

1 Spatial interactions on an Arctic shelf: Bottom dwelling cod ambush small pelagic fish hunting
2 for krill

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11

12 [Abstract](#)

13 Predator-prey spatial interactions are difficult to observe in marine systems since predators,
14 prey and resources are all typically mobile and responsive to each other. Furthermore, vertical
15 light gradients over the day add an extra dimension to the space use of visual predators and
16 their prey. We visited a bank area in the northern Barents Sea with cold bottom waters (~1°C),
17 and combined conventional trawl and acoustic sampling with novel broadband hydroacoustic
18 techniques to obtain long range, fine scale observations on interactions between cod, their
19 planktivore prey (capelin and polar cod), and krill. We caught cod in the demersal trawls but
20 could not distinguish them with the vessel acoustics. However, broadband acoustics mounted
21 on a submersible probe allowed us to follow the feeding behaviour of individual cod, revealing
22 that cod remained mostly passive within 10 m of the bottom throughout the diel cycle. In the
23 morning, cod lifted slightly from the seabed to ambush capelin, which corresponded with more
24 fresh prey in cod stomachs in the morning. During daylight, krill pushed towards the bottom,
25 sharing habitat with cod, while the planktivores aggregated in pelagic schools at the cost of lost
26 feeding opportunities, overlapping with their krill prey only during twilight hours. The diel
27 light cycle was an important driver of the spatial movements and aggregations, and during
28 daylight, krill appear to hide from capelin among the cod near bottom. The new broadband
29 hydroacoustic allowed us to observe real-time spatial interactions of three major players
30 ranging two orders of magnitude in size.

31 Key words: diet, predator-prey interaction, Barents Sea, *Gadus morhua*, *Mallotus villosus*

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33 1. Introduction

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35 Spatial association between predators and prey is an essential part of ecology with implications
36 for predation rates, trophic interaction strength, and community dynamics (Hassell & May
37 1974, Abrams 2007, Ahrens et al. 2012). Theory and observations of mobile organisms show
38 that prey typically avoid predator-rich areas while predators prefer prey-rich areas, giving rise

1 to a spatial game (Lima & Dill 1990, Hugie & Dill 1994, Sih 2005). While this game has been
2 extensively studied using game theoretical models and experimentally in different systems (e.g.
3 Sih 1998, Sih 2005, Hammond et al. 2007, Williams & Flaxman 2012), observations from
4 pelagic systems are scarce. Compared to most other systems, where prey typically graze on
5 immobile resources, spatial games in pelagic systems have the characteristic that all interacting
6 players (usually piscivore–planktivore–plankton) normally are responsive and mobile. In
7 addition, light intensity and the potential for visual predation not only varies with time of day
8 but also strongly with depth, which structures the distribution of organisms in the water column
9 and adds an extra vertical dimension to the spatial game. For an observer trying to investigate
10 space use in pelagic systems, darkness and low visibility in the deep are strong obstacles to
11 monitoring animal behaviour and interactions.

12 The Barents Sea is a large, high latitude marine ecosystem characterised by a complex
13 bathymetry with shallow areas, isolated banks and deeper troughs and depressions (Wassmann
14 et al. 2006). Among the most significant species interactions in the Barents Sea, both for
15 ecosystem functioning and for population dynamics and assessment of some of the worlds'
16 richest fisheries, is the relation between cod (*Gadus morhua* L.), small pelagic fish and their
17 main resource, the krill (Gjørseter 1998, Dolgov 2002, Wassmann et al. 2006). Cod is a major
18 piscivore in the Barents Sea, and often considered a top predator in the system. It is a visually
19 searching predator (Meager et al. 2010), generally found in association with the bottom, but an
20 opportunist with flexible behaviour sometimes feeding in the pelagic (Arnold et al. 1994, Godø
21 & Michalsen 2000, Andersen et al. 2017). Its main prey item is capelin (*Mallotus villosus*) but
22 it also feeds on polar cod (*Boreogadus saida*) in the northern Barents Sea during autumn
23 (Johannesen et al. 2016). Capelin and polar cod are both visually searching planktivores, with
24 adults mainly foraging on macroplankton such as krill (Orlova et al. 2009, Dalpadado &
25 Mowbray 2013). Their spatial distribution also reflects predator avoidance, and they use
26 vertical positioning and schooling as anti-predator strategies (Mowbray 2002, Benoit et al.
27 2010). Krill are also highly mobile, using vertical migration as a proactive, light-driven anti-
28 predator behaviour (Kaarvedt et al. 1996, Onsrud et al. 2004, Zhou & Dorland 2004).

29 The small scale space use, behaviour and interactions shaping the spatial game between Barents
30 Sea cod, pelagic fish and krill has not previously been studied despite the huge ecological and
31 economic importance of these organisms. The lack of such studies is likely due to
32 methodological difficulties in observing *in situ* in open ocean systems. In the present study,
33 however, we benefitted from advances in hydroacoustic technology, using broadband systems
34 that open for long-range, non-obtrusive, high-resolution studies of predator-prey interactions.
35 We used this technology in combination with extensive stomach sampling on a research cruise
36 dedicated to investigate how light drives the spatial associations and trophic interactions
37 between krill, pelagic fish and cod. Our observations reveal a tri-trophic spatial game driven
38 by the diel- and vertical gradient of light and constrained by the seabed.

39 2. Material and methods

40 2.1. Study area, timing and platform

41 The investigation was carried out during the 8th and 9th of October 2016 on the western part of
42 the Great Bank east of Svalbard in the Northern Barents Sea (77.4°N and 28°E) on board the
43 RV 'GO Sars'. We selected the location as it contained an aggregation of co-occurring cod,
44 pelagic fish and krill. The area was 160-170 meters deep with a bottom temperature of 1°C
45 (Figure 1) and was sampled with pelagic and demersal trawls, conventional narrowband ship
46 acoustics and broadband acoustics mounted on a submersible probe.

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2.2. Biological sampling and swept area abundance estimation of cod

Cod were sampled with a Campelen 1800 shrimp demersal trawl (five hauls) with a vertical opening of approximately 3-4 m, 22 mm stretched mesh size in the cod end and a cover net with 116 mm mesh size, and pelagic fish with a Harstad pelagic trawl (five hauls) with height and width of approximately 20 m and 8 mm stretched mesh size in the cod end. Pelagic trawling was conducted in depths where dense aggregations were recorded acoustically. Towing speed was approximately 3 knots for both gears, and haul duration of demersal hauls approximately 15 minutes. For pelagic hauls the trawl was monitored with acoustic sensors and towing was discontinued when the catch was estimated to be sufficiently large to obtain a representative sample.

Cod abundance by unit area was estimated from each demersal trawl haul as the number of individuals caught divided by the product of the towed distance and the sweep width (25 meter) using the StoX software (Stox, 2015).

Catches were sorted by species and total weight and the number of individuals were recorded. The total length of all individual cod, capelin and polar cod were measured to the nearest half cm. In the case of large catches, a subsample of 100 randomly selected individuals were measured.

In order to sample plankton we used a WP2 net (e.g. Dalpadado et al. 2012). All krill specimens that could be identified either from the plankton net, trawl hauls or in stomach samples (described below) belonged to the species *Thysanoessa inermis*.

We sampled stomach contents of polar cod, capelin and cod to identify feeding relationships and verify that the species were interacting. Stomach samples were taken from 50 randomly selected cod per haul excluding cod smaller than 25 cm (5 hauls, 250 individuals). We sampled stomachs from 10 randomly selected individual capelin from both demersal and pelagic hauls (10 hauls, 100 individuals), and stomachs from 10 randomly selected individual polar cod from 3 pelagic hauls (30 individuals). Cod stomachs were sampled more extensively than pelagic fish stomachs since cod have a larger size span and wider diet range than the pelagic fish. The extensive cod stomach sampling also enabled us to study diel variation in cod feeding. The stomach content was drained of excessive fluid and sorted to the lowest possible taxonomic level. Each prey species was then categorized based on visual inspection into: 1: newly eaten, no digestion, 2: digestion has just started, 3: partly digested, 4: digested, can only be sorted to broad prey categories, 5: fully digested, cannot be classified. The content by prey species belonging to each category was then weighed separately.

We used Temming and Herrmann's (2003) model (eq. 1) for stomach evacuation in Atlantic cod to calculate the time it takes to evacuate a cod stomach, given that there is no additional feeding during the period of evacuation. Evacuation time is dependent on water temperature (T), predator mass (m_p), stomach content mass (δ_i) and a prey specific evacuation coefficient (ρ_i). Here we used the average evacuation coefficient for capelin and polar cod $(0.00749+0.00704)/2$, taken from Temming and Herrmann (2003). We calculated stomach contents for each hour starting at the time of ingestion. This was done based on the weight of

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1 the stomach content in our samples, by subtracting estimated weight of evacuated stomach
2 content per hour. The evacuation rate in grams per hour, D , is then given by:

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$$\text{Eq. 1: } D = \hat{\rho}_i m_p^{0.305} e^{0.11T} \delta_i^{0.5}$$

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3 **2.3. Acoustic recording and data processing**

4 Acoustic data were recorded from the vessel with a Simrad EK60 echosounder system
5 operating at 18, 38, 70, 120, 200 and 333 kHz. The transducers were mounted on a retractable
6 keel and the echo sounder system set up in accordance with the recommendations provided in
7 Korneliussen et al. (2008). Vessel acoustic data were logged continuously with a ping rate of
8 1 Hz on all available frequencies except during periods of acoustic probe operations (see
9 section below), when only the 18 kHz was active to avoid interference between echosounders.

10 A submersible acoustic probe (Ona & Pedersen 2006) was applied with the primary aim of
11 investigating individual fish behaviour based on target tracking. The probe is designed to be
12 submerged for close range acoustic recordings at different depths. In our set-up we mounted
13 four Simrad EK80 broadband echo sounders on the probe operating at nominal centre
14 frequencies of 38, 70, 120 and 200 kHz. All echosounders were calibrated using the standard
15 sphere method (Demer et al. 2015). We tested the acoustic probe using different experimental
16 set-ups. We had the best results when the vessel was kept in a fixed position using the Dynamic
17 Positioning System, and using the 120 kHz EK80 (configured to use a 95-160 kHz frequency
18 modulated pulse of duration 1.024 ms) about 120 m above the bottom. This range covered most
19 of the water column where predator/prey interactions could be expected and also ensured a
20 relatively large sampled volume close to the bottom where cod were expected to occur (with a
21 vertical sample resolution of 8.0 mm, sampling volume is 1.35 m³ at 120 m range given our
22 detection settings).

23 We used the Large Scale Survey System (LSSS) post-processing software (Korneliussen et al.
24 2016) for all acoustic data processing. In particular, the broadband echoes were pulse-
25 compressed (Chu & Stanton 1998 and references therein) to yield a dataset with high range
26 resolution, from which echoes of individual cod and capelin were detected and used as input
27 to tracking algorithms (see table S1 in supplementary for details on the target detection settings
28 applied). An example of detected tracks with the settings used for cod is seen in figure 2.

29 In order to investigate the vertical distribution of krill and pelagic fish, we analysed the
30 multifrequency acoustic data from the vessel. Multifrequency data were only available in the
31 periods between the deployments of the probe (see above), but these data enabled automated
32 discrimination between targets. The discrimination is based on the expected differences in
33 frequency response between pelagic fish and krill and implemented using pre-processing
34 routines in LSSS (see supplementary material for details on the discrimination routines
35 applied).

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39 **2.4. Hydrography and light**

40 Casts down to 10 m above the seabed to measure conductivity, temperature and depth were
41 carried out using a Seabird 911 CTD probe. Photosynthetically active radiation (PAR) was also
42 measured during the CTD-cast and the values were used to estimate light attenuation with
43 depth. However, the sensitivity of the mounted sensor only allowed accurate measurements
44 down to about 0.1 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. In addition to the CTD light sensor, a LI-1400 radiation
45 sensor was mounted on the side railing on top of the bridge for measuring surface light at 15

1 minutes intervals. Surface light and attenuation coefficients were used to calculate ambient
2 radiance at depth to evaluate the role of light in triggering observed behavioural responses.

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4 **2.5. Statistical analyses**

5 In order to quantify to what extent the spatial distribution of pelagic fish as observed
6 acoustically was clustered or dispersed we calculated the index of dispersion (I) which is a
7 normalized measure of the dispersion of a probability distribution, and calculated as the ratio
8 of the variance to the mean (Perry et al. 2002). The index was calculated per one minute interval
9 from the 18 kHz recordings using 1 m depth resolution. For testing whether significant changes
10 in the index values occurred over the diel cycle we used the R changepoint package (Killick &
11 Eckley 2014).

12 As a test of whether or how the feeding behaviour of cod varied over the diel cycle, we
13 modelled the probability of occurrence of newly eaten pelagic fish (digestion stage 1 and 2;
14 section (b)) in a cod stomach using logistic regression assuming a binomial distribution of the
15 error term in R version 3.4.3 (R Core Team 2017).

16 **3. Results**

17 Pelagic fish and krill followed the light intensity closely over the diel cycle, descended around
18 dawn and ascended around dusk, and avoided light intensities above $0.001 \mu\text{mol photons m}^{-2}$
19 s^{-1} (Figure 3a). During daytime, krill were found close to the bottom (Figure 3b), while pelagic
20 fish remained from a few to 50 m above the bottom. During night-time both krill and pelagic
21 fish dispersed throughout the water column. The degree of aggregative behaviour (indicated
22 by the dispersion index as a measure of variance in acoustic backscatter) differed markedly
23 between night and day (Figure 3b). The values were lower and more even during night-time as
24 a result of dispersion, and variable (occasionally high) during daytime indicating clustering and
25 aggregation. Significant change points in the dispersion index were identified shortly after dusk
26 at 17.22 and shortly prior to dawn at 1.13 UTC.

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2 We were not able to distinguish echo recordings of cod from the standard narrowband vessel-
3 mounted echosounder data, due to low vertical resolution. However, the submerged probe and
4 high range resolution of the broadband acoustics rendered cod readily detectable and
5 identifiable (see Figure 2 for an example echogram). Cod stayed within 10 m of the bottom
6 through the periods of observations with the probe, but cod tracks were more abundant,
7 extended over a higher vertical range, and reached higher above the seabed in the morning
8 (indicating higher activity) than at other times of the day (Figure 4). The indication of increased
9 activity level in the morning corresponded with a higher probability of finding fresh pelagic
10 fish in the cod stomachs at this time of the day (Figure 4, detailed results from the logistic
11 model are found in table S1 in supplementary).

12 Pelagic fish tracks were more abundant after dark when schools dispersed and single
13 individuals could be acoustically resolved as tracks (Figure 4). The distance above bottom was
14 higher in the day than during the night. During the transition from dusk to darkness, some
15 pelagic fish approached the bottom zone which they had avoided during daylight hours (Figure
16 4).

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2 The average cod abundance per area was estimated to be 6488 cod per km² in our study area
3 with the results varying from 1351 to 10355 cod per km² depending on trawl sample. Most cod
4 were longer than 25 cm. Of the 250 cod stomachs analysed, 18% were empty. Empty stomachs
5 were more frequent for smaller cod. Of the stomachs containing food, 78% contained pelagic
6 fish (See fig. S1 in supplementary material for more details on the cod diet).

7 The evacuation rate of the cod stomachs over time is shown in Figure 5. For the fullest
8 stomach found in our study, it would take more than ten days to reach complete evacuation
9 and it would take about 50 hours to digest half of a median sized meal.

10 The pelagic trawl samples were dominated by capelin >15 cm in length, whereas the polar cod
11 caught were mostly less than 13 cm in length. Overall, 2.2 times more capelin than polar cod
12 were caught in the pelagic hauls. However, potential differences in catchability between the
13 species could not be determined and the actual ratio of the two species in the area could
14 therefore not be determined. Of the 99 capelin stomachs analysed, 52% were empty. Of the
15 stomachs containing food, 48% contained krill, while the others mostly contained highly
16 digested unidentifiable crustaceans. All 29 polar cod stomachs contained food, mostly krill and
17 unidentified crustaceans (See fig. S2 in supplementary material for more details on the diet of
18 pelagic fish).

19 4. Discussion

20 The spatial associations and interactions between cod, pelagic fish and krill were dynamic and
21 closely followed the diel cycle. Cod were visible only with high-resolution broadband acoustics
22 since they resided close to the seabed and barely lifted from the bottom, except during the early
23 morning hours, when they also had more fresh prey in the stomachs. Krill stayed close to the
24 bottom during daytime sharing habitat with the cod, but dispersed and overlapped spatially
25 with pelagic fish during night. The planktivores aggregated in pelagic schools during day only
26 approaching the bottom to hunt krill around dusk and dawn, probably to reduce predation risk
27 from cod.

28 Cod seemed to take advantage of the time-window when the combination of light levels and
29 prey distribution was optimal for efficient visual hunting. Previous studies have shown that
30 the diel feeding rhythms of cod are flexible (Meager et al. 2018 and references therein), and
31 optimal foraging theory predicts that predators should optimise the energy gained feeding per
32 unit time relative to the energy spent for food search, capture and digestion (MacArthur &
33 Pianka 1966). Cod diel cycle behaviour is most likely a reflection of such an optimisation
34 (Løkkeborg et al. 1989, Løkkeborg 1998). About 1/3 of the cod had newly eaten pelagic fish
35 in the stomachs in the morning, indicating that an average cod fed on pelagic fish only every
36 third day (Figure 4). The low feeding rate is probably related to low temperatures. The cold
37 waters restrict rapid vertical movements since cod have a physoclist swimbladder and the
38 process of secreting gas into the swimbladder is slow at low temperatures (Harden Jones &
39 Scholes 1985). In addition, digestion rate is very slow at the temperatures observed in our
40 study area (Gill 2003), and the low temperatures are likely also influencing other processes
41 relevant for predation such as swimming speed and vision (Fritsches et al. 2005, Ohlund et al.
42 2015).

43 The pelagic fish showed a strong diel vertical migration and adjusted their position in the water
44 column to depths where low light levels may inhibit efficient prey detection by visual predators

1 (Warrant & Johnsen 2013). When light levels were sufficient to permit visual prey search all
2 the way down to the seabed, the pelagic fish responded by aggregating and forming schools
3 higher up in the water column – a common anti-predator strategy (Pitcher & Parrish 1993).
4 Both diel vertical migration and schooling in the pelagic come at the cost of lost feeding
5 opportunities on krill, which resided among the cod close to the seabed during daytime. Except
6 for night-time, the highest spatial overlap between pelagic fish and krill were around dusk and
7 dawn, and most interactions likely occurred then. However, our results further showed that a
8 majority of capelin guts were empty, suggesting that most capelin assessed predation risk as
9 too high to engage in foraging. Polar cod apparently assessed danger differently, but stomach
10 data here are too scant to allow for a good comparison with capelin.

11 Krill is the key organism for understanding spatial distributions in this tri-trophic game since
12 it attracts the pelagic fish to enter the preferred habitat for cod. It is not clear how beneficial
13 the situation is for krill on the banks at this time of year. On the one hand, the shallow depths
14 of the bank areas limit krill from undertaking extensive vertical migrations out of the zone
15 where they are visible to predators (Kaartvedt et al. 1996; Onsrud et al. 2004; Zhou and Dorland
16 2004). Light penetrates down to the bottom during daytime and krill are blocked from
17 descending further down to escape the threats of visual predation (Aarflot et al. 2018). On the
18 other hand, bottom association appears to effectively reduce the predation risk for krill in our
19 system, since the pelagic fish school and aggregate at a safe distance from the sea floor that is
20 occupied by cod. Paradoxically, krill may therefore gain safety by “hiding among the cod”.

21 Oceanic banks are among the most productive marine areas, and trophic interactions here are
22 important for the productivity and dynamics of entire ocean ecosystems. Still, studies are scarce
23 since observation conditions are very challenging. We demonstrate here that spatial games
24 between key players in an open ocean bank system can be observed with modern technology.
25 In particular, real-time, high resolution, concurrent spatial information of deep-water
26 organisms spanning over a wide size range can be obtained using broadband acoustics. Such
27 techniques open up new possibilities for unobtrusive investigations of marine predator-prey
28 interactions *in situ*.

29
30 *Acknowledgements.* We thank the crew and captain of ‘G.O. Sars’ for excellent assistance and
31 collaboration during the survey. We thank Ronald Pedersen, Asgeir Steinsland and Ole Sverre
32 Fossheim for outstanding technical assistance and Ørjan Sørensen, Kirsti Børve Eriksen[‡], and
33 Inger Marie Beck for superb assistance in the lab during the survey. The project was financed
34 by the Norwegian Research Council project number 243676/E40.

35 [‡]Deceased 7 November 2018

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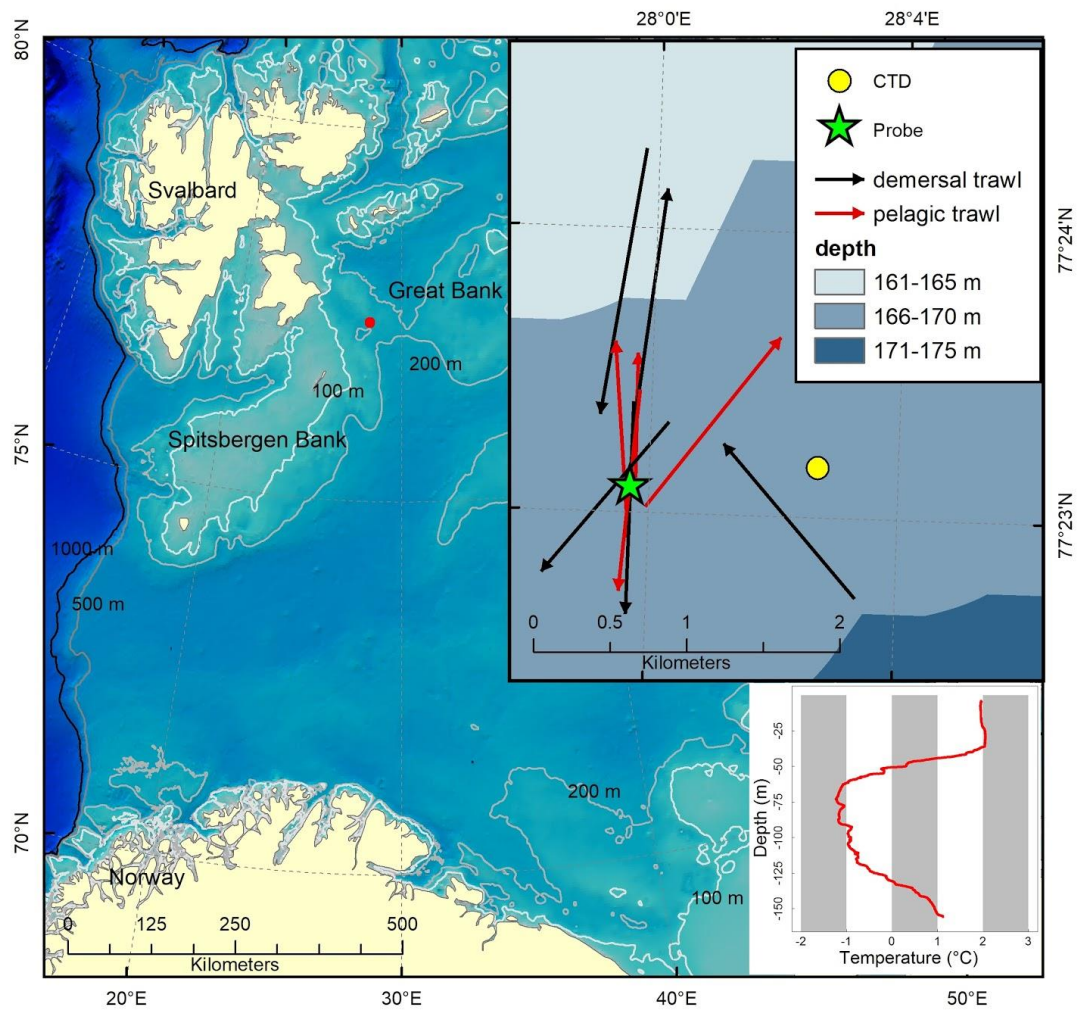
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1 Figures

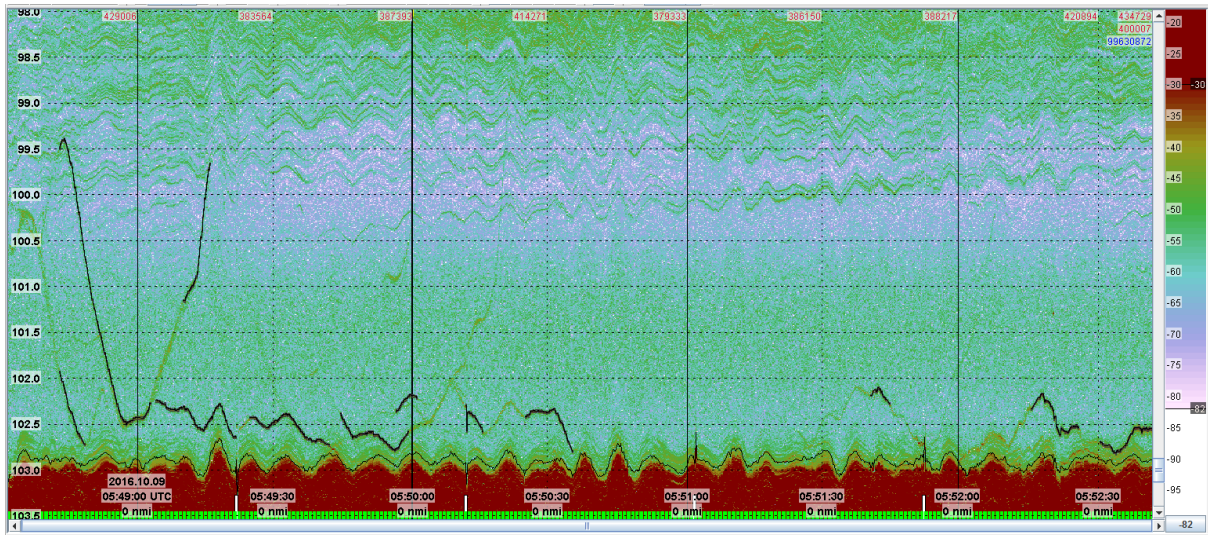


2

3 **Figure 1.** Overview of study area (red dot on the map) including trawl positions (upper right panel) and vertical
 4 temperature profile (lower right panel). Yellow dot marks position of the Conductivity Temperature Depth
 5 (CTD)-cast, and green star the position of the submersible acoustic probe (see section c).

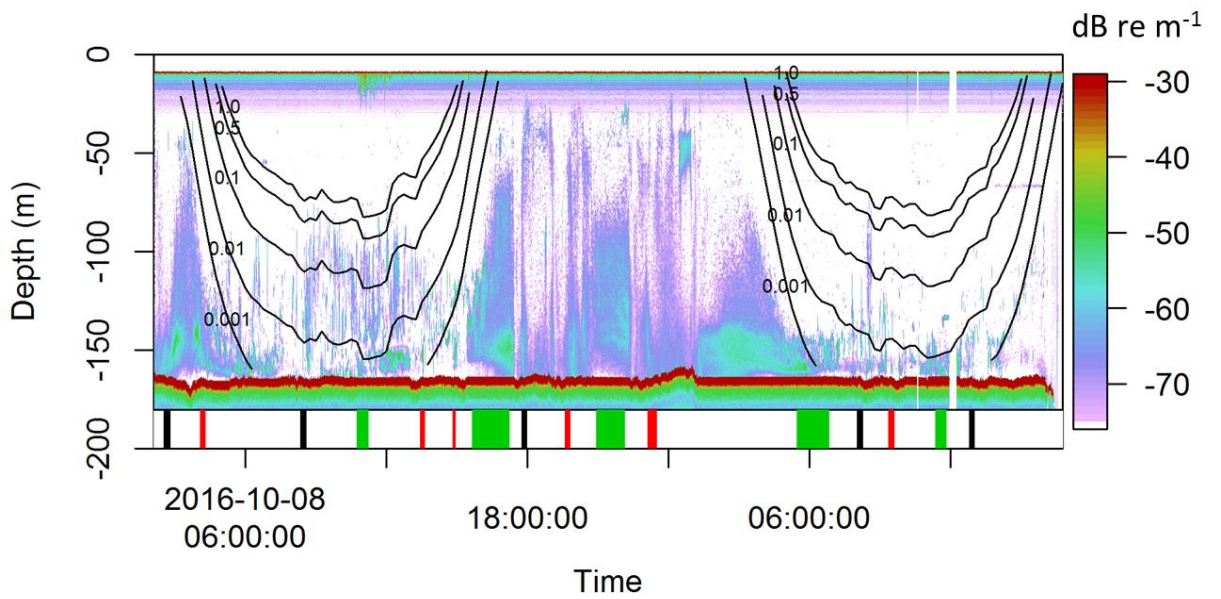
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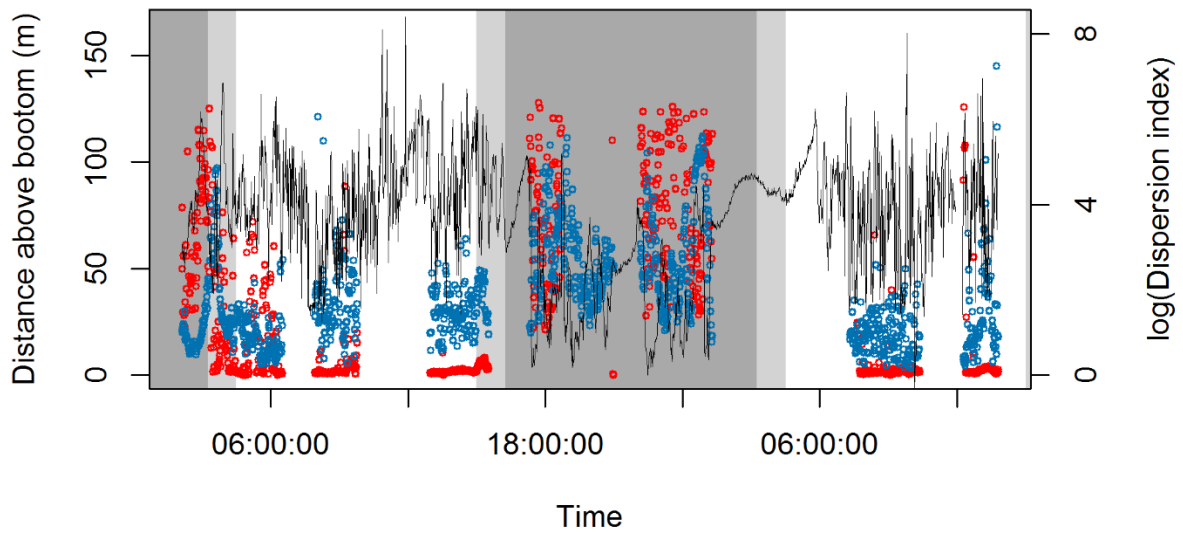


1
 2 **Figure 2.** Echogram example showing cod tracks (marked in black) recorded over a period of 4 minutes with
 3 the vessel lying still using the dynamic positioning system. Individual pelagic fish (capelin and polar cod) are
 4 visible in the upper part of the excerpt as green tracks. The data are pulse compressed (95-160 kHz) from a
 5 Simrad EK80 echo sounder mounted on an acoustic probe at a depth of ca. 60 m. The values on the left refer to
 6 vertical distance from the acoustic probe.

7 a)

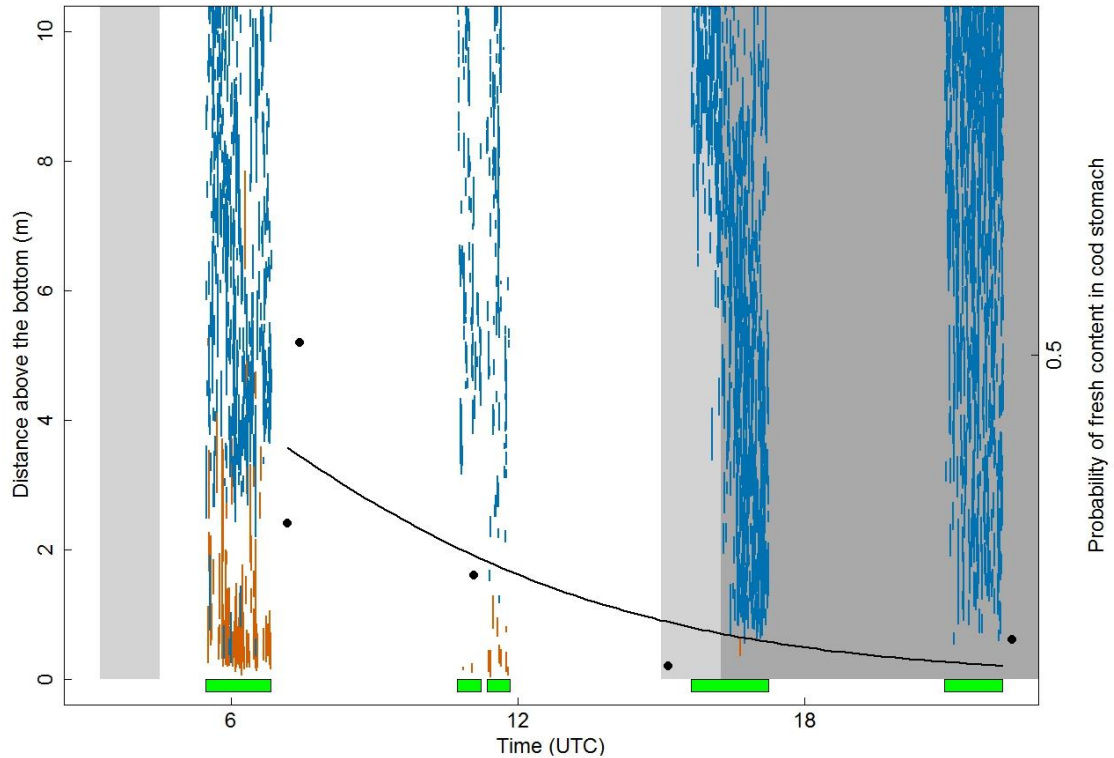


8 b)



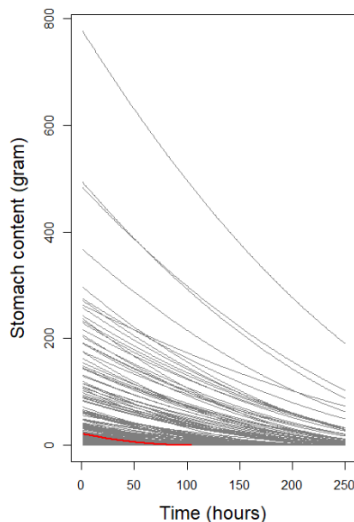
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2 **Figure 3. a)** Acoustic echogram showing distribution of pelagic fish in the water column during a day-night-day
 3 cycle. Low values (purple colours) indicate dispersed distribution while high values (green colours) indicate
 4 dense aggregations. The acoustic probe was deployed during periods marked in green below the main panel, and
 5 timing of trawl hauls are marked in red (pelagic) and black (demersal). The echogram recordings are from the
 6 vessel mounted 18 kHz echosounder and displays backscatter in units of S_v (dB re m^{-1}) at a temporal resolution
 7 of 15 second and vertical resolution 19 cm. The superimposed depth contours mark five discrete light levels
 8 based on daily surface irradiance measurements (IM_s), $W m^{-2}$, $\mu mol m^{-2}s^{-1}$, with light at depth (IM_D) calculated
 9 as: $IM_D = IM_s * e^{(-0.064 * D)}$. **b)** Mean depth distribution of krill (red) and pelagic fish (blue) derived from acoustic
 10 recordings. The black line is the dispersion index with high values indicating patchy distribution of the pelagic
 11 fish and low values uniform distribution. Light grey sectors correspond to dawn (3.15-4.30) or dusk (15-16.15),
 12 dark grey to night-time and white to daytime (see text for further details).



1

2 **Figure 4.** Overview of acoustic tracks of pelagic fish (blue) and cod (brown) within 10 m from the detected
 3 seabed, using the probe (green and grey shading as in Figs. 2 and 3). The length of the vertical lines corresponds
 4 to the vertical range of a given fish track. The tracks are extracted from a 120 kHz broadband echosounder
 5 mounted on a probe submerged to 120 m above the bottom. The black dots denote observed probability of
 6 finding fresh content in cod stomachs at a given time of the day (N=50 stomachs per sampling point), and the
 7 fully drawn line denotes the fit of a GLM-model. The model predicts probability of newly swallowed prey
 8 (binomial) as a function of hours past dawn with a binomial distribution of the error term.



9

10 **Figure 5.** The time it takes to fully evacuate a cod stomach at the bottom temperature (1.5° C) in our study area.
 11 Each line represents a stomach sample (non-empty stomachs of cod > 25 cm, n=204), the y axis is the stomach
 12 content weight in grams and on the x-axis hours after ingestion. The red line denotes evacuation of a stomach
 13 with median content.