Here, biodiversity should not be treated as a single variable: taxonomic diversity describes which organisms are present, community composition describes their relative representation, and functional diversity captures variation in traits relevant to carbon transport, whereas abundance and biomass greatly regulate the magnitude of the biological pool available for migration. Species and populations may differ greatly in body size, migration amplitude, trophic position, metabolic demand, behavior, and life-history strategy, resulting in large differences in their contributions to active carbon transport. Trait-based approaches therefore represent a particularly promising framework for connecting species identity and functional diversity with ecosystem-level carbon sequestration. The growing availability of large biological datasets presents both opportunities and challenges. Zooplankton observations are currently distributed across numerous repositories, stored in different formats, and characterized by varying levels of taxonomic and methodological consistency. Harmonization of these datasets is, therefore, essential for developing interoperable databases that can support large-scale ecological analyses and global assessments of active carbon transport. Recent syntheses of zooplankton trait data have already shown the potential of this approach for identifying broad ecological patterns and improving parameterization of ecosystem models [118].

Contemporary models increasingly recognize the importance of active carbon transport mediated by respiration, excretion, egestion, and mortality at depth. However, model outputs remain highly sensitive to assumptions regarding migration behavior, metabolic rates, community composition, and species interactions. Reliable parameterization, therefore, requires integration of field observations, remote sensing products, molecular analyses, acoustic observations, and ecosystem models [22,40,119]. In particular, molecular observations can improve taxonomic and genetic resolution, acoustics can constrain migratory biomass and its temporal dynamics, imaging and nets can provide organism size and taxonomic calibration, and biologging can constrain individual migration behavior and energetic expenditure.

The future of AMP research therefore lies not in any single methodological advance but in the effective integration of multiple approaches. By combining imaging systems, molecular ecology, acoustics, biologging technologies, autonomous observing platforms, and ecosystem modeling, researchers are beginning to move beyond biomass estimates toward a mechanistic understanding of how biodiversity regulates active carbon sequestration in the ocean.

3.6. Remaining Uncertainties in Biodiversity-Mediated Carbon Export

The principal methodological trade-offs are therefore between taxonomic resolution, spatial and temporal coverage, and quantitative estimation of biomass and carbon flux (Table 2). Net sampling provides the highest taxonomic resolution and remains essential for species-level identification and biomass calibration, but offers limited spatial and temporal coverage. Optical imaging provides continuous observations of organisms and particles and improves detection of fragile taxa, but its taxonomic resolution is generally lower and its quantitative coverage decreases for large, fast-moving nekton. Molecular approaches greatly expand taxonomic and genetic resolution but provide limited direct information on biomass and migration behavior. Acoustic methods offer broad spatial and temporal coverage of migratory biomass but generally lack taxonomic resolution. Biologging provides detailed individual-level behavioral and environmental information but is currently restricted to relatively few organisms and observations. Integrating these complementary approaches is therefore essential for linking biodiversity with the magnitude and efficiency of active carbon transport.

Despite substantial methodological advances, several major uncertainties continue to limit estimates of AMP strength and our ability to attribute active carbon transport to particular taxa, functional groups, and migratory strategies.

One of the most significant challenges remains uncertainty in the biomass of major migratory groups. Global biomass estimates for mesopelagic fishes and pelagic decapods vary by more than an order of magnitude, while reliable global assessments of cephalopod biomass remain unavailable. Furthermore, many global zooplankton datasets are restricted to the upper 500 m of the water column [120], excluding a substantial portion of the migratory habitat used by many species. These biomass uncertainties directly propagate into estimates of AMP strength because biomass influences the quantity of organisms available to transport and transform carbon.

Another source of uncertainty arises from partial migration. In many populations, only a fraction of individuals participates in diel, seasonal, or ontogenetic migrations, whereas the remaining individuals remain within resident habitats [121]. Such behavioral polymorphism has been documented in both zooplankton and fishes [122] and may be driven by resource competition, predation risk, reproductive strategies, and individual physiological condition. As a result, estimates based solely on migrant biomass may fail to capture the true complexity of population-level carbon transport.

Seasonal diapause represents another underappreciated component of active export. Most AMP models focus primarily on diel migrations, despite evidence that overwintering copepods and monsoon- or upwelling-driven diapause can contribute significantly to long-term carbon sequestration [41]. Because available estimates are based on relatively few species, the global importance of diapause-driven export remains uncertain.

Additional uncertainty stems from benthopelagic and demersal coupling. Extensive vertical migrations linking the water column and seafloor can bypass the pelagic food web and facilitate direct carbon transfer between pelagic and benthic ecosystems. Despite their potential importance, such pathways are never incorporated into current AMP assessments.

Similarly, reverse vertical migrations remain poorly quantified. In ecosystems where benthic and benthopelagic organisms ascend into the water column to reproduce, the upward transport of organic matter and reproductive products may partially offset downward carbon fluxes. Although these processes are unlikely to dominate global carbon budgets, they may be locally important and remain largely absent from existing models.

Overall, future progress in gaining deeper insights into active carbon transport and estimating AMP depends on both improved observations and a better representation of

biodiversity within BCP frameworks. Current models greatly simplify migratory assemblages into a limited number of functional groups, despite substantial differences among taxa, and even individuals, in behavior and metabolic rates. Therefore, incorporating species traits, functional diversity, and ecological interactions into an interoperable observational framework merits the utmost attention. An interoperable observing framework that combines taxonomic and genetic information, biomass measurements, functional traits, migration behavior, and biogeochemical rates is essential for translating biodiversity patterns into quantitative estimates of AMP carbon transport and, ultimately, sequestration.

Table 2. Comparative strengths and limitations of methods used to quantify biodiversity and AMP.

Method	Taxonomic Resolution	Spatial Resolution	Temporal Resolution	Main Strengths	Main Limitations
Nets and trawls	High; species-level	Local/discrete	Discrete	Taxonomic identification; abundance; size structure; biomass calibration	Net avoidance; damage to fragile taxa; limited coverage
In situ visual observation	Moderate	Local, high	High during observation	Fragile gelatinous taxa; behavior; in situ context	Expensive; limited spatial coverage
Optical imaging	Low–moderate to moderate	High	High/continuous	Continuous observations; size spectra; fragile organisms; particles	Limited taxonomic resolution; detection gap for large plankton and nekton
eDNA and metabarcoding	High potential	High when spatially sampled	Moderate	Cryptic diversity; broad taxonomic coverage; genetic information	Primer/PCR bias; incomplete databases; DNA degradation; read abundance $\neq$ biomass
Meta-transcriptomics	High	Moderate	Moderate	Physiological activity; functional responses	Complex interpretation; limited quantitative biomass information
Stable isotopes	Functional/trophic rather than taxonomic	Local–regional	Moderate	Trophic pathways; carbon sources; trophic position	limited population/global coverage
Lipidomics	Functional	Local–regional	Moderate	Lipid storage; diapause; lipid pump	Taxon-specific interpretation; limited global coverage
Acoustics	Low without calibration	Very high	Very high/continuous	Migratory biomass; scattering layers; DVM dynamics	Low taxonomic resolution; target-strength assumptions
Biologging	Species/individual	Individual trajectories	Very high	Migration depth; behavior; energetics; environmental exposure	Few individuals; limited population/global coverage

4. The Mechanics of Active Carbon Transport: Biodiversity Pathways of Deep Carbon Injection

For clarity, we use “carbon transport” for the physical relocation of carbon by migrating organisms, “carbon export” for transfer below a specified reference depth, and “carbon injection” for the release of transported carbon at depth through respiration, excretion, egestion, mortality, or subsequent trophic processing. Neither export nor injection necessarily represents long-term sequestration: sequestration requires sufficiently

prolonged isolation of carbon from atmospheric exchange and depends on subsequent remineralization and ocean circulation.

Vertical migrations transfer carbon from the surface ocean to depth through the daily or seasonal movement of organisms rather than by gravitational settling of particles. The magnitude of this active transport depends not only on migratory biomass but also on the taxonomic composition. Four principal direct pathways of carbon transfer by migrating organisms are recognized (Figure 4): (1) respiration, (2) excretion, (3) egestion, and (4) mortality. These pathways describe the immediate fate of carbon carried by migrants below the euphotic zone. Trophic relay represents a complementary, indirect mechanism rather than a fifth flux pathway: carbon transferred by migrants can subsequently be passed to resident or deeper-living predators and then processed through respiration, excretion, egestion, mortality, or biomass transfer. The pathways operate simultaneously, and their relative importance varies among ecosystems according to species composition, migration behavior, food-web structure, and environmental conditions.

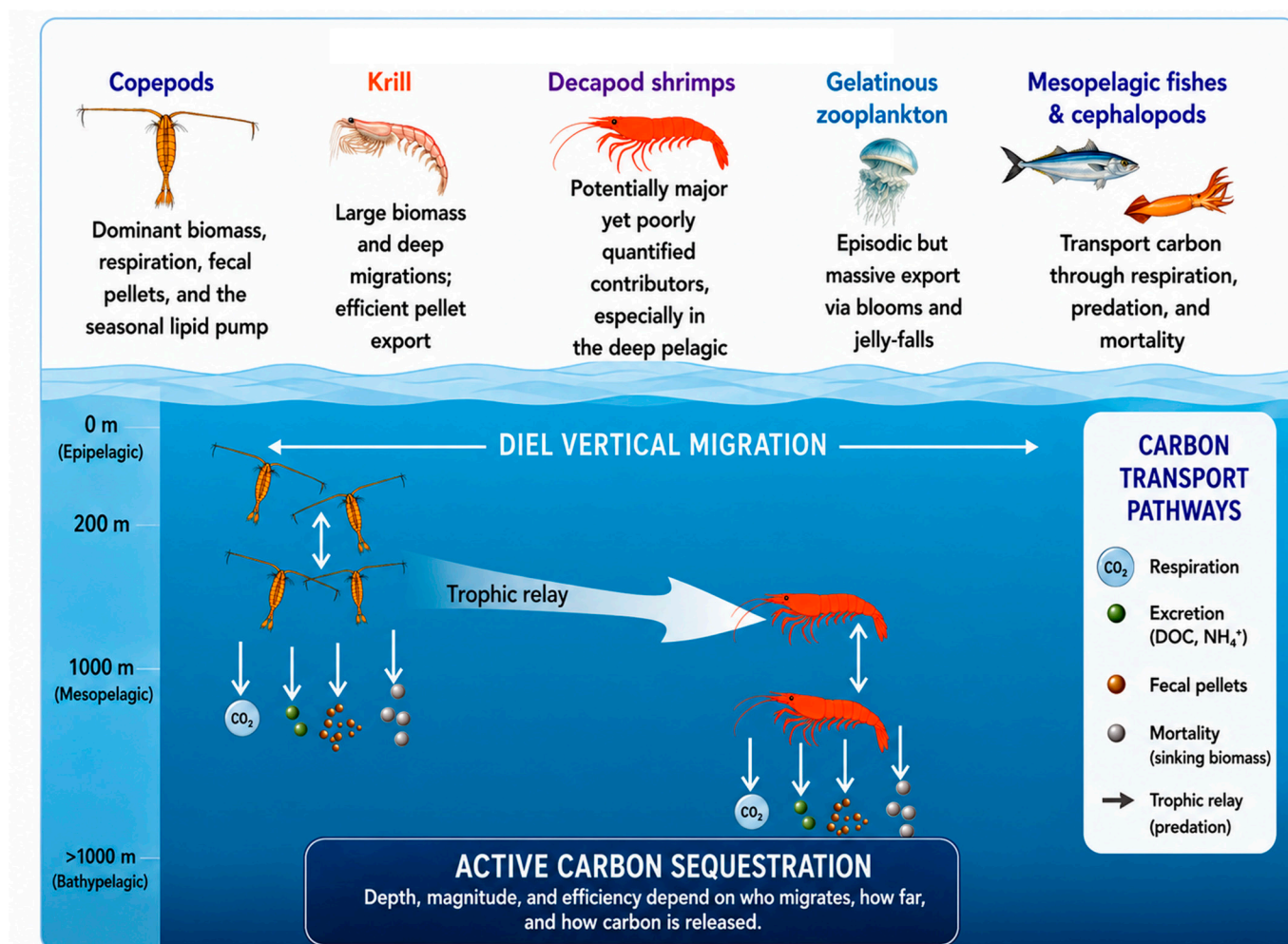


Figure 4. The mechanics of active carbon transport: biodiversity pathways of deep carbon injection.

4.1. Respiration: Metabolic Carbon Injection at Depth

Respiration is generally considered the largest component of the AMP because it converts recently assimilated organic carbon into dissolved inorganic carbon below the euphotic zone [12]. During daytime residence in the mesopelagic and upper bathypelagic, vertically migrating organisms respire carbon acquired while feeding near the surface during the previous night. Respiration at depth therefore represents carbon in-

jection into the ocean interior rather than direct evidence of long-term sequestration. The fraction of respired carbon that ultimately remains isolated from the atmosphere depends on the depth and duration of residence, subsequent transport and remineralization, and circulation pathways.

Estimated global, full-ocean-depth-integrated mesozooplankton respiration has been estimated at approximately 13 Gt C yr⁻¹, equivalent to 17–32% of global primary production [12]. This estimate, however, represents total respiratory carbon processing across the ocean rather than AMP export specifically; only the fraction of respiration occurring below the defined reference depth and attributable to vertically migrating biomass represents active carbon injection associated with the AMP. Roughly half of the carbon assimilated by zooplankton is ultimately respired, although this proportion varies among taxa according to body size, metabolic strategy, and environmental temperature [123].

The magnitude of respiratory export is largely controlled by biological traits. Mass-specific respiration decreases with increasing body size but increases with temperature, producing pronounced geographic patterns [124]. Consequently, warm subtropical and tropical ecosystems dominated by small-bodied zooplankton generally have higher respiration per unit biomass than polar systems dominated by larger species [75]. In oligotrophic subtropical gyres, respiratory export may equal or exceed passive particulate organic carbon (POC) flux [18,21].

Respiratory flux also varies over time because metabolic activity closely follows food availability. During phytoplankton blooms, enhanced feeding promotes rapid biomass accumulation and elevated metabolic rates, resulting in pulses of respiratory carbon export [39,125]. Seasonal changes in community composition further modify these patterns as different migratory taxa dominate at different stages of the annual production cycle.

Respiration is commonly estimated from oxygen consumption, which is converted to carbon production using respiratory quotients and elemental stoichiometry. However, recent studies indicate that respiratory stoichiometry varies with temperature and physiological condition rather than remaining constant, introducing additional uncertainty into biogeochemical estimates [126]. Direct measurements of respiration under in situ pressure and temperature conditions remain technically challenging, particularly for fragile or deep-living species.

The respiratory carbon injection associated with migrating biomass below a reference depth can be approximated as

$$F_{\text{resp}} = B_{\text{mig}} \times R_{\text{sp}} \times t_{\text{depth}}$$

where F_{resp} is respiratory carbon injection below the reference depth (mg C m⁻² d⁻¹), B_{mig} is migratory biomass (mg C m⁻²), R_{sp} is the mass-specific respiration rate at depth (mg C mg C⁻¹ h⁻¹), and t_{depth} is the duration of residence below the reference depth per daily cycle (h d⁻¹).

Although conceptually straightforward, each parameter remains uncertain. Migratory biomass is difficult to estimate accurately because many species avoid nets or occupy depth ranges that are inadequately sampled. Respiration rates vary among species, body sizes, and physiological states, while residence time changes with migration amplitude, latitude, season, and local light conditions. These uncertainties propagate directly into estimates of respiratory carbon export.

4.2. Excretion: Dissolved Carbon Transfer to the Mesopelagic Microbial Loop

Excretion transfers dissolved organic and inorganic compounds such as dissolved organic carbon (DOC), ammonium, and urea, from migrating organisms to the sur-

rounding water. Although less conspicuous than particulate export, this pathway supplies labile substrates that sustain microbial production and nutrient recycling in the mesopelagic zone [127,128].

DOC originates from several biological processes. It is released during sloppy feeding, when prey is mechanically fragmented before ingestion, through metabolic excretion, leakage of digestive products from guts and food vacuoles, and dissolution of fecal pellets [129]. Collectively, these processes release approximately 10–30% of previously ingested particulate carbon as dissolved organic matter [127]. In crustacean zooplankton, excretion and sloppy feeding dominate DOC production [130], whereas gelatinous taxa additionally release large quantities of carbon-rich mucus [131]. In copepods alone, sloppy feeding may convert between 7% and 70% of ingested carbon into DOC, depending on prey characteristics [129]. Because these pathways are difficult to separate experimentally, they are usually treated together when estimating excretory carbon flux [12].

Species traits strongly influence DOC production. Prey size is particularly important because large prey items are more likely to be fragmented during capture and handling, increasing DOC release, whereas very small prey is ingested intact [129]. Feeding strategy also affects excretion rates. Carnivores often release more DOC than omnivores despite similar ingestion rates [132], while gelatinous zooplankton contribute additional dissolved carbon through continuous mucus production [131]. Community composition therefore largely regulates both the quantity and chemical composition of dissolved organic matter injected below the euphotic zone.

Environmental conditions further modify excretory flux. High food concentrations increase feeding activity and consequently DOC production, whereas food quality influences the chemical composition and subsequent degradation of dissolved organic matter. The composition of phytoplankton prey also affects DOC release. For example, fecal pellets produced by copepods feeding on cryptophytes or dinoflagellates release dissolved organic carbon more rapidly than pellets derived from diatom diets [133]. Pellet fragmentation through coprophagy and microbial degradation further enhances DOC release after excretion [127].

Compared with respiration, excretory export contributes a smaller fraction of total active carbon transport. Nevertheless, because dissolved compounds are immediately available for microbial uptake, excretion provides a continuous source of carbon and nutrients that fuels mesopelagic microbial communities and links vertical migration directly to microbial carbon cycling. Quantifying this pathway remains challenging because DOC production depends simultaneously on species composition, feeding behavior, prey characteristics, and environmental conditions, all of which vary across ecosystems and seasons.

4.3. Egestion: Fecal Pellet Production and Deep Particulate Carbon Export

Egestive flux results from the production of fecal pellets at depth after migrants have fed in surface waters. By transporting ingested carbon below the euphotic zone before pellet production, vertically migrating organisms bypass much of the intense remineralization that occurs in surface waters. Fecal pellets released below the euphotic zone therefore have a greater probability of contributing to particulate carbon export to depth than pellets produced in the epipelagic[6].

The magnitude of egestive flux is largely regulated by species-specific feeding and pellet production. Zooplankton differ markedly in ingestion rates, gut passage time, pellet size, density, and composition, producing pellets that vary greatly in sinking velocity and degradation. Large crustaceans and euphausiids generally produce larger, denser pellets than small copepods, whereas gelatinous zooplankton, particularly salps,

generate exceptionally large carbon-rich pellets that sink rapidly and transport organic matter efficiently to depth [134]. Consequently, changes in community composition can substantially alter the efficiency of particulate carbon export even when total zooplankton biomass remains similar.

Food availability strongly regulates pellet production. High phytoplankton concentrations stimulate feeding and increase pellet production, while blooms dominated by large phytoplankton cells promote the formation of large, rapidly sinking pellets [135]. Food quality also influences pellet characteristics. Under low-food conditions, slower gut passage may produce dense pellets with relatively high sinking rates, whereas rapid processing of abundant food often produces less compact pellets that sink more slowly [136]. Seasonal changes in phytoplankton communities therefore modify egestive flux by altering both feeding rates and pellet properties. For example, replacement of diatom blooms by *Phaeocystis* reduces copepod feeding efficiency, pellet production, pellet density, and sinking velocity [137].

Pellets continue to change after their release. Microbial colonization accelerates remineralization, whereas zooplankton modify pellets through coprophagy, fragmentation (coprorhexy), and loosening (coprochaly), all of which increase surface area available for microbial decomposition and reduce vertical carbon transport [138,139]. Copepods frequently fragment large pellets produced by other organisms, preventing rapid sinking and generating smaller particles that remain suspended longer in the water column [140]. Some of these fragments are subsequently consumed by appendicularians and repackaged into new pellets, further modifying particle size distributions and carbon flux [140]. Pellets may be further augmented by DVM of zooplankton in response to feeding and survival cues [141]. These biological transformations make pellet export considerably more dynamic than simple sinking models suggest.

Temperature also influences egestive flux by regulating microbial activity. Higher temperatures accelerate microbial degradation and heterotrophic respiration, increasing remineralization of particulate organic carbon in the upper ocean and reducing the efficiency of export to depth [142]. The balance between pellet production, sinking, fragmentation, and remineralization therefore modulates the net contribution of egestive flux to the biological carbon pump.

Although egestive export is highly variable, it can represent a substantial fraction of active carbon transport in ecosystems dominated by large crustaceans or gelatinous filter feeders. Salp blooms are highly effective at transferring carbon because their fecal pellets typically sink at rates exceeding 500–1000 m d⁻¹, delivering organic matter to the deep ocean within days; by contrast, pellets from other dominant taxa (copepods, krill) typically sink at only 50–100 m d⁻¹ [143]. Rapid sinking, however, indicates efficient particle transport rather than necessarily long-term sequestration, which depends on the depth reached and subsequent remineralization and circulation.

4.4. Mortality: Carcass Flux and Carbon Transfer Through the Ghost Pump

Mortality transfers carbon to depth through two complementary pathways: predation on migrating organisms by resident deep-sea consumers and the sinking of carcasses. Both processes retain surface-derived carbon below the euphotic zone and contribute to BCP [20,65]. Unlike respiration or excretion, mortality transfers carbon as biomass, making trophic interactions an integral component of the active biological carbon pump.

Predatory mortality occurs when resident mesopelagic fishes and other non-migrating predators consume vertically migrating prey during their daytime residence at depth. Carbon assimilated near the surface is thereby incorporated directly into deep food webs, where it is subsequently respired, excreted, or transferred to higher

trophic levels [16]. The strength of this pathway depends on predator abundance, prey availability, and food-web structure, linking biodiversity to BCP.

Non-predatory mortality, often referred to as the “ghost carbon pump,” represents an additional source of particulate carbon export. Carcasses produced by senescence, starvation, disease, parasitism, or environmental stress sink through the water column as discrete organic particles [20]. In marine copepods, carcasses typically represent 5–30% of total abundance [144] and non-predatory processes therefore account for approximately one-quarter to one-third of total mortality in epipelagic populations [145]. Gelatinous zooplankton also experience episodic mass mortality during blooms of salps, pyrosomes, and scyphozoans, generating “jelly-falls” that deliver large quantities of organic carbon to the deep sea [146]. Appendicularians contribute through the frequent abandonment of rapidly sinking mucous houses, providing another important source of particulate organic matter [147].

Mortality rates vary among ecosystems because they are controlled by both biological and environmental factors. Senescence produces predictable increases in mortality after reproduction [148], whereas starvation becomes important during periods of low primary production or in oligotrophic waters [149]. Disease and parasitism can cause substantial episodic mortality, although their contribution remains poorly quantified [150]. Environmental stress further modifies mortality patterns. Hypoxia associated with expanding oxygen minimum zones increases mortality in many taxa [151], while elevated temperatures and marine heatwaves reduce physiological tolerance and increase mortality rates [152,153]. Global analyses indicate that copepod mortality increases exponentially with temperature, suggesting that climate warming may increase carcass production [145].

The contribution of carcasses to carbon export depends not only on mortality rates but also on their fate after death. Zooplankton carcasses generally sink rapidly because their physical properties differ from those of fecal pellets and marine snow. Small copepod carcasses sink at rates ranging from several tens to more than 100 m day⁻¹ [154], whereas larger organisms such as krill may exceed 1500–3000 m day⁻¹ [155]. Actual sinking rates vary with turbulence, stratification, microbial degradation, fragmentation, and scavenging [156,157]. Carcasses may also be intercepted by pelagic consumers before reaching the deep ocean, reducing export while simultaneously supporting meso-pelagic food webs [20].

Mortality remains one of the least quantified pathways because estimates of carcass production, predation rates, and degradation vary widely among ecosystems, and direct observations remain scarce. Improved field observations and mechanistic models are therefore needed to quantify the role of mortality in the active biological carbon pump.

Importantly, mortalities transfer carbon from migrating organisms to depth via predatory and non-predatory pathways. Predation converts migrant biomass into deep-resident consumer biomass, while non-predatory mortality produces sinking carcasses and particulate matter. These mechanisms differ from the trophic relay discussed below: predatory mortality is the initial removal of migrant biomass by a predator, whereas trophic relay is the subsequent carbon redistribution through the food web. Therefore, trophic relay must not be treated as an independent flux alongside predatory mortality in AMP carbon budgets.

4.5. Trophic Relay: Extending Carbon Transfer Beyond Vertical Migration

Trophic relay is best viewed as an indirect extension of AMP carbon transfer rather than as a fifth independent pathway. It begins when vertically migrating organisms are consumed by resident or deeper-living predators during or after their descent. The resulting carbon is subsequently redistributed through predator respiration, excretion,

egestion, mortality, and further trophic interactions. Thus, trophic relay can increase the depth and residence time of carbon initially transported by migrants, but its contribution should not be summed independently with the predatory mortality flux from which it originates. Carbon acquired by migrants in surface waters is transferred to resident mesopelagic predators, which permanently inhabit deeper layers. By consuming vertically migrating prey during their daytime residence, these predators retain surface-derived carbon within deep food webs, where it is subsequently respired, excreted, incorporated into biomass, or transferred to higher trophic levels.

The efficiency of the trophic relay depends on predator diversity, prey availability, and the structure of mesopelagic food webs. Ecosystems with abundant resident predators may therefore retain a larger fraction of actively transported carbon at depth than ecosystems in which migrants complete most trophic processing after returning to the deep layers.

Carbon transfer may be further enhanced through predator–predator interactions. Deep migrators descending from the lower mesopelagic can prey upon shallower migrants returning from the epipelagic, a mechanism described as the “migratory ladder” [158]. Because these predators subsequently return to greater depths, potentially increasing the depth and residence time of carbon in the ocean interior beyond that achieved by a single migration. This process may therefore enhance the probability of long-term sequestration, but the magnitude of this effect remains poorly constrained.

Despite its potential importance, trophic relay is likely the least understood of the AMP. Quantifying its contribution requires detailed information on predator diets, trophic interactions, and migration behaviour, which can be obtained through stable isotope analyses, molecular dietary techniques, gut-content analyses, and ecosystem modelling. Incorporating these interactions into carbon export models remains a major challenge.

4.6. From Individual Pathways to the Active Biological Carbon Pump

Respiration, excretion, egestion, and mortality represent the principal direct pathways determining the immediate fate of carbon transported by vertically migrating organisms. Trophic relay operates across these pathways by transferring migrant-derived carbon to resident or deeper-living consumers, where it may subsequently undergo respiration, excretion, egestion, mortality, or further trophic transfer. These processes therefore form an interconnected network rather than five independent fluxes. Although each pathway is often considered independently, they operate simultaneously within the same individuals and populations. Carbon assimilated during surface feeding may be respired at depth, released as dissolved organic matter, packaged into fecal pellets, transferred to predators, or exported through carcass sinking. The relative importance of each pathway depends on the biological characteristics of the migrating and resident communities and the environmental conditions under which migration occurs.

Biodiversity is therefore central to the functioning of the AMP. Taxonomic diversity underlies the availability of organismal pathways, community composition guides which taxa dominate local transport, functional diversity regulates the mechanisms and efficiency of carbon transfer, and abundance and biomass govern the magnitude of transport generated by these traits. Community composition integrates these taxonomic and functional differences and therefore influences the relative contributions of respiration, excretion, egestion, mortality, and trophic relay. Consequently, changes in community composition may alter active carbon transport even when total biomass remains unchanged.

Environmental factors further regulate the balance among pathways. Temperature influences metabolism, oxygen availability constrains migration depth and survival,

food availability controls feeding intensity and pellet production, and seasonal changes restructure pelagic communities. These interacting drivers produce substantial spatial and temporal variability in active carbon export, explaining why estimates differ among ecosystems and observational approaches.

Despite considerable progress, quantifying the integrated contribution of these pathways remains challenging. Current estimates are limited by uncertainties in migratory biomass, species composition, migration behaviour, metabolic rates, trophic interactions, and mortality. Most global models still simplify these biological processes and consequently are likely to underestimate the contribution of active transport to the BCP [7].

Future progress will depend on combining the methodological advances discussed in Section 3 with mechanistic ecosystem models that explicitly incorporate biodiversity. Integrating optical observations, acoustics, molecular tools, biochemical tracers, autonomous platforms, and trait-based modelling will provide more realistic estimates of active carbon transport and carbon export across ecosystems, while allowing the fraction of exported carbon that is ultimately retained in the ocean interior to be evaluated separately as long-term sequestration. Such integration will improve predictions of how changing marine biodiversity may alter both the magnitude of active carbon transport and the efficiency with which transported carbon is retained at depth.

5. Geographic Patterns of the Active Migrant Pump

The efficiency of the AMP varies markedly among oceanic regions because it depends on both the diversity of migrating organisms and the environmental conditions that shape their metabolism and behavior (Figure 5). At the basin scale, distinct physical and biological settings favor different mechanisms of active carbon transport. These regional comparisons should, however, be interpreted cautiously because published AMP estimates differ in sampling strategy, depth horizon, temporal coverage, and definitions of active carbon export. Consequently, the percentages reported below provide an overview of regional patterns rather than strictly comparable estimates of AMP efficiency. The principal environmental and biological characteristics of these regions are summarized in Table 3.

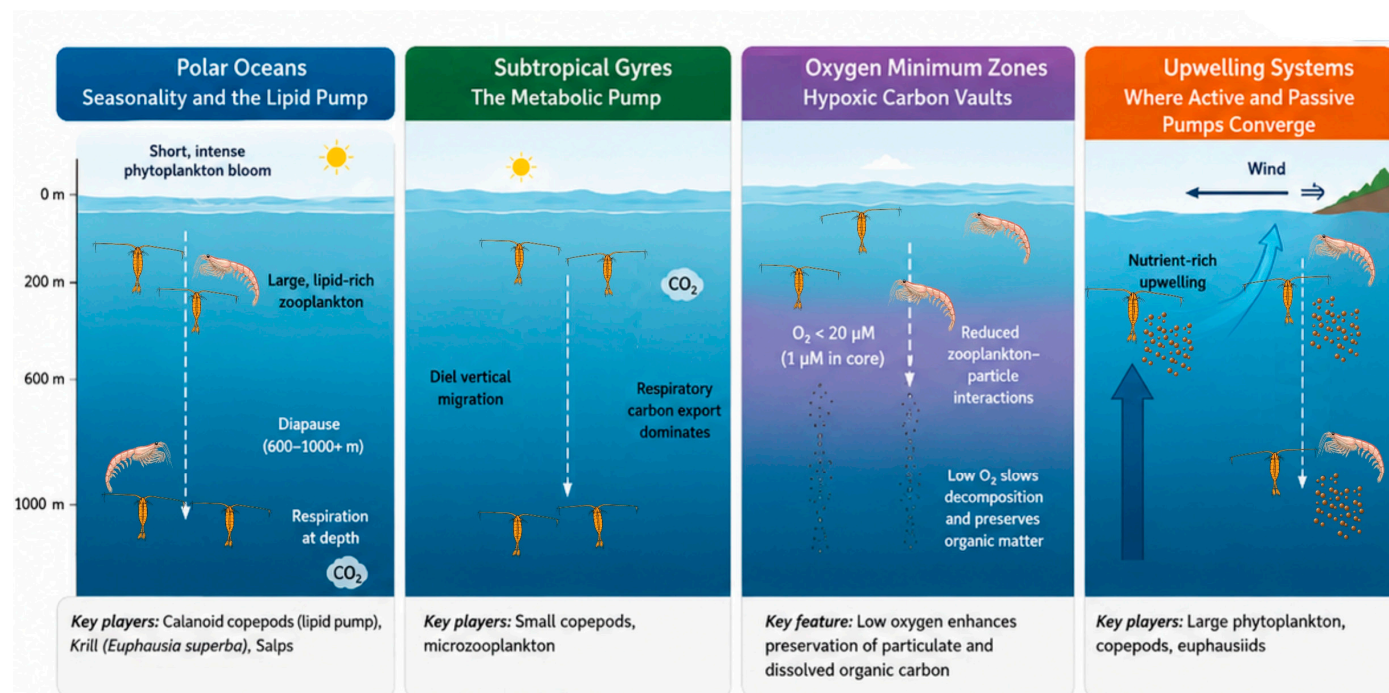


Figure 5. Geographic patterns of the active migrant pump.**Table 3.** Geographic variation in the active migrant pump.

Region	Major environmental characteristics	Dominant Migratory Taxa	Dominant AMP Mechanism	Estimated AMP Contribution
Polar oceans	Strong seasonality; intense seasonal production; prolonged winter; deep seasonal mixing	Calanoid copepods, krill, salps	Seasonal/ontogenetic migration; lipid pump; respiration and egestion	~12–15% of total export in North Atlantic/North Pacific budgets [10]
Subtropical gyres	Strong stratification; permanent nutrient limitation; low primary production; high temperature	Copepods, microzooplankton, pelagic decapods, fishes	DVM; predominantly respiratory transport	~2% in available global regional budget [10] but highly likely underestimated [15]
Oxygen minimum zones	Severe hypoxia; compressed oxygenated habitat; reduced aerobic respiration	Hypoxia-tolerant zooplankton and micronekton	Deep daytime residence; respiration and egestion; altered particle processing	Not sufficiently constrained
Upwelling systems	High nutrient supply; high primary production; strong physical export	Copepods, krill, micronekton, fishes	DVM and seasonal migration; respiration, egestion, mortality	~11% in available regional/global budget [10]

5.1. Polar Oceans: Seasonality and the Lipid Pump

The Arctic and Southern Oceans are defined by extreme seasonality in primary production. Short, intense phytoplankton blooms during summer are followed by prolonged winters with little or no photosynthetic activity. These seasonal cycles support a characteristic mode of active carbon transport dominated by large, lipid-rich zooplankton that rapidly exploit brief periods of high productivity before transporting carbon to depth during seasonal migrations [159].

The most efficient mechanism in these regions, and arguably one of the most efficient within the global ocean, is the lipid pump. Calanoid copepods accumulate large lipid reserves during the productive season and subsequently descend to depths of 600–1000 m or more to overwinter in diapause [24,159]. Because lipids contain abundant carbon but relatively little nitrogen or phosphorus, respiration during diapause exports carbon while leaving most nutrients in surface waters, thereby enhancing the efficiency of the BCP and supporting future phytoplankton production [159]. Respiration during deep diapause transfers carbon from migrant biomass into the ocean interior and may increase its residence time away from the atmosphere. However, respiratory carbon release at depth represents carbon injection rather than direct evidence of long-term sequestration; the duration of isolation ultimately depends on subsequent remineralization, mixing, and circulation [2].

The Antarctic krill forms dense swarms that perform extensive vertical migrations linking surface phytoplankton production with deep-ocean carbon cycling [44,45]. In addition to respiratory transport, krill contribute substantially through the production of large, compact fecal pellets that sink rapidly and efficiently export particulate carbon to depth.

Gelatinous zooplankton, particularly salps, represent a third important component of high-latitude export. Their episodic blooms generate large quantities of rapidly sinking fecal pellets and introduce considerable temporal variability into carbon export [56,143].

The North Atlantic and North Pacific show among the highest carbon export rates in the global ocean (approximately $38\text{--}42\text{ g C m}^{-2}\text{ yr}^{-1}$). Export is dominated by the gravitational pump (59–75%), followed by the mixing pump (12–26%) and the AMP (12–15%) [10]. These proportions, however, should be interpreted as study-specific estimates rather than standardized basin-wide AMP efficiencies, because the underlying estimates may differ in sampling period, depth horizon, and operational definition of active export.

5.2. Subtropical Gyres: The Metabolic Pump

Subtropical gyres occupy vast regions of the open ocean characterized by persistent nutrient limitation, strong stratification, and low primary production. Nevertheless, active carbon transport remains significant because elevated temperatures enhance metabolic activity. Marine communities in these oligotrophic systems have adapted to chronic resource limitation through altered turnover rates, complex ecological interactions [160], and efficient use of available metabolic substrates [161].

Temperature strongly regulates metabolic rates [124], making respiratory export the dominant component of the AMP in subtropical waters. The magnitude of this respiratory pathway depends not only on temperature but also on the taxonomic and functional composition of the migrant community. Specifically, body size, biomass, metabolic rate, migration amplitude, and residence time at depth jointly underly the amount of carbon transferred and the location of its release. Long-term observations indicate that respiration by vertically migrating zooplankton can equal or even exceed passive particulate carbon export [162,163]. At the same time, the energetic costs of diel vertical migration increase in warm waters, forcing organisms to balance predator avoidance against metabolic expenditure.

The structure of oligotrophic food webs further influences carbon export. Small phytoplankton support communities dominated by copepods and microzooplankton [164]. This food web produces small fecal pellets that sink slowly and are readily degraded by microbes or reprocessed by zooplankton. Consequently, a greater proportion of organic carbon is recycled within the upper ocean, reducing the efficiency of passive export.

Despite these constraints, the AMP remains an important export pathway in subtropical gyres. Recent studies also indicate that processes traditionally overlooked in BCP models such as viral infection, parasitism, and predation, may substantially influence carbon export. Viral lysis can either retain fixed carbon in surface waters [165] or promote aggregate formation and enhance sinking [166]. Likewise, radiolarians and alveolates have emerged as potentially important contributors to carbon export in nutrient-poor subtropical oceans [167].

Subtropical gyres show the lowest carbon export rates among the major ocean biomes (approximately $21\text{ g C m}^{-2}\text{ yr}^{-1}$). Export is dominated by the gravitational pump (approximately 75%), followed by the mixing pump (23%) and the AMP (2%) [10]. The relatively small contribution attributed to the AMP may be underestimated if conventional sampling poorly captures strongly migrating decapods. The substantially higher deep-pelagic shrimp biomass reported recently [15] provides a basis for this hypothesis, but high biomass alone does not demonstrate a proportionally high contribution to active carbon export. Direct measurements linking decapod biomass, migration amplitude, metabolic rates, and carbon release at depth are therefore needed to test whether their contribution to the AMP is systematically underestimated [15].

5.3. Oxygen Minimum Zones: Hypoxic Carbon Vaults

Oxygen minimum zones (OMZs), defined by oxygen concentrations below $20\text{ }\mu\text{M}$ and reaching as little as $1\text{ }\mu\text{M}$ in their cores, occupy approximately 8% of the global

ocean. Permanent OMZs occur in the Pacific Ocean (Eastern South Pacific, Eastern Tropical North Pacific, Eastern Subtropical North Pacific (25–52°N), the western Bering Sea, and the Gulf of Alaska) and the Indian Ocean (the Arabian Sea and the Bay of Bengal) [168]. These hypoxic layers profoundly modify pelagic ecosystems and thereby alter both the composition and vertical behavior of migrating communities, with consequences for active carbon transport [169].

For many organisms, OMZs compress the vertical habitat by imposing physiological constraints that limit migration depth [170]. In contrast, hypoxia-tolerant species can exploit these waters as refuges from visual predators, allowing deeper daytime residence and potentially increasing active carbon transport and carbon injection below the euphotic zone [111,112]. Whether this enhanced transport translates into long-term sequestration depends on the subsequent fate of the released carbon [111,112].

The fate of sinking particulate organic matter is also altered within OMZs. In oxygenated waters, particles are degraded through bacterial respiration, abiotic disaggregation [171], and ingestion and fragmentation by mesozooplankton [19,172]. Zooplankton typically fragments about half of the sinking particles before microbial degradation [19], which results in both rapidly (not fragmented, $>100 \text{ m d}^{-1}$) and slowly (fragmented, $<10 \text{ m d}^{-1}$) sinking fractions [173,174]. Within OMZs, however, zooplankton abundance declines markedly, reducing particle fragmentation and shifting remineralization toward microbial pathways, which account for approximately 70% of particle degradation [175].

Low oxygen concentrations suppress aerobic microbial respiration and slow organic matter decomposition [176], increasing the probability that sinking particles reach the deep ocean. In addition, stable hypoxic and anoxic environments favor the preservation of organic matter through processes such as sulfurization [177]. Together, these mechanisms can enhance the retention of organic carbon within OMZs and reduce its rapid remineralization or return to surface waters. OMZs may therefore act as important regional carbon reservoirs, although the extent to which this retention represents long-term sequestration depends on the subsequent transformation and circulation of both particulate and dissolved carbon.

5.4. Upwelling Systems

Upwelling systems rank among the most productive marine ecosystems because nutrient-rich deep waters sustain high primary production [178,179]. Many are iron-limited and maintained by cross-shore transport from coastal waters together with wind-stress curl-driven upwelling [180,181]. Offshore, they grade into the oligotrophic subtropical gyres [178,182], together encompassing much of the productivity gradient observed across the global ocean.

These systems illustrate particularly well the interaction between biological and physical pathways of carbon transport and export. Passive particle sinking, active transport by vertically migrating organisms, and physical transport through subduction and vertical mixing can all transfer carbon below the surface ocean, but these processes do not necessarily represent equivalent contributions to long-term sequestration. The most comprehensive observational budget indicates that passive sinking remains the dominant pathway, whereas active transport represents the second largest contributor. In the California Current, for example, regional passive sinking was estimated at $\sim 1.9 \text{ kmol C m}^{-2} \text{ yr}^{-1}$, compared with active transport of $\sim 0.5 \text{ kmol C m}^{-2}$ and the physical pump of $\sim 0.4 \text{ kmol C m}^{-2}$. This budget, calculated from 100 m to the seafloor, provides an estimate of carbon export across the specified depth horizon rather than a direct measure of the fraction undergoing long-term sequestration [183].

Globally, upwelling and adjacent mesotrophic tropical regions export approximately $30 \text{ g C m}^{-2} \text{ yr}^{-1}$, exceeding subtropical gyres but remaining below the highly

productive polar oceans. Carbon export is dominated by the gravitational pump (82%), followed by the AMP (11%) and the mixing pump (7%) [10]. The larger contribution of active transport compared with oligotrophic regions is likely a result of the greater biomass of both plankton and vertically migrating consumers, together with enhanced production of large, rapidly sinking pellets and corpses.

5.5. Global View on the Active Migrant Pump

The regional trends outlined above show that the efficiency of the AMP emerges from interactions between environmental forcing and biological diversity. Importantly, these controls operate through the characteristics of migrant communities rather than independently: environmental forcing influences which taxa can migrate and to what depth, while community composition, biomass, and functional traits shape how the transported carbon is processed after migration. Across the global ocean, five major factors govern the magnitude of active carbon transport:

- Thermal structure, which regulates metabolic rates, energetic costs of migration, and the depth and duration of residence.
- Oxygen availability, which explains vertical habitat boundaries, migration behavior, and the depth at which carbon is released.
- Seasonality, which controls the timing and magnitude of diel and seasonal migrations, including the lipid pump.
- Taxonomic and functional diversity, which shapes the identity of migratory taxa and their feeding modes, body size, metabolic rates, migration amplitudes, and carbon-processing pathways.
- Migratory biomass and community composition, which moderate the magnitude of carbon transported and the relative contribution of respiration, excretion, egestion, mortality, and subsequent trophic relay

The regional patterns therefore indicate that there is no single global “AMP”: its magnitude and mechanism emerge from the interaction between environmental forcing, migratory biomass, community composition, and functional traits. Polar systems emphasize seasonal and ontogenetic transport by lipid-rich migrants; subtropical gyres are characterized by metabolically costly DVM and potentially important but poorly quantified contributions from deep-pelagic taxa; OMZs modify migration depth and carbon processing through oxygen limitation; and productive upwelling systems combine substantial biological transport with strong gravitational and physical export. Quantitative comparisons among these regions remain constrained by differences in observation methods, depth horizons, temporal coverage, and definitions of active export. Future trait-based models [118] should therefore distinguish carbon transport and export from subsequent carbon retention and sequestration through the representation of taxonomic composition, biomass, functional traits, and migratory behavior.

6. Environmental Change Reshapes Biodiversity and the Active Migrant Pump

The active migrant pump (AMP) is shaped by the interaction of physical forcing, biogeochemical conditions, and biodiversity. Climate change can therefore influence the AMP both directly, by altering stratification, circulation, oxygen availability, temperature, and sea-ice cover, and indirectly, by restructuring the diversity, abundance, physiology, and behavior of migrating organisms. These interacting changes modify migration depth and timing, metabolic rates, trophic interactions, and the pathways through which carbon is transported and released below the euphotic zone [12,36,184].

The response of the AMP varies geographically because migrant communities differ among ocean basins and because species differ in physiological tolerance, functional traits, and behavioral plasticity. Environmental change acts as a selective filter [185], but its effects on carbon transport depend on how physical forcing interacts with the resulting changes in community composition and ecosystem function. This section examines how major climate-related drivers—deoxygenation, warming, acidification, and sea-ice loss—alter migrating communities and the efficiency and depth of active carbon transport, with particular attention to potential nonlinear responses and interactions among multiple stressors (Figure 6).

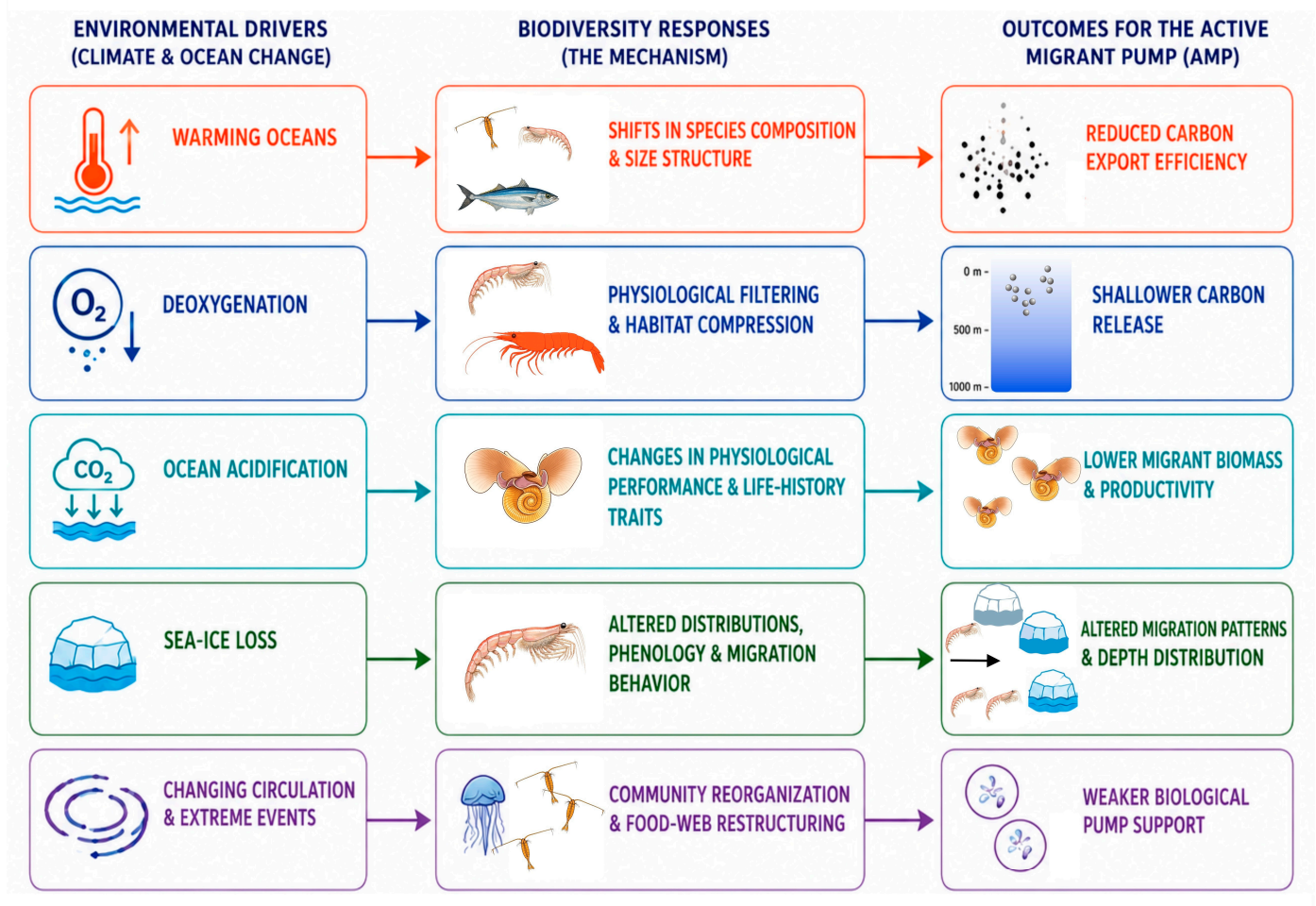


Figure 6. Changing environmental factors drive the active migrant pump (AMP) through their impact on biodiversity.

6.1. Deoxygenation: Restructuring Vertical Biodiversity

Ocean deoxygenation is among the most pervasive consequences of climate change. Reduced oxygen solubility in warmer waters, increasing stratification, and changes in ocean circulation are expanding both the area and volume of oxygen minimum zones (OMZs), where oxygen concentrations become too low to support many marine organisms [186,187]. Together with other anthropogenic stressors, this expansion creates multiple interacting pressures to which many pelagic ecosystems have limited resilience [188]. Model projections suggest that the global volume of OMZs may increase by more than 50% by the end of this century [189]. For vertically migrating organisms, expanding OMZs represent both a physiological constraint and a major ecological filter that reshapes migration patterns, community composition, and active carbon transport [190].

Species differ greatly in their tolerance of hypoxia. Oxygen-sensitive taxa experience reduced growth, impaired reproduction, and increasing mortality as oxygen concentrations decline [191]. Many are forced to occur in shallower, better-oxygenated waters, producing habitat compression that alters predator–prey interactions and reorganizes pelagic food webs [192]. For the AMP, this compression reduces the depth at which respiratory and excretory carbon is released, decreasing the probability that transported carbon remains isolated from the atmosphere for long periods.

OMZ expansion also modifies marine biogeochemistry. Oxygen-deficient waters remove approximately 30–50% of the ocean's fixed nitrogen [193] and alter coupled nitrogen, sulfur, iron, and phosphorus cycling, ultimately influencing primary production and food-web structure [194]. These changes propagate upward through pelagic communities and indirectly affect both migrant abundance and the efficiency of active carbon transport.

The response of hypoxia-tolerant migrants can be opposite. Crustaceans and mollusks have evolved physiological adaptations that allow prolonged residence in oxygen-poor waters [195–197]. By occupying hypoxic layers during daytime, these species can exploit refuge from visually hunting predators such as tunas and billfishes [198]. Expansion of OMZs may thus permit some tolerant migrants to maintain or even deepen their daytime distributions, potentially increasing the depth of carbon injection. However, metabolic suppression and reduced aerobic respiration under severe hypoxia can simultaneously decrease the magnitude of respiratory carbon flux [8,197]. Thus, deeper migration does not necessarily translate into greater carbon sequestration: the AMP mirrors a trade-off between how much carbon is transported and how deeply it is released. The net effect depends on the balance among migrant biomass, migration depth, residence time, and species-specific metabolic rates.

Consequently, deoxygenation is expected to reorganize rather than simply increase or decrease the AMP. Oxygen-sensitive species may contribute less by becoming restricted to shallower habitats, whereas hypoxia-tolerant specialists may transfer carbon deeper but at lower mass-specific metabolic rates. The resulting change in community composition and functional traits may therefore be more important for the future AMP than changes in total migrant biomass alone.

6.2. Warming Oceans: Smaller Organisms, Higher Metabolism

Ocean warming strengthens vertical stratification, suppresses nutrient supply to surface waters, and fundamentally alters the structure and functioning of pelagic ecosystems [199]. These physical changes influence the AMP primarily through changes in stratification and productivity and indirectly through changes in species composition, body-size distributions, metabolic rates, and migratory behavior.

Metabolic rates increase predictably with temperature [123]. Consequently, warming raises energetic demands both during nocturnal feeding in surface waters and during daytime residence at depth [163]. The increased energetic cost of diel vertical migration reduces its net energetic benefit and may favor shallower migrations or lower participation in migration by some populations, thereby decreasing active carbon transport.

Warming also accelerates microbial remineralization in surface waters, shortening the residence time of sinking particles and reducing the efficiency of carbon transfer through the mesopelagic zone [200]. At the same time, enhanced stratification reduces nutrient inputs into the euphotic zone, lowering phytoplankton productivity and shifting communities toward smaller cells, particularly pico- and nanophytoplankton [201–203].

These responses may be especially important at low latitudes, where warming and stratification are projected to intensify and where relatively small changes in the abun-

dance and functional composition of migrant communities can alter the balance between respiratory carbon release at depth and recycling in surface waters. These changes propagate throughout the pelagic food web. Smaller phytoplankton favor microbial pathways and support smaller zooplankton, reducing average body size across successive trophic levels. Because body size strongly influences migration amplitude, metabolic scaling, and fecal pellet characteristics, this community-wide miniaturization weakens several components of the BCP simultaneously. Smaller migrants generally have smaller amplitude of the DVM, transport less carbon to depth, produce smaller and more slowly sinking pellets, and recycle a larger proportion of organic matter within the upper ocean [8].

The ecological consequences therefore extend beyond changes in metabolism alone. Climate-driven warming selectively favors species adapted to oligotrophic conditions while reducing populations of larger migratory taxa that dominate active carbon transport in productive systems. Changes in species composition and functional diversity are thus expected to become a major modulator of future AMP efficiency, particularly in low-latitude oceans where warming and stratification are projected to intensify most strongly.

6.3. Ocean Acidification: Changing Calcifiers, Changing Carbon Export

Ocean acidification is expected to alter the carbonate component of marine carbon cycling, with model projections indicating substantial but highly model-dependent changes in CaCO_3 export [204–208]. Ocean acidification can affect the AMP through changes in the physiology, survival, calcification, and ecological functions of migrating organisms. Its effects are particularly relevant where calcifying plankton contribute to particle production or ballast and where acid–base regulation increases the energetic costs of migration.

Acidification reduces calcification in several planktonic groups, including pteropods and foraminifera [209,210], and can alter the functional composition of calcifying communities [211]. Reduced production of CaCO_3 may weaken mineral ballasting of organic particles, potentially slowing particle sinking and increasing remineralization in the upper ocean [212]. Thus, acidification can modify active transport not only through the physiology of migrants themselves but also through interactions between migrating organisms and the particles they produce or modify.

The consequences may be particularly relevant for crustaceans, which constitute major components of the AMP. Although many decapods tolerate reduced pH, acidification can compromise growth, survival, and exoskeletal calcification. Maintaining acid–base balance under acidified conditions requires additional metabolic expenditure, potentially diverting energy from locomotion, growth, and diel vertical migration [213]. Similar energetic constraints may affect other crustacean migrants. Because these trade-offs remain poorly quantified, the effects of acidification on the abundance, migration behavior, and carbon-transfer efficiency of crustacean-dominated AMP communities remain uncertain.

For the AMP, the key implication is that changes in calcifying plankton may modify particle ballasting and sinking in addition to altering the physiology of migrating organisms [212,213].

6.4. The Arctic as a Case Study: Rapid Biodiversity Reorganization in a Changing Polar Ocean

Polar oceans are experiencing some of the fastest environmental changes on Earth, including rapid warming, sea-ice loss, freshening, and increasing water-column stratification. These changes can influence the AMP through both physical and biological pathways. Declining sea-ice cover increases light penetration into surface waters and

may stimulate primary production, while warming and freshening alter stratification, nutrient supply, and habitat structure. Increased food availability, along with stronger light-driven migration and a longer annual period suitable for vertical migration, may locally enhance active carbon transport in newly ice-free regions. Conversely, shifts in species composition and phenology may reduce the abundance or seasonal performance of the large migratory taxa that currently dominate polar active transport.

The biodiversity response is equally complex. Arctic pelagic ecosystems are dominated by a relatively small number of large-bodied, lipid-rich zooplankton species whose seasonal migrations underpin the exceptionally efficient polar lipid pump [159]. Changes in the abundance or phenology of these key species therefore have disproportionate consequences for carbon transport compared with equivalent biomass changes in lower-latitude systems.

DVM in Polar Regions were traditionally assumed to cease during the Polar Night because of the absence of a regular day–night light cycle. Recent observations have overturned this assumption by demonstrating that zooplankton continue to migrate throughout the year, using weak environmental cues such as moonlight [214] and even auroral illumination [215]. These findings suggest that active carbon transport continues year-round and that the ecological controls of migration are considerably more complex than previously recognized.

Future changes in Arctic biodiversity will guide whether the AMP strengthens or weakens under continued climate change. Increased primary production and prolonged migration seasons enhance carbon export in some regions, whereas shifts in species composition, phenology, and trophic interactions reduce the abundance of the large migratory copepods and euphausiids that currently dominate active transport. The balance between these opposing processes remains one of the major uncertainties in predicting the future role of polar oceans in global carbon sequestration.

6.5. Multiple Stressors: When Biodiversity Meets Climate Synergy

Warming, acidification, changing circulation, and altered seasonality can interact to produce biological responses greater than those expected from individual stressors considered separately. Such interactions are particularly important when several environmental changes simultaneously affect the physiology, phenology, and habitat of key migrant taxa. The Arctic provides a well-resolved example: atlantification is reshaping pelagic communities through the combined influence of warming, changing water masses, and associated chemical and ecological changes.

Atlantification creates a potential winter bottleneck for Arctic copepods. Because large lipid-rich *Calanus* species are principal drivers of the seasonal lipid pump, changes in their survival and physiology can disproportionately affect one of the most efficient components of polar active carbon transport [216]. During the Polar Night, these copepods depend largely on stored lipids to survive, molt, and reproduce. First, warming and acidification act synergistically to increase mortality. A 53-day incubation experiment revealed that while warming alone has little effect and acidification alone may even enhance survival, their combined effect approximately doubles mortality rates (25% under the combined treatment compared to 13% under acidification alone) [216]. Second, warming accelerates development, forcing premature transition from juvenile to adult stages during winter and substantially increasing metabolic demand. Third, elevated metabolism rapidly depletes lipid reserves, causing copepods to exhaust their stored energy one to four months before the onset of the spring phytoplankton bloom. Finally, transcriptomic analyses reveal increased DNA damage together with reduced investment in cellular repair and maintenance [216].

Together, these responses generate pronounced phenological mismatches between copepod life cycles and seasonal food availability. Subsequently, reduced overwinter survival propagates through pelagic food webs and weakens the seasonal lipid pump, illustrating how multiple environmental stressors can alter carbon transport through changes in the abundance, physiology, and phenology of key migrant taxa.

6.6. Biodiversity at a Threshold: Nonlinear Responses of the Active Migrant Pump

The response of the AMP to climate change is inherently nonlinear because it emerges from interactions among environmental forcing, species diversity, and ecological processes. Roughly, ocean deoxygenation modifies vertical habitat structure, warming increases metabolic costs, stronger stratification reorganizes productivity and therefore food webs, and acidification alters metabolic rates, particle production and sinking dynamics. These drivers do not operate independently: warming enhances stratification, which further intensifies nutrient limitation and deoxygenation, warming and acidification frequently interact synergistically, etc. As a result, even insignificant environmental changes may trigger disproportionate shifts in community structure and, thereby, carbon export efficiency.

The future efficiency of the AMP will therefore depend less on total biomass than on changes in taxonomic composition, functional diversity, body-size structure, migration amplitude, and the relative abundance of migrating versus resident organisms. Communities dominated by large-bodied, deeply migrating organisms are expected to sustain efficient active carbon transport, whereas increasing dominance of smaller, surface-restricted taxa will reduce the depth and magnitude of active carbon transfer. Importantly, these effects can operate in opposite directions: a shift toward hypoxia-tolerant taxa, for example, may increase migration depth while simultaneously reducing respiratory carbon flux through metabolic suppression. Thus, environmental change can alter not only the amount of carbon transported but also the pathway, depth, and eventual fate of that carbon. These interactions highlight a central uncertainty for future AMP projections. Current assessments often represent migrant communities using simplified functional groups, whereas environmental change is likely to reorganize species composition and functional traits unevenly across regions. Predicting future AMP therefore requires models that jointly represent environmental forcing, biodiversity, migration behavior, and the major mechanisms of active carbon transport.

Overall, despite substantial advances in understanding the AMP, major uncertainties remain regarding how environmental change will alter the composition, biomass, functional traits, and behavior of migrating communities and how these changes will translate into carbon transport and sequestration. Uncertainties are particularly large for deep-migrating taxa, migration depth and participation, species-specific metabolic responses, and interactions among multiple stressors. Most current estimates rely on simplified representations of community structure and migration behavior and therefore insufficiently capture the taxonomic and functional diversity of marine migrants. Future AMP assessments should consequently integrate physical and biogeochemical forcing with biodiversity and trait-based representations of migration, allowing changes in community structure to be translated explicitly into changes in the magnitude, depth, and fate of active carbon transport.

7. Conclusions

The AMP is an emergent property of interactions among environmental forcing and the biological organization of migrating communities. Although commonly described as a mechanism of carbon transport, the magnitude, depth, and efficiency of active carbon transfer depend on which species are present, their relative abundance and biomass,

their functional traits, and their migration behaviour, all operating within a given physical and biogeochemical environment. Species identity and community composition shape the available biological strategies, whereas functional traits influence how these strategies translate biomass into respiration, excretion, egestion, mortality, and trophic transfer at depth. Thus, changes in biodiversity can alter the pathways and efficiency of active carbon transport even when total migrant biomass remains unchanged. Every component of the AMP, from carbon acquisition in surface waters to its release or storage at depth, is mediated by species-specific physiological and ecological traits. Consequently, changes in marine biodiversity translate into changes in the magnitude and pathways of ocean carbon sequestration. Notably, this conceptual statement remains a hypothesis that requires further empirical confirmation and supporting evidence.

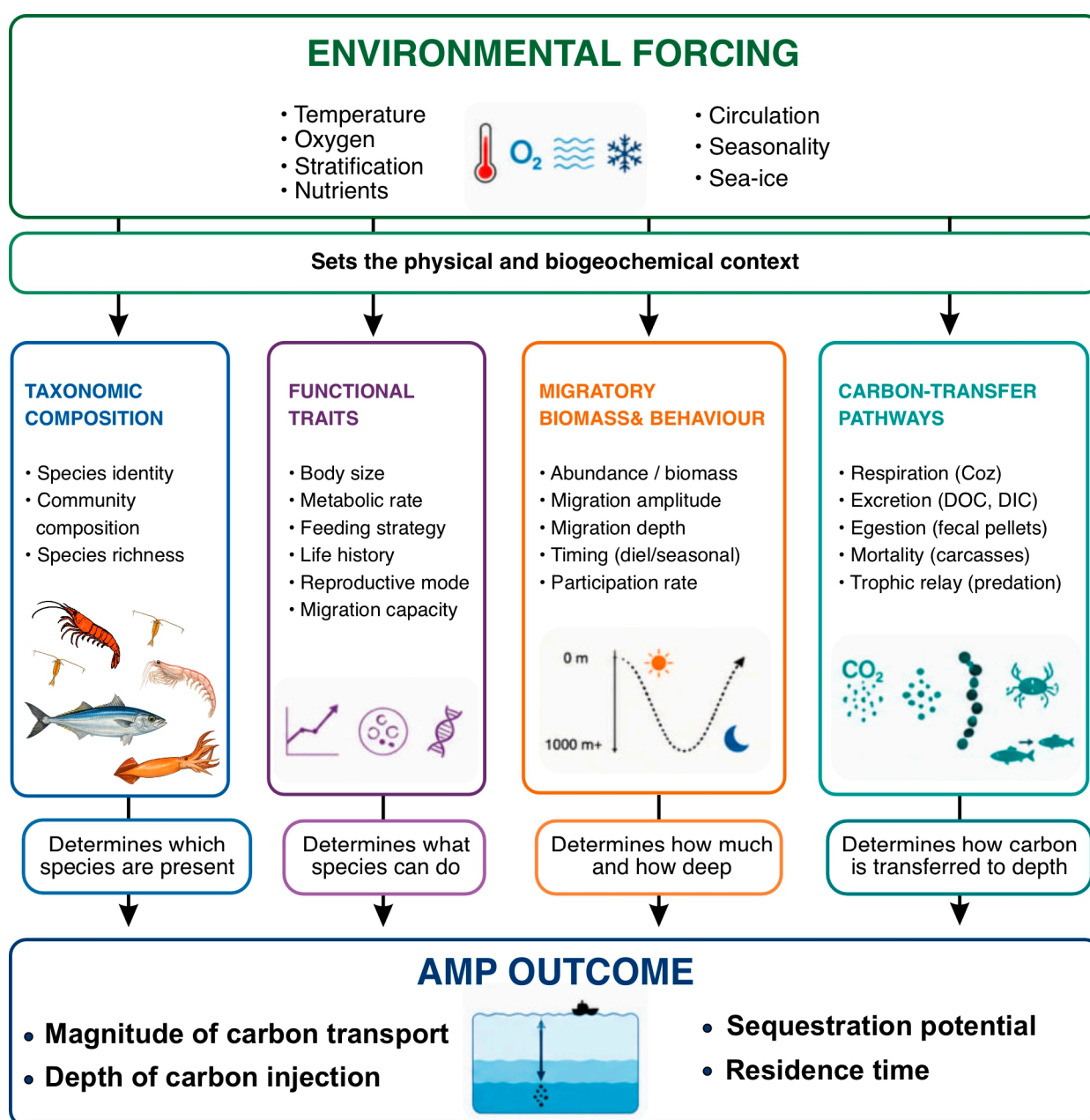


Figure 7. The pulse of the pelagic: biodiversity's role in translating environmental forcing into the AMP.

The different dimensions of biodiversity contribute to the AMP in distinct but interconnected ways. Species richness influences the number of potentially available bio-

logical strategies, but species identity and community composition are often more directly relevant to carbon transfer because taxa differ markedly in body size, migration depth, metabolic rate, feeding mode, and life history. Copepods, krill, decapod shrimps, gelatinous zooplankton, fishes, and cephalopods therefore contribute through different combinations of respiratory, egestive, mortality, and trophic-relay pathways. Changes in the relative abundance of these taxa can alter AMP efficiency without any corresponding change in species richness. Conversely, loss of species may have relatively little effect if functionally similar taxa compensate for their contribution, whereas the loss of a functionally distinctive migrant may have disproportionately large consequences. Copepods dominate global biomass and underpin respiratory export, fecal pellet production, and the seasonal lipid pump. Krill amplify export through their large biomass and rapidly sinking fecal pellets. Decapod shrimps may represent a much larger component of active transport than currently recognized, particularly in the deep pelagic ocean where their abundance remains poorly constrained. Gelatinous zooplankton generate episodic but potentially enormous export events through salp blooms and jelly-falls, whereas mesopelagic fishes and cephalopods transport carbon across multiple trophic levels through respiration, predation, and mortality. The efficiency of the AMP greatly depends on the changing balance among these diverse biological vectors.

Functional diversity is expected to determine how the biological composition of a migrant community is translated into carbon transport. Body size, metabolic rate, migration amplitude, feeding strategy, reproductive behavior, and life-history traits all regulate the partitioning of carbon among respiratory, excretory, egestive, mortality, and trophic-relay pathways. Consequently, communities composed of organisms with similar biomass may differ substantially in their contribution to carbon transport if their functional traits differ. Species-rich communities do not necessarily generate proportionally greater active carbon transport if additional species contribute little biomass or have similar functional roles. Functional redundancy may therefore buffer the AMP against some losses of species, whereas changes in the abundance of functionally distinctive migrants may produce disproportionate effects.

Environmental forcing interacts with these biological dimensions to regulate the regional expression of the AMP. High-latitude oceans are dominated by lipid-rich copepods and krill that maximize seasonal carbon export through diapause and large fecal pellets. Subtropical gyres rely primarily on metabolic transport by smaller migrators adapted to nutrient-poor environments. Oxygen minimum zones favor hypoxia-tolerant specialists capable of injecting carbon to greater depths, whereas productive upwelling systems combine intense passive export with large migratory biomass. These examples illustrate that regional AMP efficiency cannot be attributed to physical forcing or biodiversity alone; rather, it emerges from their interaction with community composition, biomass, functional traits, and migration behaviour.

Climate change can modify the AMP through both direct physical and biogeochemical effects and indirect effects mediated by biodiversity. Ocean warming, deoxygenation, acidification, altered stratification, and changing seasonality directly modify the environmental conditions governing migration, metabolism, remineralization, and carbon transfer, while simultaneously altering species distributions, community composition, body-size structure, trophic interactions, and migratory behaviour. The resulting response, therefore, depends on the interaction between environmental forcing and biological reorganization. Changes in species identity and relative abundance can alter carbon-transfer pathways even when total migrant biomass remains stable, whereas changes in biomass or migration depth can modify fluxes even without major changes in species richness.

Several major uncertainties in AMP assessments should be noted. First, biomass estimates for important migrants (pelagic shrimps, gelatinous zooplankton, cephalopods, and mesopelagic fishes) are poorly constrained. Second, species identity and community composition are often insufficiently resolved, making it difficult to determine whether changes in biomass represent changes in the abundance of the same functional groups or replacement by organisms with different ecological traits. Furthermore, respiratory, excretory, egestive, mortality, and trophic-relay fluxes are generally assessed separately in spite of their biological coupling. Finally, global and basin-scale estimates of AMP insufficiently represent species-specific traits, functional diversity, and behavioural variability, and rely on simplified assumptions regarding migration behavior, community composition, and metabolic rates.

Several knowledge gaps deserve particular attention:

- Quantifying the biomass and migration behavior of poorly sampled taxa, especially deep-pelagic decapods, gelatinous zooplankton, and cephalopods.
- Resolving species identity and community composition together with biomass, rather than treating migrant assemblages as homogeneous functional groups.
- Resolving species-specific metabolic rates under natural environmental conditions, including interactive responses to warming, hypoxia, and acidification.
- Better constraining mortality pathways and trophic relay, which remain among the least quantified components of the AMP.
- Incorporating seasonal, ontogenetic, benthopelagic, and reproductive migrations into carbon budget estimates alongside DVM.
- Quantifying functional diversity and identifying functionally distinctive versus redundant migrant taxa to determine when changes in species composition are likely to alter AMP efficiency.
- Integrating biodiversity explicitly into Earth System Models using trait-based rather than biomass-based approaches.

Ultimately, understanding and predicting the AMP requires moving beyond carbon fluxes and total biomass toward a mechanistic representation of the biological communities that generate active carbon transfer. Our synthesis indicates a hierarchical but interactive pathway in which taxonomic composition and species identity shape the pool of available biological strategies; functional traits govern how organisms acquire, process, and transport carbon; migratory biomass and behaviour influence the magnitude and depth of transport; and respiration, excretion, egestion, mortality, and trophic relay underly the ultimate fate of that carbon. Environmental forcing acts across all stages by modifying species distributions, physiological performance, migration behaviour, and the efficiency of carbon processing. Thus, AMP efficiency is best conceptualized as the outcome of interactions among taxonomic composition → functional traits → migratory biomass and behaviour → carbon-transfer pathways, all embedded within environmental forcing (Figure 7). This framework also explains why changes in species richness or biomass alone may be poor predictors of AMP change: the biogeochemical consequences of biodiversity or biomass loss or gain depend on which species are affected, what functional roles they perform, and how their abundance and behaviour change. The author synthesizes these insights by proposing that while confirming these multi-layered interactions requires further empirical verification and extended analyses, integrating them into observations and Earth System Models will provide a more mechanistic basis for predicting how marine biodiversity and environmental change will reshape the biological carbon pump.

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References

1. Chavez, F.P.; Messié, M.; Pennington, J.T. Marine primary production in relation to climate variability and change. *Annu. Rev. Mar. Sci.* **2011**, *3*, 227–260.
2. DeVries, T.; Weber, T. The export and fate of organic matter in the ocean: New constraints from combining satellite and in situ data. *Glob. Biogeochem. Cycles* **2017**, *31*, 535–555.
3. Iversen, M.H. Carbon export in the ocean: A biologist's perspective. *Annu. Rev. Mar. Sci.* **2023**, *15*, 357–381.
4. Ricour, F.; Guidi, L.; Gehlen, M.; DeVries, T.; Legendre, L. Century-scale carbon sequestration flux throughout the ocean by the biological pump. *Nat. Geosci.* **2023**, *16*, 1105–1113.
5. Martin, J.H.; Knauer, G.A.; Karl, D.M.; Broenkow, W.W. VERTEX: Carbon cycling in the northeast Pacific. *Deep Sea Res. Part A Oceanogr. Res. Pap.* **1987**, *34*, 267–285.
6. Turner, J.T. Zooplankton fecal pellets, marine snow, phytodetritus and the ocean's biological pump. *Prog. Oceanogr.* **2015**, *130*, 205–248.
7. Boyd, P.W.; Claustre, H.; Levy, M.; Siegel, D.A.; Weber, T. Multi-faceted particle pumps drive carbon sequestration in the ocean. *Nature* **2019**, *568*, 327–335. <https://doi.org/10.1038/s41586-019-1098-2>.
8. Stukel, M.R.; Décima, M.; Kelly, T.B.; Landry, M.R.; Nodder, S.D.; Ohman, M.D.; Yingling, N. Relationships between plankton size spectra, net primary production, and the biological carbon pump. *Glob. Biogeochem. Cycles* **2024**, *38*, e2023GB007994.
9. Bach, L.T.; Stange, P.; Taucher, J.; Achterberg, E.P.; Alguero-Muñiz, M.; Horn, H.; Esposito, M.; Riebesell, U. The influence of plankton community structure on sinking velocity and remineralization rate of marine aggregates. *Glob. Biogeochem. Cycles* **2019**, *33*, 971–994.
10. Nowicki, M.; DeVries, T.; Siegel, D.A. Quantifying the carbon export and sequestration pathways of the ocean's biological carbon pump. *Glob. Biogeochem. Cycles* **2022**, *36*, e2021GB007083.
11. Longhurst, A.R. *The Ecology of the Seas*; Academic Press: London, UK, 1976; pp. 116–137.
12. Steinberg, D.K.; Landry, M.R. Zooplankton and the ocean carbon cycle. *Annu. Rev. Mar. Sci.* **2017**, *9*, 413–444.
13. Vereshchaka, A.; Abyzova, G.; Lunina, A.; Musaeva, E.; Sutton, T. A novel approach reveals high zooplankton standing stock deep in the sea. *Biogeosciences* **2016**, *13*, 6261–6271.
14. Vereshchaka, A.; Abyzova, G.; Lunina, A.; Musaeva, E. The deep-sea zooplankton of the North, Central, and South Atlantic: Biomass, abundance, diversity. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **2017**, *137*, 89–101.
15. Vereshchaka, A.L.; Lunina, A.A.; Sutton, T. Assessing deep-pelagic shrimp biomass to 3000 m in the Atlantic Ocean and ramifications of upscaled global biomass. *Sci. Rep.* **2019**, *9*, 5946.
16. Hays, G.C. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* **2003**, *503*, 163–170.
17. Bandara, K.; Varpe, Ø.; Wijewardene, L.; Tverberg, V.; Eiane, K. Two hundred years of zooplankton vertical migration research. *Biol. Rev.* **2021**, *96*, 1547–1589.
18. Steinberg, D.K.; Carlson, C.A.; Bates, N.R.; Goldthwait, S.A.; Madin, L.P.; Michaels, A.F. Zooplankton vertical migration and the active transport of dissolved organic and inorganic carbon in the Sargasso Sea. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **2000**, *47*, 137–158.
19. Giering, S.L.C.; Sanders, R.; Lampitt, R.S.; Anderson, T.R.; Tamburini, C.; Boutrif, M.; Zubkov, M.V.; Marsay, C.M.; Henson, S.A.; Saw, K.; et al. Reconciliation of the carbon budget in the ocean's twilight zone. *Nature* **2014**, *507*, 480–483.
20. Calbet, A. Life after death in the pelagic: Non-predatory zooplankton mortality and the “ghost carbon pump”. *Limnol. Oceanogr. Lett.* **2026**, *11*, e70130.
21. Cavan, E.L.; Belcher, A.; Atkinson, A.; Hill, S.L.; Kawaguchi, S.; McCormack, S.; Meyer, B.; Nicol, S.; Tarling, G.A.; Boyd, P.W. The importance of Antarctic krill in biogeochemical cycles. *Nat. Commun.* **2019**, *10*, 4742.

22. Clements, D.J.; Stamieszkin, K.; Bianchi, D.; Blanco-Bercial, L.; Record, N.R.; Rodriguez-Perez, R.B.; Maas, A.E. Active carbon transport by diel vertical migrating zooplankton: Calculated and modeled, but never measured. *Annu. Rev. Mar. Sci.* **2025**, *18*, 301–326.
23. Mowatt-Larssen, T.; Steinberg, D.K.; Latour, R.; Muffelman, S.; Montalvo, M.; Nolan, M.; Hilton, E. Ontogenetic vertical migration, seasonality, and long-term increase in mesopelagic fish larvae in the subtropical North Atlantic Ocean. *Mar. Ecol. Prog. Ser.* **2025**, *769*, 107–124.
24. Visser, A.W.; Grønning, J.; Jónasdóttir, S.H. *Calanus hyperboreus* and the lipid pump. *Limnol. Oceanogr.* **2017**, *62*, 1155–1165.
25. Sahoo, I.; Kondamudi, R.B.; Tatiparthi, S.; Siddela, D.V. Seasonal variation in the diversity of holoplankton and meroplankton in relation to primary productivity and physicochemical parameters in the nearshore regions of the Visakhapatnam Coast, India. *Adv. Oceanogr. Limnol.* **2025**, *16*, 1.
26. Denda, A.; Mohn, C.; Wehrmann, H.; Christiansen, B. Microzooplankton and meroplanktonic larvae at two seamounts in the subtropical and tropical northeastern Atlantic. *J. Mar. Biol. Assoc. U. K.* **2017**, *97*, 1–27.
27. Vereshchaka, A.L. Macroplankton in the near-bottom layer of continental slopes and seamounts. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **1995**, *42*, 1639–1668.
28. Omori, M.; Konagaya, T.; Noya, K. History and present status of the fishery of *Sergestes lucens* (Penaeidea, Decapoda, Crustacea) in Suruga Bay, Japan. *J. Cons. Int. Explor. Mer* **1973**, *35*, 61–77.
29. Vereshchaka, A.L.; Anokhina, L.L. Composition and dynamics of the Black Sea benthopelagic plankton and its contribution to the near-shore plankton communities. *PLoS ONE* **2014**, *9*, e99595.
30. Vereshchaka, A.L.; Anokhina, L.L. Biodiversity and diel variation of the benthohyponeuston: A case study of the northeastern Black Sea. *Estuar. Coast. Shelf Sci.* **2015**, *167*, 487–498.
31. Giangrande, A. Polychaete reproductive patterns, life cycles and life histories: An overview. *Oceanogr. Mar. Biol. Annu. Rev.* **1997**, *35*, 323–386.
32. Metaxas, A.; Scheibling, R.E. Rapid egg transport following coral mass spawning at Ningaloo Reef, Western Australia. *Bull. Mar. Sci.* **2016**, *92*, 529–544.
33. Burd, A.B. Modeling the vertical flux of organic carbon in the global ocean. *Annu. Rev. Mar. Sci.* **2024**, *16*, 135–161.
34. Ochoa, J.; Maske, H.; Sheinbaum, J.; Candela, J. Diel and lunar cycles of vertical migration extending to below 1000 m in the ocean and the vertical connectivity of depth-tiered populations. *Limnol. Oceanogr.* **2013**, *58*, 1207–1214.
35. Isla, A.; Scharek, R.; Latasa, M. Zooplankton diel vertical migration and contribution to deep active carbon flux in the north-western Mediterranean. *J. Mar. Syst.* **2015**, *143*, 86–97.
36. Bianchi, D.; Stock, C.; Galbraith, E.D.; Sarmiento, J.L. Diel vertical migration: Ecological controls and impacts on the biological pump in a one-dimensional ocean model. *Glob. Biogeochem. Cycles* **2013**, *27*, 478–491.
37. Vereshchaka, A. Navigating the zooplankton realm: Oceans of diversity beneath the sea surface. *Diversity* **2024**, *16*, 717.
38. Feng, M.; Lin, S.; Zhang, W.; Wang, C.; Liu, H.; Cheung, S.; Stukel, M.R.; Irving, J.P.; Li, N. Micro-/meso-scale distinction and horizontal migration of tintinnid (*Ciliophora*: Tintinnida) assemblages in three regions around the North Pacific Ocean. *Front. Mar. Sci.* **2022**, *9*, 863549.
39. Briones-Fourzán, P.; Hendrickx, M.E. Ecology and diversity of marine decapod crustaceans. *Diversity* **2022**, *14*, 614.
40. Wang, S.; Zhang, F.; Li, Q.; Zang, W.; Chi, X.; Tao, Z.; Sun, S. Zooplankton diel vertical migration and its mediated active carbon flux in the South China Sea under the influence of mesoscale eddies. *J. Plankton Res.* **2025**, *47*, fbaf031.
41. Pinti, J.; Jónasdóttir, S.H.; Record, N.R.; Visser, A.W. The global contribution of seasonally migrating copepods to the biological carbon pump. *Limnol. Oceanogr.* **2023**, *68*, 1147–1160.
42. Bradford-Grieve, J.M.; Nodder, S.D.; Jillett, J.B.; Currie, K.; Lassey, K.R. Potential contribution that the copepod *Neocalanus tonsus* makes to downward carbon flux in the Southern Ocean. *J. Plankton Res.* **2001**, *23*, 963–975.
43. Vereshchaka, A.L.; Anokhina, L.L. The neritic benthopelagic fauna: Which factors explain nocturnal distribution better? *Cont. Shelf Res.* **2017**, *145*, 43–58.
44. Vereshchaka, A.L.; Anokhina, L.L. The benthoneuston of the Black Sea: Composition and environmental factors influencing its nocturnal dynamic. *Cont. Shelf Res.* **2017**, *140*, 60–74.
45. Tarling, G.A.; Johnson, M.L. Satiation gives krill that sinking feeling. *Curr. Biol.* **2006**, *16*, R83–R84.
46. Bernard, K.S.; Tarling, G.A.; Atkinson, A.; Cavan, E.L.; Cleary, A.C.; Dalpadado, P.; Díaz-Astudillo, M.; Dorman, J.; Edwards, M.; Färber-Lorda, J. Ecological roles, climate-driven responses, and critical knowledge gaps of krill in the global ocean. *ICES J. Mar. Sci.* **2026**, *83*, fsag090.

47. Werner, T.; Huenerlage, K.; Verheye, H.; Buchholz, F. Thermal constraints on the respiration and excretion rates of krill, *Euphausia hansenii* and *Nematoscelis megalops*, in the northern Benguela upwelling system off Namibia. *Afr. J. Mar. Sci.* **2012**, *34*, 391–399.
48. Watkins, J. Aggregation and vertical migration. In *Krill: Biology, Ecology and Fisheries*; Everson, I., Ed.; Blackwell Science: Oxford, UK, 2000; pp. 80–102.
49. Omori, M. The biology of pelagic shrimps in the ocean. In *Advances in Marine Biology*; Russell, F.S., Yonge, M., Eds.; Academic Press: London, UK, 1975; Volume 12, pp. 233–324.
50. Kerry, C.R.; Exeter, O.M.; Witt, M.J. Monitoring global fishing activity in proximity to seamounts using automatic identification systems. *Fish Fish.* **2022**, *23*, 733–749.
51. Pitt, K.A.; Duarte, C.M.; Lucas, C.H.; Sutherland, K.R.; Condon, R.H.; Mianzan, H.; Purcell, J.E.; Robinson, K.L.; Uye, S.-I. Jellyfish body plans provide allometric advantages beyond low carbon content. *PLoS ONE* **2013**, *8*, e72683.
52. Lucas, C.H.; Jones, D.O.B.; Hollyhead, C.J.; Condon, R.H.; Duarte, C.M.; Graham, W.M.; Robinson, K.L.; Pitt, K.A.; Schildhauer, M.; Regetz, J. Gelatinous zooplankton biomass in the global oceans: Geographic variation and environmental drivers. *Glob. Ecol. Biogeogr.* **2014**, *23*, 701–714.
53. Ishak, N.H.A.; Motoki, K.; Miyamoto, H.; Fujii, T.; Taniuchi, Y.; Kakehi, S.; Kuroda, H.; Setou, T.; Takahashi, K. Basin-scale distribution of salps and doliolids in the transition region of the North Pacific Ocean in summer: Drivers of bloom occurrence and effect on the pelagic ecosystem. *Prog. Oceanogr.* **2022**, *204*, 102793.
54. Luo, J.Y.; Condon, R.H.; Stock, C.A.; Duarte, C.M.; Lucas, C.H.; Pitt, K.A.; Cowen, R.K. Gelatinous zooplankton-mediated carbon flows in the global oceans: A data-driven modeling study. *Glob. Biogeochem. Cycles* **2020**, *34*, e2020GB006704.
55. Martin, B.; Koppelman, R.; Kassatov, P. Ecological relevance of salps and doliolids in the northern Benguela Upwelling System. *J. Plankton Res.* **2017**, *39*, 290–304.
56. Perissinotto, R.; Pakhomov, E.A. Contribution of salps to carbon flux of the marginal ice zone of the Lazarev Sea, Southern Ocean. *Mar. Biol.* **1998**, *131*, 25–32.
57. Vereshchaka, A.L. Features of the microscale distribution of the gelatinous macroplankton in the Black Sea off Gelendzhik (August 2000). *Oceanology* **2002**, *42*, 83–90.
58. Vereshchaka, A.L. Small-scale vertical distribution and behavior of the ctenophore *Beroe* in the Black Sea off Gelendzhik. *Oceanology* **2002**, *42*, 811–814.
59. Kaartvedt, S.; Titelman, J.; Røstad, A.; Klevjer, T.A. Beyond the average: Diverse individual migration patterns in a population of mesopelagic jellyfish. *Limnol. Oceanogr.* **2011**, *56*, 2189–2199.
60. Lüsckow, F.; Bahl, A.A.; Décima, M.; Steinberg, D.K.; Pakhomov, E.A. Reproductive biology, elemental composition and diel vertical migration of the cosmopolitan warm-temperate pelagic tunicate *Soestia zonaria*. *J. Plankton Res.* **2024**, *46*, 72–85.
61. Pugh, P.R. The diel migrations and distributions within a mesopelagic community in the North East Atlantic. 7. Siphonophores. *Prog. Oceanogr.* **1984**, *13*, 461–489.
62. Gjøsæter, J.; Kawaguchi, K. A review of the world resources of mesopelagic fish. *FAO Fish. Tech. Pap.* **1980**, *193*, 1–151.
63. Lam, V.; Pauly, D. Mapping the global biomass of mesopelagic fishes. *Sea Around US Proj. Newsl.* **2005**, *30*, 4–7.
64. 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. *Nat. Commun.* **2014**, *5*, 3271.
65. Davison, P.C.; Checkley, D.M., Jr.; Koslow, J.A.; Barlow, J. Carbon export mediated by mesopelagic fishes in the northeast Pacific Ocean. *Prog. Oceanogr.* **2013**, *116*, 14–30.
66. Saba, G.K.; Burd, A.B.; Dunne, J.P.; Hernández-León, S.; Martin, A.H.; Rose, K.A.; Salisbury, J.; Steinberg, D.K.; Trueman, C.N.; Wilson, R.W.; et al. Toward a better understanding of fish-based contribution to ocean carbon flux. *Limnol. Oceanogr.* **2021**, *66*, 1639–1664.
67. Aksnes, D.L.; Løtvedt, A.S.; Lindemann, C.; Calleja, M.L.; Morán, X.A.G.; Kaartvedt, S.; Thingstad, T.F. Effects of migrating mesopelagic fishes on the biological carbon pump. *Mar. Ecol. Prog. Ser.* **2023**, *717*, 107–126.
68. Watanabe, H.; Kubodera, T.; Moku, M.; Kawaguchi, K. Diel vertical migration of squid in the warm core ring and cold water masses in the transition region of the western North Pacific. *Mar. Ecol. Prog. Ser.* **2006**, *315*, 187–197.
69. Arkhipkin, A.I.; Hendrickson, L.C.; Payá, I.; Pierce, G.J.; Roa-Ureta, R.H.; Robin, J.P.; Winter, A. Stock assessment and management of cephalopods: Advances and challenges for short-lived fishery resources. *ICES J. Mar. Sci.* **2021**, *78*, 714–730.
70. Rodhouse, P.G.; Nigmatullin, C.M. Role as consumers. *Philos. Trans. Biol. Sci.* **1996**, *351*, 1003–1022.

71. Arkhipkin, A.I.; Nigmatullin, C.M.; Parkyn, D.C.; Winter, A.; Csirke, J. High seas fisheries: The Achilles' heel of major straddling squid resources. *Rev. Fish Biol. Fish.* **2023**, *33*, 453–474.
72. Hoving, H.J.T.; Bush, S.L.; Haddock, S.H.D.; Robison, B.H. Bathyal feasting: Post-spawning squid as a source of carbon for deep-sea benthic communities. *Proc. R. Soc. B Biol. Sci.* **2017**, *284*, 20172096.
73. Bahlburg, D.; Hüppe, L.; Böhrer, T.; Thorpe, S.E.; Murphy, E.J.; Berger, U.; Meyer, B. Plasticity and seasonality of the vertical migration behaviour of Antarctic krill using acoustic data from fishing vessels. *R. Soc. Open Sci.* **2023**, *10*, 230520.
74. Seuront, L. What do the geometric and stochastic properties of swimming behaviour have to teach us about zooplankton behavioural ecology? *J. Plankton Res.* **2025**, *47*, fbae075.
75. Vedenin, A.; Kulagin, D.; Musaeva, E.; Vereshchaka, A. The Southern Polar Front as a key to mesoplankton migratory behavior. *Sci. Rep.* **2020**, *10*, 14046.
76. Maszczyk, P.; Zebrowski, M.L.; Lee, J.S.; Wang, Y.; Yang, Z.; Wierzbicka, M.; Rutkowska, K.M.; Liu, Q.; Babkiewicz, E. Uneven resources, uneven fish: Zooplankton patchiness drives variability in fish growth and metabolism. *Proc. R. Soc. B Biol. Sci.* **2026**, *293*, 20260119.
77. Christiansen, S.; Bråthen, M.P.; Moksnes, F.L.; Schmedling, C.A.; Thorsby, S.J.; Titelman, J.; Kaartvedt, S. Extensive avoidance behaviour of krill from predators and nets. *ICES J. Mar. Sci.* **2024**, *81*, 1764–1773.
78. Vedenin, A.A.; Musaeva, E.I.; Zasko, D.N.; Vereshchaka, A.L. Zooplankton communities in the Drake Passage through environmental boundaries: A snapshot of 2010, early spring. *PeerJ* **2019**, *7*, e7994.
79. Vereshchaka, A.; Musaeva, E.; Lunina, A. Biogeography of the Southern Ocean: Environmental factors driving mesoplankton distribution south of Africa. *PeerJ* **2021**, *9*, e11411.
80. Vedenin, A.; Musaeva, E.; Vereshchaka, A. Three-dimensional distribution of mesoplankton assemblages in the Central Atlantic. *Glob. Ecol. Biogeogr.* **2022**, *31*, 1345–1365.
81. Vinogradov, M.E.; Vereshchaka, A.L.; Shushkina, E.A. The vertical structure of zooplankton in the oligotrophic areas of the North Atlantic and the effect of hydrothermal fields. *Oceanology* **1996**, *36*, 64–71.
82. Orlov, A.M. Contemporary ichthyological and fisheries research of deepwater fish: New advances, current challenges, and future developments. *J. Mar. Sci. Eng.* **2022**, *10*, 166. <https://doi.org/10.3390/jmse10020166>.
83. Orlov, A.M.; Tuponogov, V.N. Past and present ichthyological and fisheries research at the Emperor Seamounts: Lessons from the Soviet/Russian experience in the Central North Pacific. *Rev. Fish. Sci. Aquac.* **2026**, *34*, 94–111. <https://doi.org/10.1080/23308249.2025.2523058>.
84. Strand, E.; Boms, C.; Bagoien, E.; Knutsen, T.; Arnesen, H.; Mozfar, B. Comparison of two multiple plankton samplers: MOCNESS and Multinet Mammoth. *Limnol. Oceanogr. Methods* **2022**, *20*, 595–604.
85. Long, A.P.; O'Donnell, C.; Haberland, D.; Lawton, C.; Doyle, T.K. A novel platform for monitoring gelatinous mesozooplankton: The high-speed Gulf VII sampler quantifies gelatinous mesozooplankton similar to a ring net. *Limnol. Oceanogr. Methods* **2020**, *18*, 696–706.
86. Vereshchaka, A.; Anokhina, L.; Kulagin, D.; Lunina, A. Precision of mesoplankton sampling: A case study based on three net series in the South Atlantic and in the Black Sea. *Mar. Environ. Res.* **2023**, *183*, 105848.
87. Vereshchaka, A.L.; Vinogradov, G.M. Visual observations of the vertical distribution of plankton throughout the water column above Broken Spur vent field, Mid-Atlantic Ridge. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **1999**, *46*, 1615–1632.
88. Stemmann, L.; Youngbluth, M.; Robert, K.; Hosia, A.; Picheral, M.; Paterson, H.; Ibanez, F.; Guidi, L.; Lombard, F.; Gorsky, G. Global zoogeography of fragile macrozooplankton in the upper 100–1000 m inferred from the Underwater Video Profiler. *ICES J. Mar. Sci.* **2008**, *65*, 433–442.
89. Kiko, R.; Picheral, M.; Antoine, D.; Babin, M.; Berline, L.; Biard, T.; Boss, E.; Brandt, P.; Carlotti, F.; Christiansen, S.; et al. A global marine particle size distribution dataset obtained with the Underwater Vision Profiler 5. *Earth Syst. Sci. Data* **2022**, *14*, 3741–3768.
90. Laget, M.; Accardo, A.; Picheral, M.; Catalano, C.; Guidi, L.; Biard, T. Combining the Underwater Vision Profiler 6 with sediment traps to measure in situ velocity of marine particles. *Limnol. Oceanogr. Methods* **2026**, *24*, e70052.
91. Vinogradov, G.M.; Vereshchaka, A.L.; Musaeva, E.I.; Dyakonov, V.Y. Vertical zooplankton distribution over the Porcupine Abyssal Plain (Northeast Atlantic) in the summer of 2002. *Oceanology* **2003**, *43*, 512–523.
92. Pantiukhin, D.; Verhaegen, G.; Kraan, C.; Jerosch, K.; Neitzel, P.; Hoving, H.J.T.; Havermans, C. Optical observations and spatio-temporal projections of gelatinous zooplankton in the Fram Strait, a gateway to a changing Arctic Ocean. *Front. Mar. Sci.* **2023**, *10*, 987700.

93. Lindeque, P.K.; Parry, H.E.; Harmer, R.A.; Somerfield, P.J.; Atkinson, A. Next generation sequencing reveals the hidden diversity of zooplankton assemblages. *PLoS ONE* **2013**, *8*, e81327.
94. Bachy, C.; López-García, P.; Vereshchaka, A.; Moreira, D. Diversity and vertical distribution of microbial eukaryotes in snow, sea ice and seawater near the North Pole at the end of the polar night. *Front. Microbiol.* **2011**, *2*, 106.
95. Lara, E.; Moreira, D.; Vereshchaka, A.; López-García, P. Pan-oceanic distribution of new highly diverse clades of deep-sea diplomonads. *Environ. Microbiol.* **2009**, *11*, 47–55.
96. López-García, P.; Vereshchaka, A.; Moreira, D. Eukaryotic diversity associated with carbonates and the fluid–seawater interface in the Lost City hydrothermal field. *Environ. Microbiol.* **2007**, *9*, 546–554.
97. Sahu, A.; Kumar, N.; Singh, C.P.; Singh, M. Environmental DNA (eDNA): A powerful technique for biodiversity conservation. *J. Nat. Conserv.* **2023**, *71*, 126325.
98. Van Vu, S.; Putra, A.; Aini, S.; Abedin, I.; Lee, S.R.; Kim, A.R.; Kang, H.-E.; Le, T.T.; Nguyen, H.H.; Van Doan, H.; et al. Unravelling the Population Genetic Dynamics of the Ivory Snail (*Babylonia areolata*) in Vietnam: Guiding Sustainable Aquaculture Development. *Thalass. Int. J. Mar. Sci.* **2026**, *42*, 107.
99. Keller, I.; Alexander, J.M.; Holderegger, R.; Edwards, P.J. Widespread phenotypic and genetic divergence along altitudinal gradients in animals. *J. Evol. Biol.* **2013**, *26*, 2527–2543.
100. Feng, Y.; Sun, D.; Shao, Q.; Fang, C.; Wang, C. Mesozooplankton biodiversity, vertical assemblages, and diel migration in the western tropical Pacific Ocean revealed by eDNA metabarcoding and morphological methods. *Front. Mar. Sci.* **2022**, *9*, 1004410.
101. Lenz, P.H.; Lieberman, B.; Cieslak, M.C.; Roncalli, V.; Hartline, D.K. Transcriptomics and metatranscriptomics in zooplankton: Wave of the future? *J. Plankton Res.* **2021**, *43*, 3–9.
102. Williams, R.L.; Wakeham, S.; McKinney, R.; Wishner, K.F. Trophic ecology and vertical patterns of carbon and nitrogen stable isotopes in zooplankton from oxygen minimum zone regions. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **2014**, *90*, 36–47.
103. Rey, F.; Melo, T.; Lopes, D.; Couto, D.; Marques, F.; Domingues, M.R. Applications of lipidomics in marine organisms: Progress, challenges and future perspectives. *Mol. Omics* **2022**, *18*, 357–386.
104. Stanton, T.K. 30 years of advances in active bioacoustics: A personal perspective. *Methods Oceanogr.* **2012**, *1*, 49–77.
105. Wiebe, P.H.; Benfield, M.C. From the Hensen net toward four-dimensional biological oceanography. *Prog. Oceanogr.* **2003**, *56*, 7–136.
106. Lee, W.-J.; Chu, D.; Dosso, S.E. How much more informative are broadband compared to narrowband echoes for biological interpretation? *J. Acoust. Soc. Am.* **2019**, *146*, 2899.
107. van Haren, H.; Compton, T.J. Diel vertical migration in deep-sea plankton is finely tuned to latitudinal and seasonal day length. *PLoS ONE* **2013**, *8*, e64435.
108. Cisewski, B.; Hátún, H.; Kristiansen, I.; Hansen, B.; Larsen, K.M.H.; Eliassen, S.K.; Jacobsen, J.A. Vertical migration of pelagic and mesopelagic scatterers from ADCP backscatter data in the southern Norwegian Sea. *Front. Mar. Sci.* **2021**, *7*, 542386.
109. Chun, S.; La, H.S.; Son, W.; Kim, Y.C.; Cho, K.H.; Yang, E.J. Detection method for diel vertical migration pattern using 2D cross-correlation with ADCP backscatter time-series data. *Methods Ecol. Evol.* **2022**, *13*, 1475–1487.
110. Cisewski, B.; Strass, V.H.; Rhein, M.; Krägfesky, S. Seasonal variation of diel vertical migration of zooplankton from ADCP backscatter time series data in the Lazarev Sea, Antarctica. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **2010**, *57*, 78–94.
111. Skaret, G.; Johansen, G.O.; Johnsen, E.; Fall, J.; Fiksen, Ø.; Englund, G.; Fauchald, P.; Gjøsæter, H.; Macaulay, G.J.; Johannesen, E. Diel vertical movements determine spatial interactions between cod, pelagic fish and krill on an Arctic shelf bank. *Mar. Ecol. Prog. Ser.* **2020**, *638*, 13–23.
112. Bertrand, A.; Ballón, M.; Chaigneau, A. Acoustic observation of living organisms reveals the upper limit of the oxygen minimum zone. *PLoS ONE* **2010**, *5*, e10330.
113. Riquelme-Bugueño, R.; Pérez-Santos, I.; Alegría, N.; Vargas, C.A.; Urbina, M.A.; Escibano, R. Diel vertical migration into anoxic and high- $p\text{CO}_2$ waters: Acoustic and net-based krill observations in the Humboldt Current. *Sci. Rep.* **2020**, *10*, 17181.
114. Beltran, R.S.; Kilpatrick, A.M.; Picardi, S.; Abrahms, B.; Barrile, G.M.; Oestreich, W.K.; Smith, J.A.; Czapanskiy, M.F.; Favilla, A.B.; Reisinger, R.R.; et al. Maximizing biological insights from instruments attached to animals. *Trends Ecol. Evol.* **2025**, *40*, 37–46.
115. Hays, G.C.; Scott, R. Global patterns for upper ceilings on migration distance in sea turtles and comparisons with fish, birds and mammals. *Funct. Ecol.* **2013**, *27*, 748–756.
116. Gemmell, B.J.; Colin, S.P.; Costello, J.H. Movement ecology of gelatinous zooplankton: Approaches, challenges and future directions. *J. Exp. Biol.* **2025**, *228*, JEB247987.

117. Watanabe, Y.Y.; Papastamatiou, Y.P. Biologging and biotelemetry: Tools for understanding the lives and environments of marine animals. *Annu. Rev. Anim. Biosci.* **2023**, *11*, 247–267.
118. Pata, P.R.; Hunt, B.P. Harmonizing marine zooplankton trait data toward a mechanistic understanding of ecosystem functioning. *Limnol. Oceanogr.* **2025**, *70*, S8–S27.
119. Baker, K.; Halfter, S.; Scoulding, B.; Swadling, K.M.; Richards, S.A.; Bressac, M.; Sutton, C.A.; Boyd, P.W. Carbon injection potential of the mesopelagic-migrant pump in the Southern Ocean during summer. *Front. Mar. Sci.* **2025**, *12*, 1461723.
120. Drago, L.; Panaiotis, T.; Irisson, J.O.; Babin, M.; Biard, T.; Carlotti, F.; Coppola, L.; Guidi, L.; Hauss, H.; Karp-Boss, L.; et al. Global distribution of zooplankton biomass estimated by in situ imaging and machine learning. *Front. Mar. Sci.* **2022**, *9*, 894372.
121. Peller, T.; Guichard, F.; Altermatt, F. The significance of partial migration for food web and ecosystem dynamics. *Ecol. Lett.* **2023**, *26*, 3–22.
122. Mehner, T.; Kasprzak, P. Partial diel vertical migrations in pelagic fish. *J. Anim. Ecol.* **2011**, *80*, 761–770.
123. Ikeda, T.; Kanno, Y.; Ozaki, K.; Shinada, A. Metabolic rates of epipelagic marine copepods as a function of body mass and temperature. *Mar. Biol.* **2001**, *139*, 587–596.
124. Ikeda, T. Respiration and ammonia excretion by marine metazooplankton taxa: Synthesis toward a global bathymetric model. *Mar. Biol.* **2014**, *161*, 2753–2766.
125. Wikner, J.; Vikström, K.; Verma, A. Regulation of marine plankton respiration: A test of models. *Front. Mar. Sci.* **2023**, *10*, 1134699.
126. Moreno, A.R.; Garcia, C.A.; Larkin, A.A.; Lee, J.A.; Wang, W.L.; Moore, J.K.; Primeau, F.W.; Martiny, A.C. Latitudinal gradient in the respiration quotient and the implications for ocean oxygen availability. *Proc. Natl. Acad. Sci. USA* **2020**, *117*, 22866–22872.
127. Carlson, C.A.; Hansell, D.A. DOM sources, sinks, reactivity, and budgets. In *Biogeochemistry of Marine Dissolved Organic Matter*, 2nd ed.; Hansell, D.A., Carlson, C.A., Eds.; Academic Press: San Diego, CA, USA, 2014; pp. 65–126.
128. Hygum, B.H.; Petersen, J.W.; Søndergaard, M. Dissolved organic carbon released by zooplankton grazing activity—A high-quality substrate pool for bacteria. *J. Plankton Res.* **1997**, *19*, 97–111.
129. Møller, E.F. Production of dissolved organic carbon by sloppy feeding in the copepods *Acartia tonsa*, *Centropages typicus* and *Temora longicornis*. *Limnol. Oceanogr.* **2007**, *52*, 79–84.
130. Saba, G.K.; Steinberg, D.K.; Bronk, D.A. The relative importance of sloppy feeding, excretion, and fecal pellet leaching in the release of dissolved carbon and nitrogen by *Acartia tonsa* copepods. *J. Exp. Mar. Biol. Ecol.* **2011**, *404*, 47–56.
131. Condon, R.H.; Steinberg, D.K.; del Giorgio, P.A.; Bouvier, T.C.; Bronk, D.A.; Graham, W.M.; Ducklow, H.W. Jellyfish blooms result in a major microbial respiratory sink of carbon in marine systems. *Proc. Natl. Acad. Sci. USA* **2011**, *108*, 10225–10230.
132. Saba, G.K.; Steinberg, D.K.; Bronk, D.A. Effects of diet on release of dissolved organic and inorganic nutrients by the copepod *Acartia tonsa*. *Mar. Ecol. Prog. Ser.* **2009**, *386*, 147–161.
133. Thor, P.; Dam, H.G.; Rogers, D.R. Fate of organic carbon released from decomposing copepod fecal pellets in relation to bacterial production and ectoenzymatic activity. *Aquat. Microb. Ecol.* **2003**, *33*, 279–288.
134. Steinberg, D.K.; Stamieszkin, K.; Maas, A.E.; Durkin, C.A.; Passow, U.; Estapa, M.L.; Omand, M.M.; McDonnell, A.M.P.; Karp-Boss, L.; Galbraith, M.; et al. The outsized role of salps in carbon export in the subarctic Northeast Pacific Ocean. *Glob. Biogeochem. Cycles* **2023**, *37*, e2022GB007523.
135. Dagg, M.J.; Jackson, G.A.; Checkley, D.M., Jr. The distribution and vertical flux of fecal pellets from large zooplankton in Monterey Bay and coastal California. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **2014**, *94*, 72–86.
136. Atkinson, A.; Schmidt, K.; Fielding, S.; Kawaguchi, S.; Geissler, P.A. Variable food absorption by Antarctic krill: Relationships between diet, egestion rate and the composition and sinking rates of their fecal pellets. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **2012**, *59*, 147–158.
137. Frangoulis, C.; Belkhiria, S.; Goffart, A.; Hecq, J.H. Dynamics of copepod faecal pellets in relation to a *Phaeocystis*-dominated phytoplankton bloom: Characteristics, production and flux. *J. Plankton Res.* **2001**, *23*, 75–88.
138. Belcher, A.; Iversen, M.; Manno, C.; Henson, S.A.; Tarling, G.A.; Sanders, R. The role of particle-associated microbes in remineralization of fecal pellets in the upper mesopelagic of the Scotia Sea, Antarctica. *Limnol. Oceanogr.* **2016**, *61*, 1049–1064.
139. Iversen, M.H.; Poulsen, L.K. Coprorhexy, coprophagy, and coprochaly in the copepods *Calanus helgolandicus*, *Pseudocalanus elongatus*, and *Oithona similis*. *Mar. Ecol. Prog. Ser.* **2007**, *350*, 79–89.
140. Sampei, M.; Forest, A.; Sasaki, H.; Hattori, H.; Makabe, R.; Fukuchi, M.; Fortier, L. Attenuation of the vertical flux of copepod fecal pellets under Arctic sea ice: Evidence for an active detrital food web in winter. *Polar Biol.* **2009**, *32*, 225–232.

141. 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.; Koppelman, R.; et al. Mesopelagic zone ecology and biogeochemistry—A synthesis. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **2010**, *57*, 1504–1518.
142. Bendtsen, J.; Hilligsøe, K.M.; Hansen, J.L.; Richardson, K. Analysis of remineralisation, lability, temperature sensitivity and structural composition of organic matter from the upper ocean. *Prog. Oceanogr.* **2015**, *130*, 125–145.
143. Longhurst, A.R.; Harrison, W.G. The biological pump: Profiles of plankton production and consumption in the upper ocean. *Prog. Oceanogr.* **1989**, *22*, 47–123.
144. Elliott, D.T.; Tang, K.W. Simple staining method for differentiating live and dead marine zooplankton in field samples. *Limnol. Oceanogr. Methods* **2009**, *7*, 585–594.
145. Hirst, A.G.; Kiørboe, T. Mortality of marine planktonic copepods: Global rates and patterns. *Mar. Ecol. Prog. Ser.* **2002**, *230*, 195–209.
146. Orlov, P.; Pakhomov, E.A. The fate of salp blooms: Decomposition and sinking of salp carcasses. *Mar. Biol.* **2024**, *171*, 85.
147. Lombard, F.; Kiørboe, T. Marine snow originating from appendicularian houses: Age-dependent settling characteristics. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **2010**, *57*, 1304–1313.
148. Saiz, E.; Calbet, A.; Griffell, K. Sex-dependent effects of caloric restriction on copepod ageing. *Sci. Rep.* **2017**, *7*, 12662.
149. Tang, K.W.; Elliott, D.T. Copepod carcasses: Occurrence, fate and ecological importance. In *Copepods: Diversity, Habitat and Behaviour*; Seuront, L., Ed.; Nova Science Publishers: New York, NY, USA, 2014.
150. Skovgaard, A.; Saiz, E. Protistan parasites in marine zooplankton. *Mar. Ecol. Prog. Ser.* **2006**, *327*, 37–49.
151. Vaquer-Sunyer, R.; Duarte, C.M. Thresholds of hypoxia for marine biodiversity. *Proc. Natl. Acad. Sci. USA* **2008**, *105*, 15452–15457.
152. de Juan, C.; Calbet, A.; Saiz, E. Shifts in survival and reproduction after chronic warming enhance the potential of a marine copepod to persist under extreme heat events. *J. Plankton Res.* **2023**, *45*, 751–762.
153. Deschamps, M.M.; Boersma, M.; Gimenez, L. Responses of the mesozooplankton community to marine heatwaves: Challenges and solutions based on a long-term time series. *J. Anim. Ecol.* **2024**, *93*, 1524–1540.
154. Elliott, D.T.; Tang, K.W.; Shields, A.G. Dead in the water: The fate of copepod carcasses in the York River Estuary, Virginia. *Limnol. Oceanogr.* **2010**, *55*, 1821–1834.
155. Franco-Cisterna, B.; Glud, A.; Bristow, L.A.; Rudra, A.; Sanei, H.; Winding, M.H.; Nielsen, T.G.; Glud, R.N.; Stief, P. Sinking krill carcasses as hotspots of microbial carbon and nitrogen cycling in the Arctic. *Front. Mar. Sci.* **2022**, *9*, 1019727.
156. Perharič Bailey, Č.E.; Vodopivec, M.; Herndl, G.J.; Tinta, T.; Ličer, M. Dynamic Sinking and Surface-Area Based Decay Modeling Reduce Estimates of Gelatinous Zooplankton-Mediated Carbon Export to the Deep Sea. *Glob. Biogeochem. Cycles* **2026**, *40*, e2025GB008937.
157. Litvinyuk, D.; Mukhanov, V.; Evstigneev, V. Zooplankton mortality, decomposition, and sedimentation in the Black Sea using vital dye and short-term sediment traps. *J. Mar. Sci. Eng.* **2022**, *10*, 1031.
158. Vinogradov, M.E. Feeding of deep-sea zooplankton. *Rapp. P. V. Réun. Cons. Int. Explor. Mer.* **1962**, *153*, 114–120.
159. Jónasdóttir, S.H.; Visser, A.W.; Richardson, K.; Heath, M.R. Seasonal copepod lipid pump promotes carbon sequestration in the deep North Atlantic. *Proc. Natl. Acad. Sci. USA* **2015**, *112*, 12122–12126.
160. Kitano, H. Biological robustness. *Nat. Rev. Genet.* **2004**, *5*, 826–837.
161. Azam, F. Microbial control of oceanic carbon flux: The plot thickens. *Science* **1998**, *280*, 694–696.
162. Steinberg, D.K.; Carlson, C.A.; Bates, N.R.; Johnson, R.J.; Michaels, A.F.; Knap, A.H. Overview of the US JGOFS Bermuda Atlantic Time-series Study (BATS): A decade-scale look at ocean biology and biogeochemistry. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **2001**, *48*, 1405–1447.
163. Lomas, M.W.; Bates, N.R.; Johnson, R.J.; Steinberg, D.K.; Tanioka, T. Adaptive carbon export response to warming in the Sargasso Sea. *Nat. Commun.* **2022**, *13*, 1211.
164. Evans, L.E.; Hirst, A.G.; Kratina, P.; Beaugrand, G. Temperature-mediated changes in zooplankton body size: Large-scale temporal and spatial analysis. *Ecography* **2020**, *43*, 581–590.
165. Suttle, C.A. Marine viruses—Major players in the global ecosystem. *Nat. Rev. Microbiol.* **2007**, *5*, 801–812.
166. Weinbauer, M.G. Ecology of prokaryotic viruses. *FEMS Microbiol. Rev.* **2004**, *28*, 127–181.
167. Guidi, L.; Chaffron, S.; Bittner, L.; Eveillard, D.; Larhlmi, A.; Roux, S.; Darzi, Y.; Audic, S.; Berline, L.; Brum, J.R.; et al. Plankton networks driving carbon export in the oligotrophic ocean. *Nature* **2016**, *532*, 465–470.
168. Paulmier, A.; Ruiz-Pino, D. Oxygen minimum zones (OMZs) in the modern ocean. *Prog. Oceanogr.* **2009**, *80*, 113–128.

169. Ekau, W.; Auel, H.; Pörtner, H.O.; Gilbert, D. Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). *Biogeosciences* **2010**, *7*, 1669–1699.
170. Gilly, W.F.; Beman, J.M.; Litvin, S.Y.; Robison, B.H. Oceanographic and biological effects of shoaling of the oxygen minimum zone. *Annu. Rev. Mar. Sci.* **2013**, *5*, 393–420.
171. Alldredge, A.L.; Granata, T.C.; Gotschalk, C.C.; Dickey, T.D. The physical strength of marine snow and its implications for particle disaggregation in the ocean. *Limnol. Oceanogr.* **1990**, *35*, 1415–1428.
172. Mayor, D.J.; Sanders, R.; Giering, S.L.C.; Anderson, T.R. Microbial gardening in the ocean's twilight zone. *BioEssays* **2014**, *36*, 1132–1137.
173. Fabres, J.; Alonso-González, I.J.; Arístegui, J.; Lee, C.; Sanchez-Vidal, A.; Calafat, A.; Fabrés, J.; Sangrá, P.; Masqué, P.; Hernández-Guerra, A.; Benítez-Barrios, V. Role of slowly settling particles in the ocean carbon cycle. *Geophys. Res. Lett.* **2010**, *37*, L13602.
174. Riley, J.S.; Sanders, R.; Marsay, C.; Le Moigne, F.A.C.; Achterberg, E.P.; Poulton, A.J. The relative contribution of fast and slow sinking particles to ocean carbon export. *Glob. Biogeochem. Cycles* **2012**, *26*, GB1026.
175. Cavan, E.L.; Trimmer, M.; Shelley, F.; Sanders, R. Remineralization of particulate organic carbon in an ocean oxygen minimum zone. *Nat. Commun.* **2017**, *8*, 14847.
176. Chen, Q.; Tang, K.; Zhai, W.; Zhu, Z.; Yang, J.Y.T.; He, Z.; Li, M.; Kao, S.-J.; Yang, J.; Zheng, Q.; et al. Microbial responses to ocean deoxygenation: Revisiting the impacts on organic carbon cycling. *iScience* **2025**, *28*, 112767.
177. Jessen, G.L.; Lichtschlag, A.; Ramette, A.; Pantoja, S.; Rossel, P.E.; Schubert, C.J.; Struck, U.; Boetius, A. Hypoxia causes preservation of labile organic matter and changes seafloor microbial community composition (Black Sea). *Sci. Adv.* **2017**, *3*, e1601897.
178. Ohman, M.D.; Barbeau, K.; Franks, P.; Goericke, R.; Landry, M.; Miller, A. Ecological transitions in a coastal upwelling ecosystem. *Oceanography* **2013**, *26*, 210–219.
179. Jacox, M.G.; Edwards, C.A.; Hazen, E.L.; Bograd, S.J. Coastal upwelling revisited: Ekman, Bakun, and improved upwelling indices for the US West Coast. *J. Geophys. Res. Oceans* **2018**, *123*, 7332–7350.
180. Rykaczewski, R.R.; Checkley, D.M. Influence of ocean winds on the pelagic ecosystem in upwelling regions. *Proc. Natl. Acad. Sci. USA* **2008**, *105*, 1965–1970.
181. Hogle, S.L.; Dupont, C.L.; Hopkinson, B.M.; King, A.L.; Buck, K.N.; Roe, K.L.; Stuart, R.K.; Allen, A.E.; Mann, E.L.; Johnson, Z.I.; et al. Pervasive iron limitation at subsurface chlorophyll maxima of the California Current. *Proc. Natl. Acad. Sci. USA* **2018**, *115*, 13300–13305.
182. Taylor, A.G.; Landry, M.R. Phytoplankton biomass and size structure across trophic gradients in the southern California Current and adjacent ocean ecosystems. *Mar. Ecol. Prog. Ser.* **2018**, *592*, 1–17.
183. Stukel, M.R.; Irving, J.P.; Kelly, T.B.; Ohman, M.D.; Fender, C.K.; Yingling, N. Carbon sequestration by multiple biological pump pathways in a coastal upwelling biome. *Nat. Commun.* **2023**, *14*, 2024.
184. Brierley, A.S.; Kingsford, M.J. Impacts of climate change on marine organisms and ecosystems. *Curr. Biol.* **2009**, *19*, R602–R614.
185. Ferretti, S.; Macali, A.; Mazza, V.; Carere, C. Marine heatwaves as selective filters on the behaviour of native and non-native invertebrates. *Biol. Invasions* **2025**, *27*, 218.
186. Keeling, R.F.; Körtzinger, A.; Gruber, N. Ocean deoxygenation in a warming world. *Annu. Rev. Mar. Sci.* **2010**, *2*, 199–229.
187. Kim, H.; Franco, A.C.; Sumaila, U.R. A selected review of impacts of ocean deoxygenation on fish and fisheries. *Fishes* **2023**, *8*, 316.
188. Diaz, R.J.; Rosenberg, R. Spreading dead zones and consequences for marine ecosystems. *Science* **2008**, *321*, 926–929.
189. Oschlies, A.; Schulz, K.G.; Riebesell, U.; Schmittner, A. Simulated 21st century increase in oceanic suboxia by CO₂-enhanced biotic carbon export. *Glob. Biogeochem. Cycles* **2008**, *22*, GB4008.
190. Ditkovsky, S.; Resplandy, L.; Dalaut, L.; Barrier, N.; Lengaigne, M.; Maury, O. Sensitivity of fish diel vertical migration depths to future changes in the Pacific Ocean oxygen minimum zone. *Front. Mar. Sci.* **2026**, *12*, 1716557.
191. Tremblay, N.; Abele, D. Response of three krill species to hypoxia and warming: An experimental approach to oxygen minimum zone expansion in coastal ecosystems. *Mar. Ecol.* **2016**, *37*, 179–199.
192. Färber Lorda, J.; Färber, B. Autumn vertical distribution of zooplankton in the oxygen minimum zone of the Eastern Tropical North Pacific. *Mar. Environ. Res.* **2023**, *190*, 106116.
193. Schubotz, F.; Xie, S.; Lipp, J.S.; Hinrichs, K.; Wakeham, S.G. Intact polar lipids in the water column of the eastern tropical North Pacific: Abundance and structural variety of non-phosphorus lipids. *Biogeosciences* **2018**, *15*, 6481–6501.

194. Xing, J.; Deng, Y.; Ren, J.; Hein, J.R.; Xian, H.; Li, L.; Jiang, X.; Yang, Y.; He, G.; Qiu, H.; et al. Oxygen minimum-zone expansion controls critical metal enrichment and growth rates in a ferromanganese crust from the central Pacific Ocean. *J. Geophys. Res. Oceans* **2025**, *130*, e2025JC022450.
195. Altieri, A.H. Dead zones enhance key fisheries species by providing predation refuge. *Ecology* **2008**, *89*, 2808–2818.
196. Jorquera, E.; Brante, A.; Urzúa, Á.; Sanders, T.; Ellis, R.P.; Wilson, R.; Urbina, M.A. Effects of elevated CO₂ on the critical oxygen tension (P_{crit}) and aerobic metabolism of two oxygen minimum zone (OMZ)-hypoxia-tolerant squat lobster species. *Sci. Total Environ.* **2024**, *957*, 177508.
197. Seibel, B.A. Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. *J. Exp. Biol.* **2011**, *214*, 326–336.
198. Prince, E.D.; Goodyear, C.P. Hypoxia-based habitat compression of tropical pelagic fishes. *Fish. Oceanogr.* **2006**, *15*, 451–464.
199. Boscolo-Galazzo, F.; Crichton, K.A.; Barker, S.; Pearson, P.N. Temperature dependency of metabolic rates in the upper ocean: A positive feedback to global climate change? *Glob. Planet. Change* **2018**, *170*, 201–212.
200. Marsay, C.M.; Sanders, R.J.; Henson, S.A.; Pabortsava, K.; Achterberg, E.P.; Lampitt, R.S. Attenuation of sinking particulate organic carbon flux through the mesopelagic ocean. *Proc. Natl. Acad. Sci. USA* **2015**, *112*, 1089–1094.
201. Lewandowska, A.M.; Boyce, D.G.; Hofmann, M.; Matthiessen, B.; Sommer, U.; Worm, B. Effects of sea surface warming on marine plankton. *Ecol. Lett.* **2014**, *17*, 614–623.
202. Edwards, K.F.; Thomas, M.K.; Klausmeier, C.A.; Litchman, E. Allometric scaling and taxonomic variation in nutrient utilization traits and maximum growth rate of phytoplankton. *Limnol. Oceanogr.* **2012**, *57*, 554–566.
203. Morán, X.A.G.; López-Urrutia, Á.; Calvo-Díaz, A.; Li, W.K.W. Increasing importance of small phytoplankton in a warmer ocean. *Glob. Change Biol.* **2010**, *16*, 1137–1144.
204. Sarmiento, J.L.; Gruber, N. *Ocean Biogeochemical Dynamics*; Princeton University Press: Princeton, NJ, USA, 2006.
205. Planchat, A.; Kwiatkowski, L.; Bopp, L.; Torres, O.; Christian, J.R.; Butenschön, M.; Lovato, T.; Séférian, R.; Chamberlain, M.A.; Aumont, O.; et al. The representation of alkalinity and the carbonate pump from CMIP5 to CMIP6 Earth system models and implications for the carbon cycle. *Biogeosciences* **2023**, *20*, 1195–1257.
206. Zeebe, R.E.; Wolf-Gladrow, D. *CO₂ in Seawater: Equilibrium, Kinetics, Isotopes*; Gulf Professional Publishing: San Diego, CA, USA, 2001; Vol. 65.
207. Planchat, A.; Bopp, L.; Kwiatkowski, L.; Torres, O. The carbonate pump feedback on alkalinity and the carbon cycle in the 21st century and beyond. *Earth Syst. Dyn.* **2024**, *15*, 565–588.
208. Wilson, J.D.; Andrews, O.; Katavouta, A.; de Melo Virissimo, F.; Death, R.M.; Adloff, M.; Baker, C.A.; Blackledge, B.; Goldsworth, F.W.; Kennedy-Asser, A.T.; et al. The biological carbon pump in CMIP6 models: 21st century trends and uncertainties. *Proc. Natl. Acad. Sci. USA* **2022**, *119*, e2204369119.
209. Leung, J.Y.; Zhang, S.; Connell, S.D. Is ocean acidification really a threat to marine calcifiers? A systematic review and meta-analysis of 980+ studies spanning two decades. *Small* **2022**, *18*, 2107407.
210. Seifert, M.; Nissen, C.; Rost, B.; Hauck, J. Cascading effects augment the direct impact of CO₂ on phytoplankton growth in a biogeochemical model. *Elem. Sci. Anth.* **2022**, *10*, 00104.
211. Bednaršek, N.; Van de Mortel, H.; Pelletier, G.; García-Reyes, M.; Feely, R.A.; Dickson, A.G. Assessment framework to predict sensitivity of marine calcifiers to ocean alkalinity enhancement: Identification of biological thresholds and importance of the precautionary principle. *Biogeosciences* **2025**, *22*, 473–498.
212. Klaas, C.; Archer, D.E. Association of sinking organic matter with various types of mineral ballast in the deep sea: Implications for the rain ratio. *Glob. Biogeochem. Cycles* **2002**, *16*, 1116.
213. Ocampo, E.H.; Nunez, J.D.; Ribeiro, P.D.; Garcia, M.P.; Bas, C.C.; Luppi, T.A. Disparate response of decapods to low pH: A meta-analysis of life history, physiology and behavior traits across life stages and environments. *Mar. Pollut. Bull.* **2024**, *202*, 116293.
214. Last, K.S.; Hobbs, L.; Berge, J.; Brierley, A.S.; Cottier, F. Moonlight drives ocean-scale mass vertical migration of zooplankton during the Arctic winter. *Curr. Biol.* **2016**, *26*, 244–251.

215. Cohen, J.H.; Berge, J.; Moline, M.A.; Johnsen, G.; Zolich, A.P. Light in the polar night. In *Polar Night Marine Ecology: Life and Light in the Dead of Night*; Berge, J., Johnsen, G., Cohen, J.H., Eds.; Springer International Publishing: Cham, Switzerland, 2020; pp. 37–66.
216. Dijkstra, J.; Søreide, J.E.; Schott, L.; Thomsen, N.; Reinardy, H.; Lutier, M.; Dinh, K.V. Stressed overwintering bottleneck hypothesis: Ocean warming and acidification synergistically disrupt Arctic zooplankton overwintering. *Glob. Change Biol. Commun.* **2026**, *1*, e70022.

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