Vol. 734: 177–180, 2024
https://doi.org/10.3354/meps14578

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published April 18

REPLY COMMENT

Biological indicators reveal mesozooplankton foray behaviour in dynamic physical environments: Reply to Kaartvedt et al. (2024)

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ABSTRACT: Kaartvedt et al. (2024; Mar Ecol Prog Ser 734:173–175) comment on the role internal waves played in the findings of Dewar-Fowler et al. (2023; Mar Ecol Prog Ser 715:27–39) that foray behaviour was present across a number of zooplankton species in the Polar Frontal Zone of the Southern Ocean. Kaartvedt et al. (2024) contend that foray behaviour may not be responsible for the capture of zooplankton by fixed-depth bi-directional net-traps because the influence of internal waves on transporting these organisms into the traps was not accounted for. In Figs. 4 & 5 of Dewar-Fowler et al. (2023), directional biases were apparent in the abundance and taxon-ratios captured by the upward and downward looking nets, which can only be explained by the active swimming and avoidance behaviours of zooplankton. This refutes the contention that physical processes such as internal waves dominated capture rates by the net-trap. Even within this physically dynamic oceanic frontal zone, biological indicators such as these biases support the assertion of Dewar-Fowler et al. (2023) that foray behaviour is detectable and prevalent within zooplankton communities.

KEY WORDS: Internal wave · Ocean mixing · Swimming behaviour · Net avoidance · Diel cycles

1. INTRODUCTION

Vertical movement of pelagic organisms is universal across all ocean environments (Hays 2003, Bianchi & Mislan 2016). Research has mainly focused on self-propelled vertical migrations during diel (Hays 2003, Bianchi & Mislan 2016), tidal (Manuel & O'Dor 1997, Petrusevich et al. 2020) and lunar (Gliwicz 1986, Last et al. 2016) cycles. Daytime catches of deep zooplankton with guts full of surface phytoplankton further indicate that intermittent forays into the surface layers from deeper depths also take place (Pearre 2003). This intermittent foray behaviour may not necessarily change the vertical distribution of zooplankton biomass, which makes this behaviour difficult to detect through traditional net and acoustic surveys, although there has been some success with Doppler-based acoustic instruments (Cottier et al. 2006). Bi-directional net traps are an innovation to gain both species-specific and state-based data on zooplankton foray behaviour. To this end, the motion-compensated upward and downward looking (MUDL) net described by Dewar-Fowler et al. (2023) enhanced the prototype design of Pierson et al. (2009) through integrating a compensation mechanism which helped maintain a fixed deployment depth while the MUDL net was tethered to a research vessel.

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2. PREVALENCE OF MIXING PROCESSES AT SAMPLING STATIONS

Oceanic environments, particularly those in regions such as the Polar Frontal Zone of the Southern Ocean, are oceanographically dynamic, with several physical processes that may vertically displace pelagic organisms, including internal waves (Lennert-Cody & Franks 1999), turbulence (Michalec et al. 2017) and eddies (Batten & Crawford 2005). These processes will act over a range of scales and are spatially variable. We considered a range of data sources to examine the prevalence of such mixing processes at each of the sampling stations of Dewar-Fowler et al. (2023). There was evidence of internal waves in at least parts of the water column at certain stations (Fig. 1), although their prevalence between depths and stations was variable. Fig. 1A,B shows echosounder images from 2 of the MUDL deployment periods where the distribution of backscatter particles in certain parts of the water column was characteristic of internal waves. Certain CTD casts (Fig. 1C) also showed vertical displacement of temperature and salinity between the downcast and upcast, indicating properties likely caused by internal waves. The internal waves highlighted in Fig. 1A,B had wave heights of 6 to 8 m and periods of 1 to 3 min, which would result in 8 to 30 cycles over the respective deployment periods (Table 1). Also notable was that MUDL net deployments were considerably deeper than these features, although the lack of zooplankton at depth may have prevented deeper internal waves from

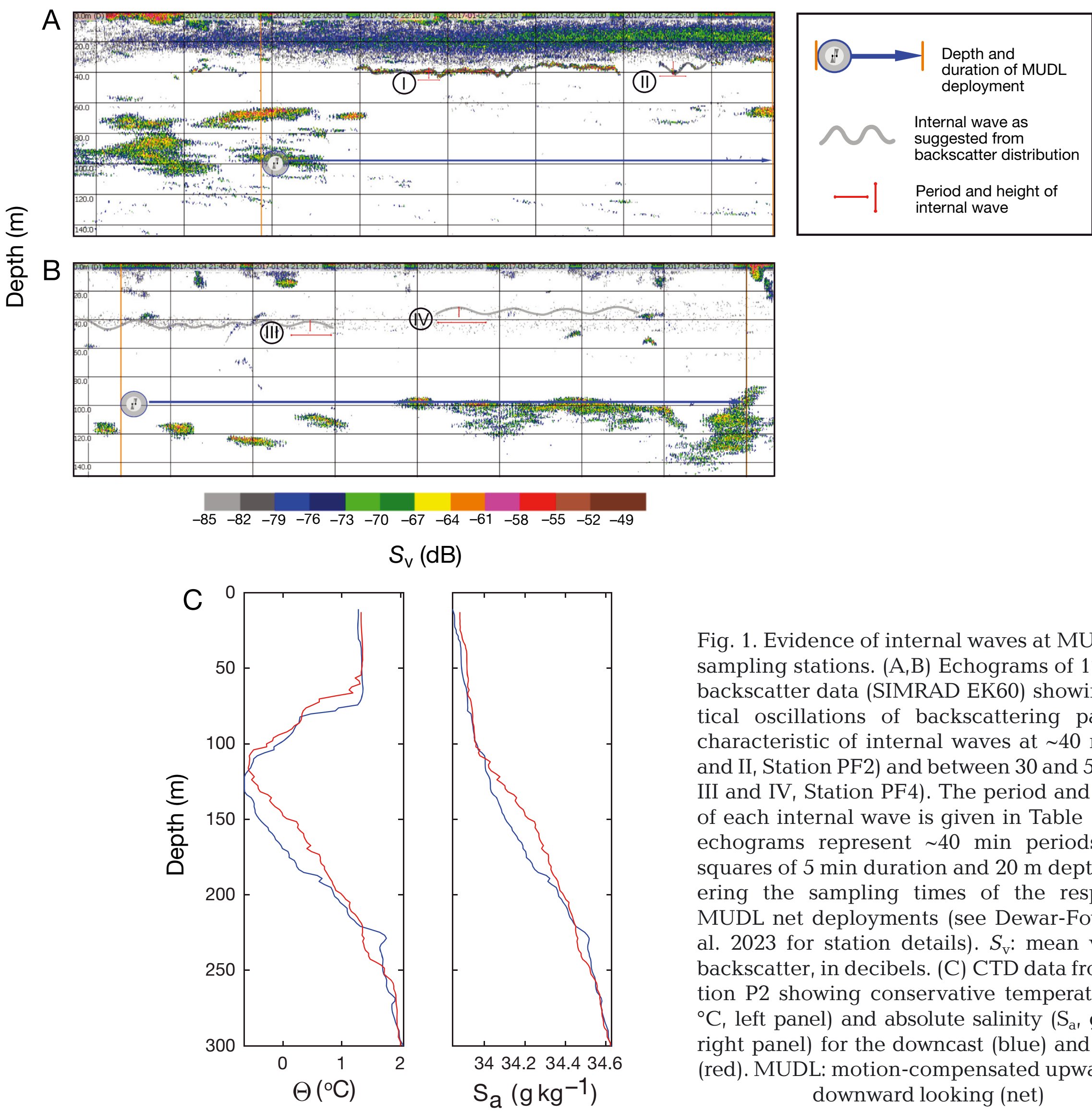

Fig. 1. Evidence of internal waves at MUDL net sampling stations. (A,B) Echograms of 120 kHz backscatter data (SIMRAD EK60) showing vertical oscillations of backscattering particles characteristic of internal waves at ~40 m (A: I and II, Station PF2) and between 30 and 50 m (B: III and IV, Station PF4). The period and height of each internal wave is given in Table 1. Both echograms represent ~40 min periods (grid squares of 5 min duration and 20 m depth) covering the sampling times of the respective MUDL net deployments (see Dewar-Fowler et al. 2023 for station details). S_v: mean volume backscatter, in decibels. (C) CTD data from Station P2 showing conservative temperature (Θ, °C, left panel) and absolute salinity (S_a, g kg^{-1}, right panel) for the downcast (blue) and upcast (red). MUDL: motion-compensated upward and downward looking (net)

Table 1. Properties of internal wave features as indicated by backscattering particle characteristics shown for Stations PF2 in Fig. 1A (internal wave features I and II) and PF4 in Fig. 1B (III and IV) during deployments in January 2017. MUDL: motion-compensated upward and downward looking (net)

Station	Start date and local time (dd/mm/yyyy)	Deployment period (min)	Internal wave	Wave period (min)	Wave height (m)	Internal wave cycles per MUDL net deployment
PF2	02/01/2017 22:05	38	I	1.30	6.67	29.23
		38	II	1.58	8.27	24.05
PF4	04/01/2017 21:43	23	III	2.43	6.67	9.47
		23	IV	2.90	6.13	7.93

being visualized. If these internal waves coincided with the deployment depth of the MUDL, they would have had the potential to move organisms into, as well as out of, the device, given the absence of any type of one-way gate in the MUDL cod-ends.

3. BIOLOGICAL INDICATORS OF FORAY BEHAVIOUR

Although not explicitly stated in Dewar-Fowler et al. (2023), it was an implicit assumption that the physical environment was not vertically static and that organisms would have been moved into and out of the trap through the action of physical forces alone. Contributing to this inward and outward movement is the potential influence of internal waves, which the analyses described in Section 2 above confirm to be present, at least in certain parts of the water column, during some deployments. However, Dewar-Fowler et al. (2023) found evidence of foray behaviour beyond such physically induced background noise. This evidence comes from 2 principal sources: (1) directional bias in captured abundance and (2) different taxon ratios between net-opening directions and times of day.

With regards to directional bias in captured abundance, Dewar-Fowler et al. (2023) found a mean (±SD) decrease of 75.6 ± 24.4% in the number of organisms captured by the downward looking net compared to the upward looking net. While physical processes may move zooplankton in and out of devices such as the MUDL net, this should not induce any directional biases when averaged across all deployments. In terms of internal waves, the upward and downward phases should be equal in magnitude, and although any one deployment may encounter more of one phase than the other, this should even out across all deployments (13 in total). Even if one phase is consistently over-encountered, the limits to this potential error still cannot account for the directional bias observed across all deployments, as we will explain. In Fig. 1, we resolved internal waves that generated between 8 and 30 cycles per deployment (Table 1). As an extreme example, internal wave feature III would generate 9.5 internal wave cycles during the MUDL deployment period. The 0.5 cycle would result in one phase (either upward or downward) being more represented than the other. The potential bias this could generate would consequently be 10/9 (i.e. 10 of phase *x* divided by 9 of phase *y*), equaling a factor of 1.11 or 11%. This bias would be lower if there were more wave cycles per deployment or if the proportion of a non-complete cycle was less or more than 0.5. This upper level of potential bias from internal waves (~11%) is much lower than the mean directional bias observed (~76%). Active swimming traits such as the avoidance of shade and escape from detected net walls better explain the causes of this bias.

Taxon-ratio analyses provide further support for the importance of swimming behaviour. Dewar-Fowler et al. (2023) found that the ratio of cyclopoid copepods to calanoid copepods varied between 3.2:1 to 1.5:1 depending on time of day and net direction. This showed that the capture potential differed considerably between taxa and that diel biological cycles had a detectable influence on relative capture rates. If physical mixing processes dominated, there should be no consistent biases in which taxa are captured by the upward and downward looking nets.

4. CONCLUSION

Dewar-Fowler et al. (2023) reported consistent directional biases in abundance and taxon ratios that cannot be explained by the action of physical processes including internal waves. A better explanation for the observed results is the presence of foray behaviour, since it incorporates factors such as directional avoidance and diel cycles. We agree with the sentiment of Kaartvedt et al. (2024) that disentangling biology from physics is a necessity for any biological oceanographic study. Here, we show that weakly swimming organisms, such as mesozooplankton, have control over their vertical location and carry out forays even within one of the most dynamic of oceanic environments.

Acknowledgements. We are grateful to Sophie Fielding for helping to prepare acoustic images to facilitate our analyses.

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Editorial responsibility:
Deborah K. Steinberg, Gloucester Point, Virginia, USA;
Christine Paetzold, Oldendorf/Luhe, Germany

Submitted: January 16, 2024
Accepted: March 14, 2024
Proofs received from author(s): April 15, 2024