The transformation of mesopelagic structure across polar fronts

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Article

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The transformation of mesopelagic structure across polar fronts

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Bold First Paragraph/Abstract:

The oceans sequester 31% of atmospheric carbon annually ¹, but the magnitude of biologically enhanced sequestration is not evenly distributed across the globe ². Measuring surface primary productivity offers a reasonable proxy for estimating carbon flux into the ocean ³ but entirely misses the processes that affect carbon export to sequestration depths. A high proportion of carbon flux is broken up ⁴ or respired ⁵ by organisms at mesopelagic depths (200-1000 m). At low and mid-latitudes, daytime biomass peaks of mesopelagic organisms are clearly present and detectable as sound-scattering layers, and up to 40% of oceanic carbon passes through these layers ^{6,7}. Here we demonstrate that acoustic backscatter, a proxy for abundance of mesopelagic fish and zooplankton decreases by up to 97% across polar fronts, revealing a distinct pelagic structure in high latitude systems. As mesopelagic fish and macrozooplankton comprise a large component of active carbon transport in the upper ocean, this latitudinal reduction in mesopelagic biomass across thermal fronts, in both the Arctic and Antarctic, suggests different carbon flux attenuation schemes exists in ocean twilight zones of polar ecosystem compared to low latitude systems. Rapid ocean warming projected at mesopelagic depths⁸ will likely disrupt vertical connectivity and alter biogeochemical cycles at high latitudes.

Main Text:

At mid-latitudes, the mesopelagic zone (i.e. depths ranging from 200 - 1000 m) houses large abundances of macrozooplankton and micronekton ^{9,10} resulting in localized mesopelagic biomass peaks ⁷. Global biomass estimates put mesopelagic fish resources between 2-20 gigatonnes, or roughly 100 times more than the annual catch of all other fisheries ¹¹. Due to sheer biomass, mesopelagic organisms play an important role in exporting carbon to depth as part of the biological carbon pump.

While physical processes (i.e. the solubility pump) are responsible for the majority of gross oceanic uptake of carbon¹², long term-sequestration is primarily achieved through the biological pump ¹³. Carbon fixed through photosynthesis near the surface is either metabolized by organisms in the water-column and on the seafloor, or is exported to depths where it is effectively removed from contact with the atmosphere for long time periods (on the order of hundreds to thousands of

years)^{13–15}. Through diel vertical migrations (DVM; i.e. the active pump)¹⁶, attenuation (feeding on the passive flux) and repackaging of organic flux⁶, mesopelagic communities link biological assemblages at the surface to those on the seafloor and are an important conduit for oceanic carbon storage^{5,17,18}. As such, the abundance and vertical distribution of large mesopelagic organisms contributes to the functioning of the biological carbon pump. As a first order approximation, biomass of mesopelagic organisms should scale with energy input to the mesopelagic zone. However, research on mesopelagic macrozooplankton and micronekton has mainly focused on low- or mid-latitude systems^{19,20} and knowledge of their vertical structure and effect on carbon fluxes at high latitudes remains scarce^{21–25}.

Scientific echosounders are frequently used to map mesopelagic deep-scattering layers (DSL). To better understand the vertical distribution of life in the mesopelagic zone, we compiled shipboard acoustic measurements of backscatter at 38 kHz recorded while crossing frontal boundaries in both the North and South Atlantic. Continuously recorded acoustic data revealed a strong latitudinal gradient in backscatter across polar fronts (i.e. isotherms delineating different water masses) at both poles (**Figure 1**). The average backscatter at 38 kHz diminished by 97 % North of the polar front in Baffin Bay and by 89% South of the polar front in the Southern Ocean. Subpolar mesopelagic habitats host diverse communities of lanternfishes, crustaceans, molluscs, and gelatinous zooplankton; each considered important contributors to downward energy flow^{26–29}. At mesopelagic depths, echosounders operating at 38 kHz are well-suited to detect larger organisms in the 2–20 cm size range that bear air inclusions, such as swim-bladders³⁰ and pneumatophores³¹. Previous studies have also reported low overall backscatter in poleward mesopelagic ecosystems^{22,24,32,33}, however the use of strictly low-frequency measurements can be biased by changes in scattering properties of fish³³. Therefore, to detect weakly scattering organisms, we compiled backscatter profiles at higher frequency and closer range using 150 kHz and 300 kHz lowered acoustic Doppler current profilers (LADCP) (**Figure 2**). The backscatter at higher frequencies diminished by 32% at 300 kHz in Baffin Bay and by 79% at 150 kHz in the Antarctic zone. The reduced backscatter at high and low frequencies reflects reduced abundances of both micronekton and macrozooplankton across polar fronts. Furthermore, the LADCP data revealed the absence of sound scattering layers below ~400 m in poleward ecosystems, in contrast to equatorial and boreal regions where they are ubiquitous features^{2,9,19,20,34}.

The coincidence of the mesopelagic boundaries with polar fronts reflects a strong relationship between temperature and pelagic vertical structure. In our data, low water column temperatures were accompanied by reduced backscatter in both low and high frequency measurements and a loss of deep-sound scattering layers, regardless of hemisphere and distance from equator. As both hemispheres have different mesopelagic communities, the link between abundance and temperature appears independent of species assemblages¹⁰. Furthermore, the potential absence of vertically migrating species such as mesopelagic fish suggests a reduction in the active carbon flux in the upper ocean. It has been hypothesized that photoperiod is a key physical constraint to the dispersal of mesopelagic fish toward the poles³⁵. While mesopelagic densities vary widely with latitude, our data shows that mesopelagic structural boundaries closely track temperature gradients, rather than light, in poleward ecosystems.

The stability of mesopelagic boundaries at polar fronts and the rate of ‘borealization’ of pelagic ecosystem structures at high latitudes under climate change remains unclear. In both hemispheres,

the boundaries we observed occur between previously defined biogeographical provinces^{2,10,36}. Not coincidentally, these provinces present distinct biogeochemical signatures with different carbon export regimes^{37–39}. In poleward systems, provincial boundaries largely follow seasonal solar irradiance and stratification patterns; however, their stability varies between hemispheres⁴⁰. In the Indian Ocean sector, poleward displacement of the Antarctic polar front is linked to changes in large-scale ocean circulation patterns⁴¹, such as the Southern Annular Mode⁴². On the other hand, portions of the Antarctic polar front are stabilized by seafloor topography and present scarce evidence of poleward movement^{43–45}. In the Davis Strait, the position of the polar front aligns with a sill which drives the bifurcation of the West Greenland current^{46,47}. Over recent decades, the position of the front has remained consistent, at least in summer months^{47,48}. Future stability of the front in Baffin Bay will likely depend on the volume of freshwater transport generated by glacial melting in West Greenland and the Canadian Arctic Archipelago^{46,49}. Overall, the Arctic contains fewer deep-water connections with other oceans than the Antarctic and its temperature gradient is stronger (**Figure 1**). The effects of any potential climate-related poleward shifts are likely to differ between hemispheres, with much larger oceanic areas affected by a similar latitudinal shift in the southern hemisphere. As the Southern Ocean is responsible for up to 40% of global oceanic carbon export⁵⁰, climate warming and resulting changes in high latitude ecosystem structures would alter global carbon export efficiency³⁹.

Conclusions

The high degree of similarity in both the northern and southern vertical profiles shows that the relationship between pelagic vertical structure and temperature is independent of the species present, and strongly suggests a major difference in carbon export across polar fronts. While the reduced backscatter is clearly associated with water-column temperature, we lack a mechanistic understanding of the causes of the observed differences. Previous studies have suggested that mesopelagic fish biomass in high latitude systems are restricted by latitudinal light gradients^{35,51,52}. The front between austral and Antarctic mesopelagic distributions, however, starts much closer to the equator than the front in the northern hemisphere, suggesting that photoperiod constraint is unlikely to be the only factor driving the position of mesopelagic boundaries. The tight coupling with temperature documented in our data demonstrates that global warming will affect vertical structures of high-latitudes marine ecosystems, particularly at mesopelagic depths⁸.

Methods

Acoustic data

Shipboard acoustics were collected by two vessels during different sampling campaigns (Supplementary Figure 1). In the Davis Strait, data were collected aboard the research icebreaker CCGS *Amundsen* during the Integrated Studies and Ecosystem Characterization of the Labrador Sea Deep Ocean (ISECOLD) cruise in July and August 2018. In the Southern Ocean, data were collected in February 2008 along the 15°W section aboard the Norwegian research vessel *G.O. Sars*. Shipboard measurements from both cruises were made using an EK60 38 kHz scientific echosounder calibrated annually using standard-sphere methods⁵³.

The lowered acoustic Doppler profilers (LADCP) were mounted on CTD-rosettes and lowered to within 5 m of the bottom. 150 kHz LADCP data for the Southern Ocean were downloaded from the National Centers for Environmental Information (NCEI) database⁵⁴. Additional LADCP

data were collected from the CCGS *Amundsen* at fourteen stations in the Labrador Sea and Baffin Bay during the ISECOLD cruise in July and August 2018.

CTD profiles

Data for temperature sections in the Davis Strait and the Southern Ocean were downloaded from the Clivar & Carbon Hydrographic Data Office (CCHDO) database^{55,56}. An additional fourteen profiles were collected in the Labrador Sea and Baffin Bay from the CCGS *Amundsen* during the 2018 campaign using a Seabird © SBE 911+. Aboard the *Amundsen*, CTD profiles were collected concurrently with a rosette-mounted LADCP.

Data processing

Backscatter from shipboard echosounders (S_v , dB re 1 m⁻¹) was calculated according to MacLennan et al. (2002). Sound-speed and absorption were calculated from CTD data and used to adjust backscatter. Percent change in backscatter was calculated following linear transformation of S_v . All calculations were made between 30-750 m depth. For display purposes, -60 dB upper and -87 dB lower thresholds were applied to the data to highlight the scattering ranges of the dominant mesopelagic signal.

Backscatter from LADCP units was calculated according to Mullinson⁽⁵⁷⁾ (eq. 1) with factory supplied calibration constants per beam. Vertical profiles of sound-speed and absorption were calculated from the concurrent CTD profiles and were used when converting the LADCP counts to (relative) backscattering values.

$$S_{V(rel,dB)} = C + 10 \log_{10}((T_x + 273.16) R^2) - L_{DBM} - P_{DBW} + 2\alpha R + 10 \log_{10}(10^{k_c(E-E_r)/10} - 1) \quad (\text{eq. 1})$$

where C is an instrument specific constant, R is the along-beam range to the measurement, L_{DBM} is $10 \log_{10}$ transmit pulse length in meters, P_{DBW} is $10 \log_{10}$ transmit power in watts, k_c is the Returned Signal Strength Indicator (RSSI) slope, α is a beam specific constant relating amplitude counts to the decibel scale. For the data from the CCGS *Amundsen*, we used instrument-specific values supplied by the manufacturer and for the Southern Ocean data we used a generic instrument value of 0.45 dB count⁻¹. α is the acoustic absorption and E , E_r are amplitude count and amplitude count at noise-floor, respectively. The high levels of sound-absorption at 300 kHz means that a hull-mounted transducer will have a very limited observational range before the signal from organisms drop below the noise-level. Backscatter from organisms depends on, among other things, the size of the organism. In general organisms much smaller than the wavelength (4.5 mm at 300 kHz and 1500 m s⁻¹ sound speed) will give very little echo. Thus, the deployment of high-frequency acoustic equipment on a lowered rig enables observation of relatively small, weakly scattering animals at depths that surpass the range of high frequency hull-mounted sounders.

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Author contributions

JC and TAK conceived of this topic, collected and analysed data, and co-wrote the manuscript. DC obtained funding and led the ISECOLD project in the Labrador Sea. MG and DC contributed to the writing of the paper as well as discussion of results and comments on the manuscript.

Competing Interests

The authors declare no competing interests

FIGURES:

Fig 1. 38 kHz acoustic backscatter across high-latitude temperature fronts. Backscatter volume strength (S_v , dB re 1 m^{-1}) collected during latitudinal transects of the Antarctic sub-polar current to the Antarctic circumpolar current (A) and the crossing of the Arctic Circle in the Davis Strait (B). Echograms display acoustic backscatter calculated for 1 km x 2.5 m intervals. Upper and lower thresholds of -87 to -60 dB were applied to facilitate visualization of the deep-scattering layer. Solid grey and red dashed lines represent S_v of upper water column (0-750 m) and a two-sided 25 km moving average, respectively. CTD transects from expeditions in similar locations were used to construct latitudinal sections across the southern polar front along the 30° W line (C) and Davis Strait and (D). Water column temperature is summarised using mean +/- standard error of water temperature between 0-750 m.

Figure 2. **150 and 300 kHz LADCP backscatter across high-latitude temperature fronts.** 150 kHz data were collected from lowered profiles at stations during latitudinal crossings from the Polar Frontal Zone (PFZ) to the Antarctic Zone (AZ) in 2008 (A). 300 kHz data were collected in the Labrador Sea and Baffin Bay in 2018 (B). Water column temperature data were collected concurrently with LADCP and are displayed as the mean $\pm$ standard error calculated between 30-750m in the Southern Ocean (C) and in the North Atlantic (D).

Supplementary Figure 1.

S1. Location of sampling events and sampling types in the Southern Ocean (left) and Labrador Sea/Davis Strait (right). Green line in left panel denotes the position of the polar front ⁵⁸.

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401

Figures

Figure 1

38 kHz acoustic backscatter across high-latitude temperature fronts. Backscatter volume strength (S_v , db re 1 m^{-1}) collected during latitudinal transects of the Antarctic sub-polar current to the Antarctic circumpolar current (A) and the crossing of the Arctic Circle in the Davis Strait (B). Echograms display acoustic backscatter calculated for $1 \text{ km} \times 2.5 \text{ m}$ intervals. Upper and lower thresholds of -87 to -60 dB were applied to facilitate visualization of the deep-scattering layer. Solid grey and red dashed lines represent S_v of upper water column (0-750 m) and a two-sided 25 km moving average, respectively. CTD transects from expeditions in similar locations were used to construct latitudinal sections across the

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Figure 2

150 and 300 kHz LADCP backscatter across high-latitude temperature fronts. 150 kHz data were collected from lowered profiles at stations during latitudinal crossings from the Polar Frontal Zone (PFZ) to the Antarctic Zone (AZ) in 2008 (A). 300 kHz data were collected in the Labrador Sea and Baffin Bay in 2018 (B). Water column temperature data were collected concurrently with LADCP and are displayed as the mean $\pm$ standard error calculated between 30-750m in the Southern Ocean (C) and in the North Atlantic (D).