



FEATURE ARTICLE: NOTE

Efficient trawl avoidance by mesopelagic fishes causes large underestimation of their biomass

Stein Kaartvedt^{1,2,*}, Arved Staby^{3,4}, Dag L. Aksnes³

¹King Abdullah University of Science and Technology, Red Sea Research Center, Thuwal 23955-6900, Saudi Arabia

²Department of Biology, University of Oslo, 0316 Oslo, Norway

³Department of Biology, University of Bergen, 5020 Bergen, Norway

⁴Present address: Institute of Marine Research, 5817 Bergen, Norway

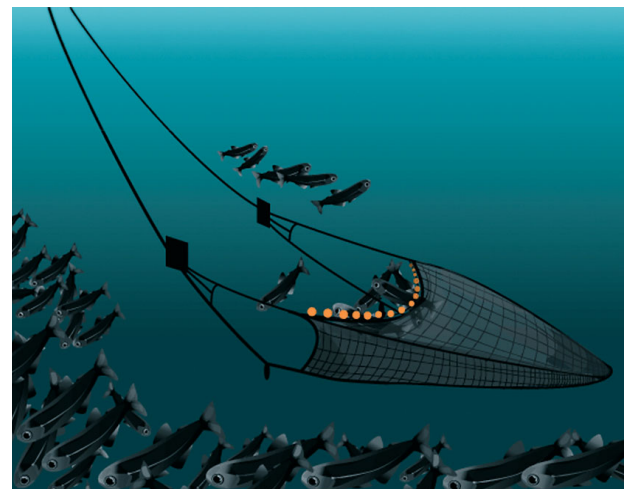
ABSTRACT: Mesopelagic fishes occur in all the world's oceans, but their abundance and consequently their ecological significance remains uncertain. The current global estimate based on net sampling prior to 1980 suggests a global abundance of one gigatonne (10^9 t) wet weight. Here we report novel evidence of efficient avoidance of such sampling by the most common myctophid fish in the Northern Atlantic, i.e. *Benthosema glaciale*. We reason that similar avoidance of nets may explain consistently higher acoustic abundance estimates of mesopelagic fish from different parts of the world's oceans. It appears that mesopelagic fish abundance may be underestimated by one order of magnitude, suggesting that the role of mesopelagic fish in the oceans might need to be revised.

KEY WORDS: Mesopelagic fish · Avoidance behavior · Trawling · Acoustics

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INTRODUCTION

Mesopelagic (200 to 1000 m depth) fishes are important planktivores and prominent prey for higher trophic levels in all the world's oceans (Gjøsæter & Kawaguchi 1980, Lam & Pauly 2005) and, because of pronounced diel vertical migrations (DVM), contribute to the biological pump whereby organic material is transported from upper layers down to the waters at depth (Hidaka et al. 2001, Hernández-León et al. 2010). The current global bio-



Mesopelagic fishes show efficient avoidance behavior in response to sampling gears.

Image: Hege Vestheim

mass estimate of mesopelagic fishes, primarily based on catches by micronekton sampling gears prior to 1980, amounts to approximately 1 gigatonne (10^9 t wet weight) (Gjøsæter & Kawaguchi 1980, Lam & Pauly 2005). This is likely an underestimate (Gjøsæter & Kawaguchi 1980) because mesopelagic fishes are not captured quantitatively by sampling gear. Subsequent gear intercomparisons have revealed marked differences in catch efficiency of mesopelagic fish between different trawl types, due to various influences from extrusion through meshes and net avoid-

*Email: stein.kaartvedt@kaust.edu.sa

ance behavior (Pakhomov & Yamamura 2010, Heino et al. 2011). However, regardless of trawl type, acoustic abundance estimates always appear to be consistently higher than the net-based estimates (Koslow et al. 1997, Kloser et al. 2009, Pakhomov & Yamamura 2010).

Myctophids (lanternfish) are the most widespread mesopelagic fish family (Saito & Murata 1998), being represented by ~250 species worldwide (Catul et al. 2011). Facilitated by the unique opportunities deep fjords provide for investigating the mesopelagic realm (Kaartvedt et al. 2009), we used echo sounders to obtain novel evidence of pronounced avoidance of a trawl by the most common myctophid fish in the Northern Atlantic, i.e. *Benthoosema glaciale*. Our results suggest that the sampling gear invokes avoidance reactions similar to those incited by approaching predators and that such efficient avoidance behavior will cause large net-based underestimation of mesopelagic fish biomass.

MATERIALS AND METHODS

Sampling and acoustic studies of avoidance of a trawl were carried out in Masfjorden (60° 52' N, 5° 25' E), Norway, on 2–3 November 2007, using the RV 'Håkon Mosby' (University of Bergen and Institute of Marine Research). Two mesopelagic fish species prevail in Masfjorden: *Maurolicus muelleri* dominates in the upper 200 m, while *Benthoosema glaciale* is mostly distributed below 200 m and is the prevailing species below ~250 m (Kaartvedt et al. 2009, Staby et al. 2011, Dypvik et al. 2012). Both species to a varying degree carry out DVM, depending on season (Kaartvedt et al. 2009, Staby et al. 2011, Dypvik et al. 2012). At the time of the present study (late fall), the population of adult *M. muelleri* had largely ceased migrating vertically (Staby et al. 2011). In the nocturnal echograms presented here, they likely dominated the acoustic backscatter above ~200 m (see Fig. 1), but they are not further dealt with in this paper, where we focus on fish in deeper waters. *B. glaciale* mostly stayed below 200 m at night (Kaartvedt et al. 2009).

We used a Harstad trawl, designed to capture small fish, which had un-stretched mesh sizes ranging from 200 mm in the front to 10 mm in the rear part. Trawl height and width is ~20 m, which provides an opening of ~400 m², the area used for calculations of volume filtered. This evidently is an overestimate of the unknown 'effective' mouth opening, which will result in an underestimate of true fish abundance.

Pelagic trawls with decreasing meshes towards the cod-end are intended to herd fish backwards until they eventually encounter meshes that are small enough for retention (e.g. Lee et al. 1996, Heino et al. 2011). Nevertheless, there will be an unknown fraction of the catch escaping through coarse meshes in the front.

The trawl was towed at 2 to 3 knots. It was equipped with a remotely controlled Multisampler cod-end (Engås et al. 1997) that was kept open during launching and retrieval of the trawl. Trawl depth was monitored during sampling by a Scanmar depth sensor located at the head rope of the trawl. Acoustic transects using the RV 'Håkon Mosby's Simrad EK60 38 kHz echo sounder (7,1° beam width) were carried out prior to, during and subsequent to a tow conducted at ~320 to 330 m depth at night; in the latter case, the vessel traversed the path of the preceding tow, assessing the distribution and abundance of mesopelagic fish along the path of the trawl.

We made acoustic abundance estimates of *Benthoosema glaciale* for the same depth and horizontal segments as the trawling, using the software Echoview. After backscatter from individual, larger fish had been removed, the remaining volume backscattering (S_v) in a rectangle corresponding to the depth of the subsequent sampling was allocated to *B. glaciale*. This is largely justified based on trawl catches in this and other studies, as well as from acoustic studies at different frequencies (Kaartvedt et al. 2008, Kaartvedt et al. 2009, Dypvik et al. 2012, although some backscatter from pelagic shrimps may have been included in the estimate. For converting total S_v values to number of fish, we used the standard relation: $N = 10^{[(S_v - TS)/10]}$ (MacLennan & Simmonds 1992), where N is number of fish and TS (target strength) is the acoustic backscatter from one individual.

In situ values for TS of individual fish were obtained by an upward-facing, calibrated echo sounder (Simrad EK60, 38 kHz, 7.1° beam width) deployed on the bottom at 390 m depth in the same fjord location and cabled to shore for long-term measurements (July 2007 to October 2008). This provided a TS of -58.4 dB for *Benthoosema glaciale* during the time of this study (Kaartvedt et al. 2009). Sizes of *B. glaciale* in catches below 300 m were 59 ± 5 mm (SD) and 60 ± 5 mm for day and night, respectively (Kaartvedt et al. 2009).

For comparison with avoidance of the trawl, data from the long-term acoustic measurements were also used to assess avoidance behavior of *Benthoosema glaciale* upon encounters with groups (here referred to as 'schools') of potentially predatory fish.

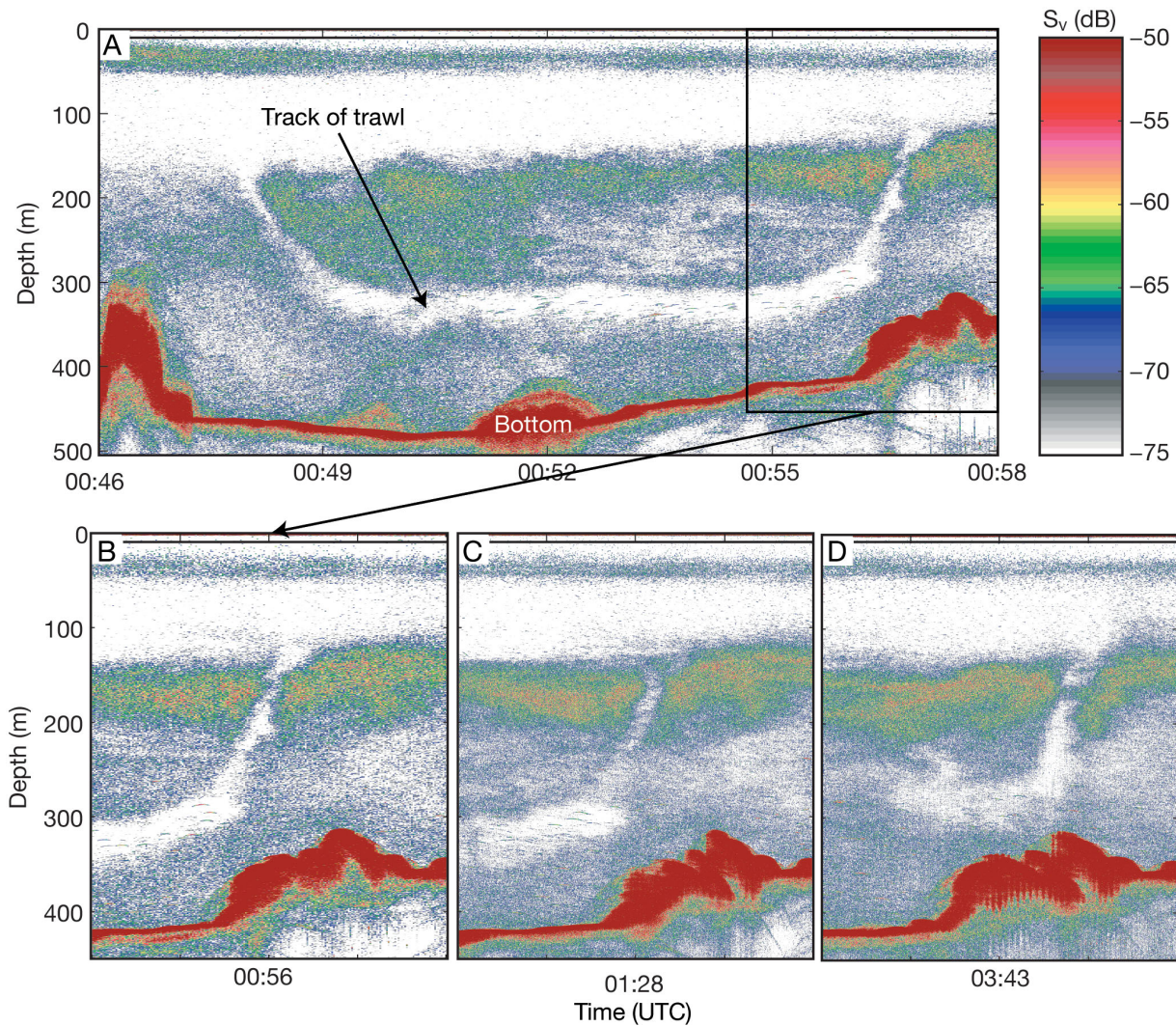


Fig. 1. Avoidance of trawl. (A) Echogram recorded when the path of a preceding trawl tow was traversed; signature with low backscatter depicts the track of the trawl. (B–D) Persistence of the void created by the trawl (deployed at ~23:30 h). The trawl had free throughflow and was not sampling on its way down (the part of the tow portrayed in B–D), so the void in the acoustic records cannot be explained by removal of fish by the gear. Color scale refers to volume backscattering strength (S_v), with brownish-red as the strongest echoes

RESULTS

A conspicuous trace (void) in the acoustic scattering layers of mesopelagic fish appeared when the path of a preceding nocturnal trawl tow of the mesopelagic was traversed while acoustic measurements were made (Fig. 1A). This void persisted for several hours in the calm fjord environment, drifting slowly at 2 to 3 cm s^{-1} (Fig. 1B–D). The void also mirrors the periods of launching and retrieval of the trawl when a remotely controlled cod-end is kept open so that there is free flow through the trawl, i.e. no capture of fish. Catches in 4 trawl samples below 300 m, including the tow responsible for the void shown in Fig. 1, were 58 ± 12 (SE) *Benthoosema glaciale*, correspond-

ing to $\sim 0.05 \pm 0.01$ ind. per 100 m^3 . The acoustic abundance estimates of *B. glaciale* for the same depth and horizontal segments as the trawling were 3.6 ± 0.5 (SE) ind. per 100 m^3 .

We made observations of natural predator avoidance behavior of mesopelagic fish (*Benthoosema glaciale*) from the bottom-mounted echo sounder (Fig. 2). Undisturbed individuals normally remain motionless, resulting in echo traces appearing as horizontal ‘lines’ since many successive echoes are received from the same individual. Nevertheless, encounters with schools of larger fish incite pronounced escape reactions (Fig. 2). Individuals diving below the—presumably predatory—school are evident in the acoustic records (Fig. 2B). Also, a 50% increase in acoustic

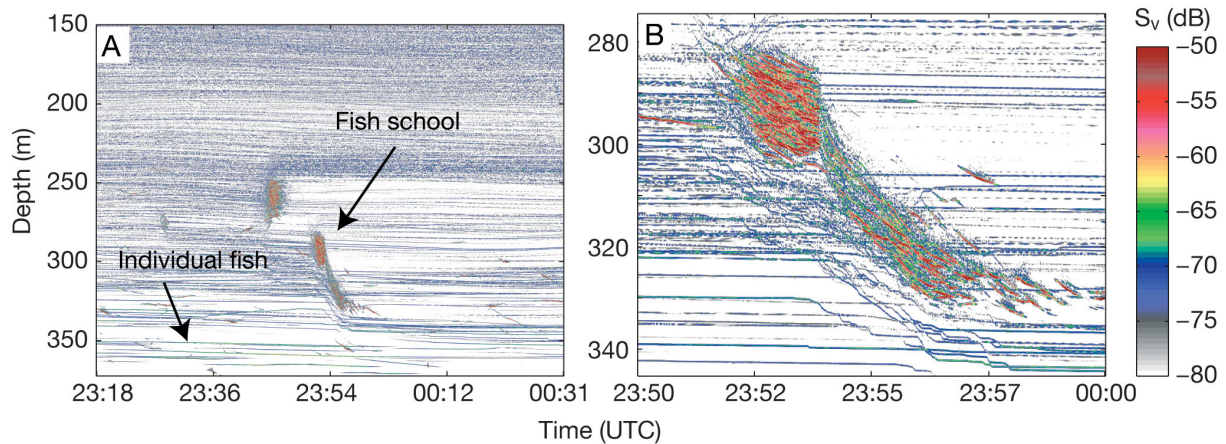


Fig. 2. *Benthosema glaciale*. Avoidance of predators. (A) Mesopelagic fish (individuals seen as blue 'lines') escape from a school of larger fish, creating a comparative void as in Fig. 1. (B) Close up, excerpt from (A). Records were made by an echo sounder deployed at 390 m depth; color scale refers to volume backscattering strength (S_v), with brownish-red as the strongest echoes

backscatter is recorded throughout the nearest 20 m above the school. This suggests additional upwards escapement, but individuals cannot be observed at this range from the echo sounder. The largest vertical distance between the school and a responding fish suggests that the approaching school is detected within a range of ~30 m.

After the encounter with the predators, the fishes resumed a lethargic behavior, leaving a persistent void in the acoustic records, much as that recorded in the wake of the trawl. This type of flight behavior upon encounter with predators was repeatedly recorded during the long-term acoustic measurements.

DISCUSSION

Our acoustic results clearly suggest avoidance behavior of mesopelagic fish from a pelagic trawl. Marked voids in the acoustic records of *Benthosema glaciale* (and of the shallower located *Maurolicus muelleri*, which is not further addressed here) encompassed periods when the trawl was kept open and thus without capture of fish, suggesting that the void is created by fish swimming away from the trawl rather than removal of fish. The void created by the trawl was similar to the void formed as a result of *B. glaciale* escaping potential predatory fishes. In both cases, the voids persisted, since *B. glaciale* resumed their lethargic behavior immediately after their flight behavior. The well-documented pattern of quiescence in mesopelagic fish (Barham 1966) evidently does not prevent prompt flight reactions.

The void created by the trawling had a vertical extent of about 30 m, which is 10 m greater than the

trawl opening. The diameter of the acoustic beam at 315 m depth is 40 m, suggesting a minimum for the horizontal extension of the void, and underlining the extent of the avoidance behavior. The behavioral observations of encounters between *Benthosema glaciale* and fish schools suggested that predators could be detected at a range of tens of meters. Fish can use several sensory stimuli to detect a moving trawl (Handegard & Tjøstheim 2005, Jamieson et al. 2006). This includes visual detection (Jamieson et al. 2006, Heino et al. 2011), and catches of myctophids have been considered to be more quantitative at night (Collins et al. 2012). However, trawls will stimulate bioluminescent flashes (Jamieson et al. 2006) and thereby also make a marked visual signal at night. Myctophids have eyes that are very sensitive to light, and bioluminescent flashes may be detected at a range of tens of meters (Warrant & Lockett 2004). While the actual mechanisms eliciting avoidance behavior is beyond the scope of this paper, visually stimulated nocturnal avoidance may very well be expected.

Acoustic abundance estimates were close to 2 orders of magnitude higher than estimates from the trawl and were roughly similar to previous acoustic estimates of *Benthosema glaciale* from Masfjorden (Bagøien et al. 2001). However, our trawl catches were lower than previous net sampling in the fjord (Kaarvedt et al. 1988, Giske et al. 1990), suggesting a lower sampling efficiency for the trawl used in our study than for the smaller gears normally used in mesopelagic studies (Gjøsæter & Kawaguchi 1980). Although not concurrent in time, results from the previous studies in Masfjorden suggest differences between net-based and acoustic abundance esti-

mates closer to one order of magnitude. Correspondingly, studies from other parts of the world's oceans also give acoustic abundance estimates of mesopelagic fish about one order of magnitude higher than net-based estimates (Koslow et al. 1997, Kloser et al. 2009, Pakhomov & Yamamura 2010).

Acoustic estimates are also affected by uncertainties and depend on fish size distribution relative to acoustic wave length, correct ascribing of acoustic backscatter to fish in scattering layers composed of different taxonomic groups, and use of appropriate TS values (Barham 1966, MacLennan & Simmonds 1992, Godø et al. 2009). However, such uncertainties do not relate to our direct observations of avoidance in the much-studied ecosystem of Masfjorden. Therefore, we conclude that efficient avoidance of sampling gear indeed causes large net-based underestimation of the most common myctophid in the northern Atlantic. To the extent that this conclusion can be generalized, our evidence suggests that avoidance may also account for pronounced discrepancies between net-based and acoustic abundance estimates of mesopelagic fishes that have been revealed in other studies.

The global estimate of mesopelagic fish that is commonly referred to in the scientific literature amounts to 948×10^6 t wet weight (Gjøsæter & Kawaguchi 1980) and was slightly revised to 999×10^6 t (Lam & Pauly 2005) to correct for minor inconsistencies in the original estimation. More important is probably the likelihood of underestimation that was pointed out in Gjøsæter & Kawaguchi (1980, p 121): 'most of the gears used to obtain the available information obviously underestimate the biomass present'. Due to lack of knowledge of the actual avoidance and underestimation of these fishes, this 30 yr old estimate is still in use (Davison & Asch 2011). If the underestimation suggested in this paper applies to the current global estimate (Gjøsæter & Kawaguchi 1980), an acoustically determined mesopelagic fish biomass of 10^{10} t is indicated for the world oceans.

A recent evaluation on the effect of fishing low trophic level species on marine ecosystems concludes that impacts of harvesting mesopelagic fishes would be consistently high across ecosystems (Smith et al. 2011). A potential upgrading of the current global estimate of mesopelagic fish to 10^{10} t—which is 100 times larger than the world's yearly fishery catch—would force us to rethink their role as predators on zooplankton, as prey for top predators, as well as daily vertical transporters of organic matter from the surface to the deeper ocean.

Acknowledgements. We thank Anders Røstad and Thor A. Klevjer for help during the long-term acoustic study. Anders Røstad made the figures.

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*Editorial responsibility: Jake Rice,
Ottawa, Ontario, Canada*

*Submitted: February 6, 2012; Accepted: April 26, 2012
Proofs received from author(s): May 16, 2012*