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Diel vertical movements determine spatial interactions between cod, pelagic fish and krill on an Arctic shelf bank

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ABSTRACT: Predator–prey spatial interactions are essential to understand ecosystem processes like predation rates and trophic interaction strength. In marine systems, such spatial interactions are highly dynamic and difficult to observe, as predators, prey and resources are mobile and responsive to each other, and also since shifting vertical light gradients strongly affect the space use of visual predators and their prey. We visited a bank area in the northern Barents Sea with cold bottom waters (~1°C), and combined conventional trawl and acoustic sampling with broadband hydroacoustics to obtain long-range, fine-scale observations of interactions between cod, their planktivore prey (capelin and polar cod) and krill. We caught cod in demersal trawl hauls but could not detect them with the vessel acoustics. However, broadband acoustics mounted on a submersible probe allowed us to track individual cod, revealing that they remained mostly within 10 m of the bottom throughout the diel cycle. In the morning, cod lifted slightly from the seabed indicating feeding activity, which corresponded with more fresh prey in cod stomachs in the morning. During daylight, krill pushed towards the bottom, sharing habitat with cod, while the planktivores aggregated in pelagic schools at the cost of lost feeding opportunities, overlapping with their krill prey only during twilight hours. The diel light cycle was an important driver of the spatial movements and aggregations, and krill appear to hide from capelin among the cod near bottom, while cod take advantage of descending pelagic fish after dawn to feed with a minimum of effort.

KEY WORDS: Diet · Predator–prey interaction · Barents Sea · *Gadus morhua* · *Mallotus villosus*

1. INTRODUCTION

Spatial overlap between predators and prey is an essential part of ecology with implications for predation rates, trophic interaction strength and community dynamics (Hassell & May 1974, Abrams 2007, Ahrens et al. 2012). Mobile prey avoid predator-rich areas while predators are attracted to prey-rich areas, clearly conflicting responses which give rise to a highly dynamic interplay (Lima & Dill 1990, Hugie & Dill 1994, Sih 2005). Predator–prey spatial associations in pelagic systems have the characteristic that predators, prey and the resource of the prey (piscivore–planktivore–zooplankton) are responsive and mobile, which gives rise to complex space use. In addition, light intensity and the potential for visual predation varies over the diel cycle, with season, latitude and depth (Langbehn et al. 2019). Several studies have addressed predator–prey interplay in pelagic systems, in particular vertical migration of

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plankton in response to predation, under different environmental conditions using theoretical models (Ohman & Romagnan 2016, Pinti et al. 2019, Pinti & Visser 2019) and field studies (see review by Hays 2003). Nevertheless, for an observer trying to investigate animal space use in pelagic systems, darkness and low visibility in the deep are strong obstacles, and interplay over several trophic levels between organisms ranging orders of magnitude in size is particularly challenging to observe.

The Barents Sea is a large, high-latitude marine ecosystem characterised by a complex bathymetry with shallow areas, isolated banks and deeper troughs and depressions (Wassmann et al. 2006). Among the most significant species interactions in the Barents Sea, both for ecosystem functioning, population dynamics and fisheries assessment, is that between cod *Gadus morhua* L., small pelagic fish and their main resource, krill (Gjøsæter 1998, Dolgov 2002, Wassmann et al. 2006). Cod is a major piscivore in the Barents Sea, and is often considered a top predator in the system. It is a visually searching predator (Meager et al. 2010), generally found in association with the bottom, but an opportunist with a wide diet and flexible behaviour sometimes feeding in the pelagic (Arnold et al. 1994, Godø & Michalsen 2000, Andersen et al. 2017). Its main prey item is capelin *Mallotus villosus*, but it also feeds on polar cod *Boreogadus saida* in the northern Barents Sea during autumn (Johannesen et al. 2012, 2016). Capelin and polar cod are both visually searching planktivores, with adults mainly foraging on macroplankton such as krill (Orlova et al. 2009, Dalpadado & Mowbray 2013). Their spatial distribution also reflects predator avoidance, and they use vertical positioning and schooling as anti-predator strategies (Mowbray 2002, Benoit et al. 2010). Krill are also highly mobile, using vertical migration as a proactive, light-driven anti-predator behaviour (Kaartvedt et al. 1996, Onsrud et al. 2004, Zhou & Dorland 2004).

The fine-scale space use and behaviour determining interactions between Barents Sea cod, pelagic fish and krill have, to the best of our knowledge, not previously been studied. At least in part, this must be attributed to difficult observing conditions in open ocean systems. In the present study, we benefitted from broadband hydroacoustics which only recently has become commercially available. The acoustic broadband technology allows for long-range, nonobtrusive, high-resolution studies of predator–prey interactions. We used this technology in combination with intensive stomach sampling on a research cruise dedicated to investigating how light drives the spatial associations and trophic interactions between krill, pelagic fish and cod. Our observations reveal a tri-trophic spatial game driven by the diel and vertical gradient of light and constrained by the seabed.

2. MATERIALS AND METHODS

2.1. Study area, timing and platform

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

2.2. Biological sampling and swept area abundance estimation of cod

Cod were sampled with a Campelen 1800 shrimp demersal trawl (5 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 (5 hauls) with height of approximately 12 m and 8 mm stretched mesh size at the cod end. Pelagic trawling was conducted at depths where dense aggregations were recorded acoustically. Towing speed was approximately 3 knots for both gears, and duration of demersal hauls was approximately 15 min. 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. All krill specimens that could be identified from the trawl hauls or in stomach samples (described below) belonged to the species *Thysanoessa inermis.*

Trawl catches were sorted by species and total weight, and the numbers of individuals were recorded. The total length of all individual cod, capelin and polar cod were measured to the nearest 0.5 cm. In the case of large catches, a subsample of 100 randomly selected individuals were measured for length.

We used the Stox software (Johnsen et al. 2019) to estimate swept area abundance by length group. Cod abundance by 5 cm length groups by unit area

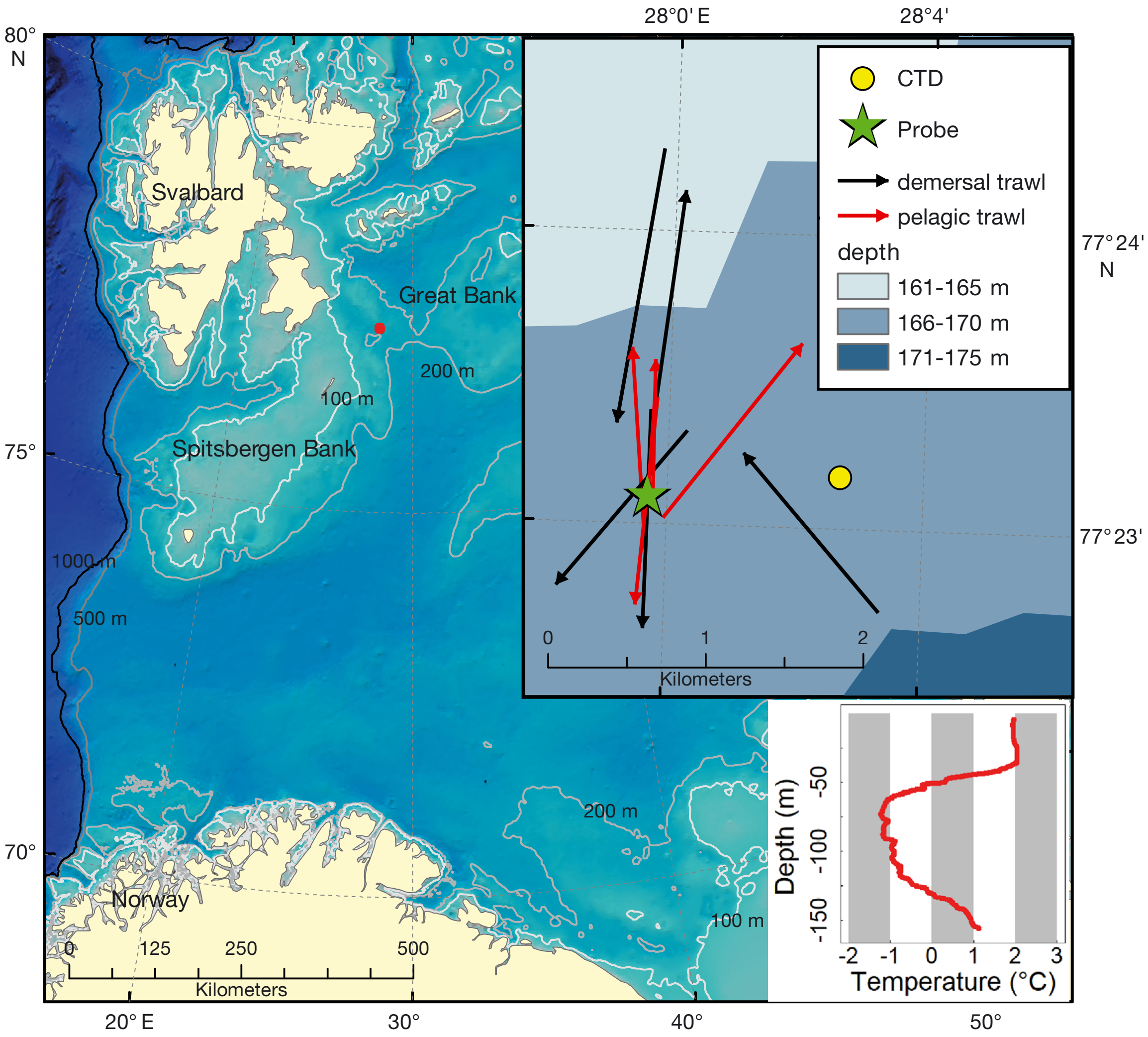

Fig. 1. Overview of study area (red dot on the map) including trawl positions (upper right panel) and vertical temperature profile (lower right panel). Yellow dot marks position of the conductivity-temperature-depth (CTD)-cast, and green star marks the position of the submersible acoustic probe (see Section 2.3)

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 m). Capelin and polar cod abundances by 1 cm length groups were calculated from each pelagic trawl as the number of individuals caught divided by the product of the towed distance and the sweep width (20 m).

We sampled stomach contents of polar cod, capelin and cod to identify feeding relationships and verify that the species were interacting. The protocol was to sample 50 randomly selected cod >25 cm per haul (5 hauls = 250 cod stomachs; however, 11 stomachs from cod <25 cm were erroneously analysed, and these were excluded from the calculations below). We sampled stomachs from 10 randomly selected individual capelin from both demersal and pelagic hauls (10 hauls), and stomachs from 10 randomly selected individual polar cod from 3 pelagic hauls. With limited capacity in the lab, we prioritized cod stomachs to be sampled more extensively than pelagic fish stomachs, since cod have a larger size span and wider diet range than the pelagic fish. The intensive 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.

Since stomach evacuation has a strong impact on feeding rate, we assessed the time it would take each individual cod to empty its stomach based on the stomach fullness at the time of sampling. We used the stomach evacuation model developed by Temming & Herrmann (2003) for Atlantic cod. Stomach contents at time *t* were found by integration:

$$S(t) = [S(0)^{0.5} - 0.5rt]^2 \qquad (1)$$

where $S(t)$ is the stomach content at time t after feeding, and r is the rate at which prey are evacuated. This rate is dependent on a prey-specific evacuation constant ($\hat{\rho}$), the mass of the predator (m_p), ambient temperature (T) and the initial prey mass consumed ($S(0)$) (Temming & Herrmann 2003):

$$r = \hat{\rho} m_p{}^{0.305} e^{0.11T} S(0)^{0.5} \qquad (2)$$

We calculated a representative prey evacuation constant for each stomach as the mean of evacuation constants for all prey in the stomach weighted by the mass of the prey. We used the prey-specific evacuation coefficients from Temming & Herrmann (2003). For prey not included by Temming & Herrmann (2003), we used coefficients from similar prey (see Supplement 1 for details; all Supplements are at www.int-res.com/articles/suppl/m638p013_supp/).

From Eq. (1), we calculated the hypothetical time needed to completely evacuate the content of the stomach for each cod sampled; evacuation was assumed to start at the time of capture and last until complete evacuation given that the cod had survived, and stayed at the same temperature without any additional feeding.

2.3. Acoustic recording and data processing

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

A submersible acoustic probe (Ona & Pedersen 2006) was applied with the primary aim of investigating individual fish behaviour based on target tracking. The probe is designed to be submerged for close-range acoustic recordings at different depths. In our set-up, we applied Simrad EK80 broadband echo sounders with 4 transducers mounted on the probe operating at nominal centre frequencies of 38, 70, 120 and 200 kHz. All echo sounders were calibrated using the standard sphere method (Demer et al. 2015). We tested the acoustic probe both with the vessel drifting and with the vessel in a fixed position using the Dynamic Positioning System, and we also tested different ranges to the target and several combinations of the available frequencies. When the vessel was kept in a fixed position, it typically enabled tracking of individual fish for a longer period than when drifting, and more importantly circumvented the potential effect that changing locations could have on the results. Only data from the fixed position periods have been included in the analyses. We preferred to run only 1 echo sounder channel at a time when tracking fish since this allowed for fast pinging (ping interval of ca. 0.18 s) without cross-talk interference between simultaneously pinging broadband channels. The 70 kHz transducer malfunctioned during the survey, and of the available frequencies left, the 120 kHz provided the best compromise between resolution and detection range for our purpose. The 120 kHz echo sounder was configured to use a 95–160 kHz frequency modulated pulse of 1.024 ms duration. Beam widths are 8.8° and 5.2° at 95 and 160 kHz, respectively. The range resolution of the pulse-compressed signal was about 10 mm, but we observed that the strong seafloor echo and pulse-compression side-lobes obscured all cod echoes until about 80 mm above the seafloor.

A range to the bottom of about 120 m covered most of the water column where predator–prey interactions could be expected and also ensured a relatively large sampled volume close to the bottom where cod were expected to occur (with a vertical sample resolution of 8.0 mm, sampling volume is 1.35 m^3 at 120 m range given our detection settings).

We used the Large Scale Survey System (LSSS) post-processing software (Korneliussen et al. 2016) for all acoustic data processing. In particular, the broadband echoes from the submersible probe were pulse-compressed (Chu & Stanton 1998 and references therein) to yield a dataset with high range resolution, from which echoes of individual cod and capelin/polar cod were detected and used as input to tracking algorithms. Visual inspection of the echograms from the probe showed fish tracks close to the seabed which corresponded with cod tracks by their echo strength and track profile. We used a small subsample of the data comprising such tracks to adjust the settings for the target detection and tracking. In LSSS, the single target detection is as presented by Soule et al. (1996) and the detection of fish tracks from the single target detection is via an alpha-beta tracker (Blackman 1986). In particular, we used a minimum target strength (TS) threshold of −36 dB re 1 m^{-1} for the detection of cod tracks. This threshold is high and above the TS expected of small cod at 120 kHz based on theoretical TS to length relationships (Foote 1980). We used this high threshold in order to minimise the possibility of including tracks from pelagic fish among the detected cod. A consequence of the high threshold is that tracks from small cod and weaker echoes from larger cod might be lost. An example of detected tracks with the settings used for cod is shown in Fig. 2. A high minimum TS threshold of −55 dB was used for pelagic fish based on a similar rationale to minimise the risk of inclusion of echo from smaller organisms, in particular krill. Details on the target detection settings we applied are provided in Table S1 in Supplement 2.

In order to investigate the vertical distribution of krill and pelagic fish, we analysed the acoustic multifrequency data from the vessel. Multifrequency data were only available in the periods between the deployments of the probe (see above), but these data enabled automated discrimination between targets. The pre-processing module KORONA in LSSS was used for removing spike noise and for bottom detection. An upper integration limit of 15 m and an offset of 0.5 m from the detected bottom were applied to the pre-processed data to avoid spurious echoes. We used the categories 'krill_north' and 'krill_thysanoessa' from the species categorization library in KORONA (Korneliussen et al. 2016) to first discriminate echoes assumed to originate from krill from other echoes. This was done by setting the minimum threshold to −82 dB re 1 m^{-1}, and data categorized as krill were exported from the 120 kHz in units of Nautical Area Scattering Coefficient (NASC; m^2 [nautical mile]$^{-2}$; MacLennan et al. 2002). We then filtered the echoes categorized as krill out of the data using the conditional masking functionality in LSSS. The remaining data were split into echo strength of >−70 dB re 1 m^{-1}, which were allocated to 'pelagic fish', and <−70 dB re 1 m^{-1}, which were allocated to 'others', and data categorized as 'pelagic fish' were exported at 38 kHz. All data were exported on a grid resolution of 1 min horizontally and 1 m vertically. Cod tracks were not observed in the echo sounder data from the vessel.

To investigate whether the fine-scale spatial distribution of pelagic fish (aggregated or dispersed) as observed acoustically changed over the diel cycle, we used the 18 kHz data which had been recorded continuously during the entire study period. The data were resolved in 1 min intervals at 1 m depth bins. At 18 kHz, krill is a very weak scatterer and since cod were only present in small vertical segments of the echogram, we considered the 18 kHz echo scattering to be a good proxy of pelagic fish distribution over the water column. Based on the data, we calculated an index of dispersion to quantify patchiness in depth distribution based on acoustic backscatter. The index of dispersion is a normalized measure of the dispersion of a probability distribution, and it is calculated as the ratio of the variance to the mean (Perry et al.

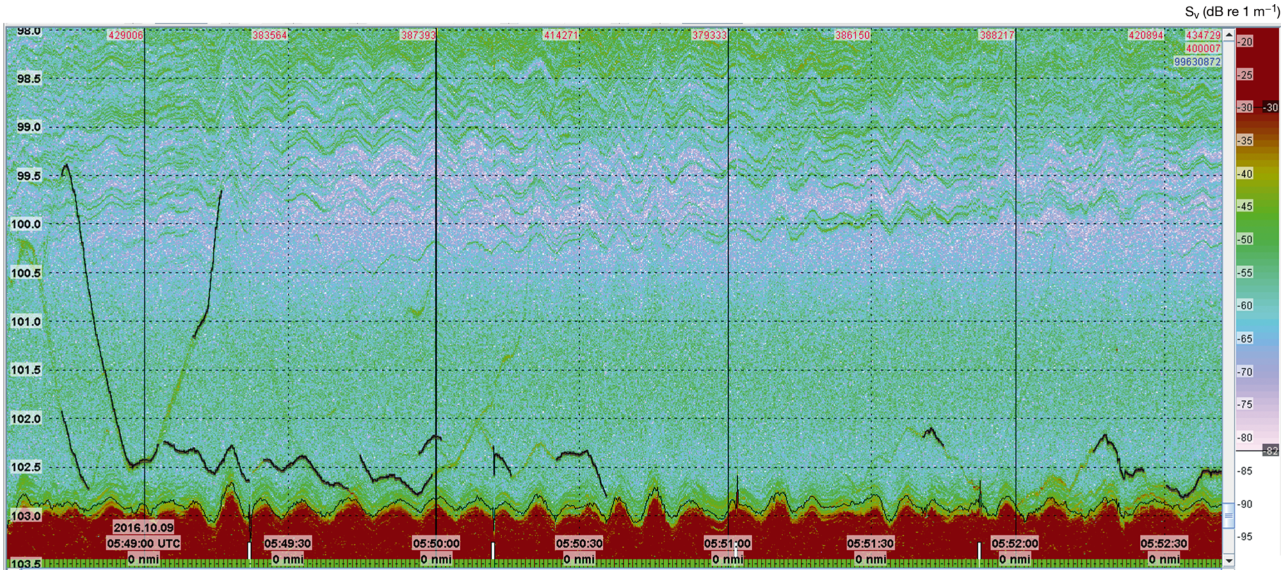

Fig. 2. Echogram example showing cod tracks (marked in black) recorded over a period of 4 min with the vessel lying still using the dynamic positioning system. Acoustic backscatter is diplayed in units of S_v (dB re 1 m^{-1}). Individual pelagic fish (capelin and polar cod) are visible in the upper part of the excerpt as green tracks. The data are pulse-compressed (95–160 kHz) from a Simrad EK80 echo sounder mounted on an acoustic probe at a depth of ca. 60 m. Values on the left refer to vertical distance (m) from the acoustic probe

2002). The index value is equal to 0 for a constant random variable, equal to 1 in a poisson distribution and >1 in a negative binomial distribution (over-dispersion) corresponding to a clustered or clumped distribution.A changepoint analysis was used to identify whether and when changes or shifts in the index of dispersion occurred (see Section 2.5).

In total, we thus worked with 3 data layers from the acoustic recordings: 120 kHz broadband data which were available from the periods of probe deployment and were used for assessing individual behaviour of cod and pelagic fish; multifrequency data from the vessel which were available from the periods between probe deployments, and were used for assessing vertical distribution of krill and pelagic fish; and finally 18 kHz data from the vessel available from the entire period and used for assessing degree of aggregation or dispersion through the diel cycle.

2.4. Hydrography and light

A CTD-cast down to 10 m above the seabed to measure conductivity, temperature and depth was carried out using a Seabird 911 CTD probe. Given that the study location was small and the duration of the study was short, we only conducted 1 cast. Photosynthetically active radiation (PAR) was also measured during the CTD cast using a Biospherical QSP-200L, SN 4654 sensor. However, the sensitivity of the mounted sensor only allowed accurate measurements down to about 0.1 µmol photons m^{-2} s^{-1}. We used the CTD data to find the local depth-averaged attenuation coefficient (K, m^{-1})

$$K = \ln[I_s/I_z]/Z \tag{3}$$

where I_s is the radiance at the surface and I_z the radiance at depth Z safely within the sensitivity range of the light sensor). This gave an attenuation coefficient of –0.064 m^{-1}, a typical value for the Barents Sea in autumn (Aarflot et al. 2019). Assuming this value throughout the water column, we calculated ambient radiance (I_D) at depth (D, in m) as:

$$I_D = I_S e^{(-0.064D)} \tag{4}$$

In addition to the CTD light sensor, a LI-1400 radiation sensor was mounted on the side railing on top of the bridge for measuring surface light at 15 min intervals. We calculated theoretical values for sunrise and sunset, dusk and dawn based on solar angle as implemented in the package 'suncalc' run with R version 3.6.1 (Thieurmel & Elmarhraoui 2019).

2.5. Statistical analyses

In order to identify whether and when changes or shifts in the index of dispersion occurred over the diel cycle, we used binary segmentation as implemented in the 'changepoint' package run with R version 3.6.1 (Killick & Eckley 2014) considering change in both mean and variance. We log-transformed the test statistic and assumed it followed a normal distribution. We set the maximum number of changepoints to 2 to reflect the expectation of change related to the 2 diel transition periods.

As a test of whether or how the feeding behaviour of cod varied over the diel cycle, we modelled the probability of occurrence of newly eaten pelagic fish (digestion stages 1 and 2; see Section 2.2) in a cod stomach (n = 239) as dependent upon hours since civil dawn using mixed logistic regression assuming a binomial distribution and with station (n = 5) as a random factor. Civil dawn and dusk are the moments when the sun is 6 degrees below the horizon in the morning or evening respectively; civil twilight is the period between civil dawn and sunrise or sunset and civil dusk. We also attempted models with cod length and stomach fullness (excluding the newly eaten pelagic fish) as independent variables. The latter was included based on the rationale that cod of different sizes may not have the same probabilities of feeding on pelagic fish, and that motivation for and possibility of feeding may be reduced as the stomach fills up with prey. The 'lme4' package run with R version 3.5.3 was used for the analysis (Bates et al. 2015). Akaike Information Criterion (AIC) was used to evaluate the quality of the different models. The R code used for the regression analyses is available in Supplement 3.

3. RESULTS

Pelagic fish followed the light intensity closely over the diel cycle, descended around dawn and ascended around dusk, and avoided light intensities above 0.001 µmol photons m^{-2} s^{-1} during these diel transition periods (Fig. 3a). During daytime, pelagic fish remained from a few to 50 m above the bottom while krill were found close to the bottom (Fig. 3b). During night-time, both krill and pelagic fish dispersed throughout the water column. The degree of pelagic fish aggregative behaviour as indicated by the dispersion index differed markedly between night and day (Fig. 3b). Lower index values during night-time indicate dispersed distribution versus more clustered and aggregated distribution during daytime. Civil dusk was at

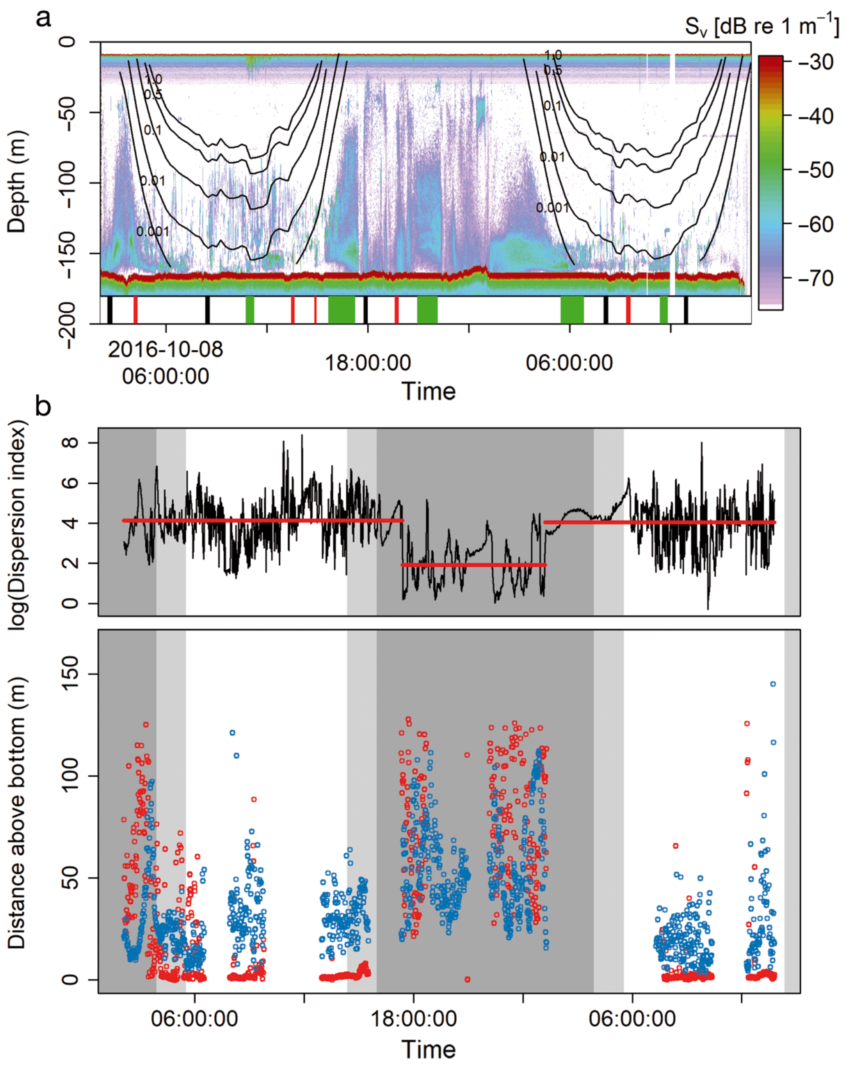

Fig. 3. (a) Acoustic echogram from October 8 and 9, 2016, showing distribution of pelagic fish in the water column during a day-night-day cycle. Low values (purple colours) indicate dispersed distribution, while high values (green colours) indicate dense aggregations. The acoustic probe was deployed during periods marked in green below the main panel, and timing of trawl hauls are marked in red (pelagic) and black (demersal). The echogram recordings are from the vessel-mounted 18 kHz echo sounder; backscatter is displayed in units of S_v (dB re 1 m^{-1}) at a temporal resolution of 15 s and vertical resolution 19 cm. The superimposed depth contours mark 5 discrete light levels based on daily surface irradiance measurements (I_s), W m^{-2}, µmol m^{-2} s^{-1}. (b) Top: Dispersion index calculated from 18 kHz acoustic data with high (low) values indicating patchy (dispersed) distribution of pelagic fish. The red horizontal lines mark segments and shifts in the dispersion index based on a breakpoint analysis. Bottom: Mean depth distribution of krill (red) and pelagic fish (blue) derived from acoustic recordings. Light grey sectors correspond to civil twilight periods, dark grey to night-time (civil dusk to civil dawn) and white to daytime

15:58 h and nautical dusk (the moment when the sun is 12 degrees below the horizon in the evening) was at 17:53 h on 8 October, while nautical dawn on 9 October was at 02:07 h and civil dawn at 04:00 h. The first significant change point in the dispersion index was identified between civil dusk and nautical dusk at 17:22 h and the second change point prior to nautical dawn at 01:13 h UTC.

Cod were caught in the demersal trawl, and we estimated the swept area density of cod at the study location to be 6488 cod km^{-2}, varying from 1351 to 10 355 cod km^{-2} depending on trawl sample. Even though the trawl samples showed that several cod were large (Fig. S1A in Supplement 2), we were not able to identify echo recordings of cod from the standard narrowband vessel-mounted echo sounder data, due to low vertical resolution.

On the echograms from the submerged probe with high range resolution due to the broadband acoustics, cod tracks were readily detectable and identifiable (see Fig. 2 for an example echogram). Cod stayed within 10 m of the bottom through the periods of observations with the probe, but cod tracks were more abundant, extended over a higher vertical range and reached higher above the seabed in the morning (indicating higher activity) than at other times of the day (Fig. 4). We could not separate confidently between capelin and polar cod using either the standard narrowband vessel-mounted echo sounder or the broadband acoustics, but pelagic fish tracks were more abundant after dark when schools dispersed and single individuals could be acoustically resolved as tracks (Fig. 4). The distance above bottom was higher for the pelagic fish in the day than during the night. During the transition from dusk to night, some pelagic fish approached the bottom zone which had been avoided during daylight hours (Fig. 4).

The indication of increased activity level of cod in the morning corresponded with a higher probability of finding fresh pelagic fish in the cod stomachs at this time of the day (Fig. 4). There was variability in the results from the stomach data that could not be attributed to the time of day (see the difference in proportion between the 2 stations both carried out around 08:00 h UTC in Fig. 4), but the probability of finding newly eaten pelagic fish in a

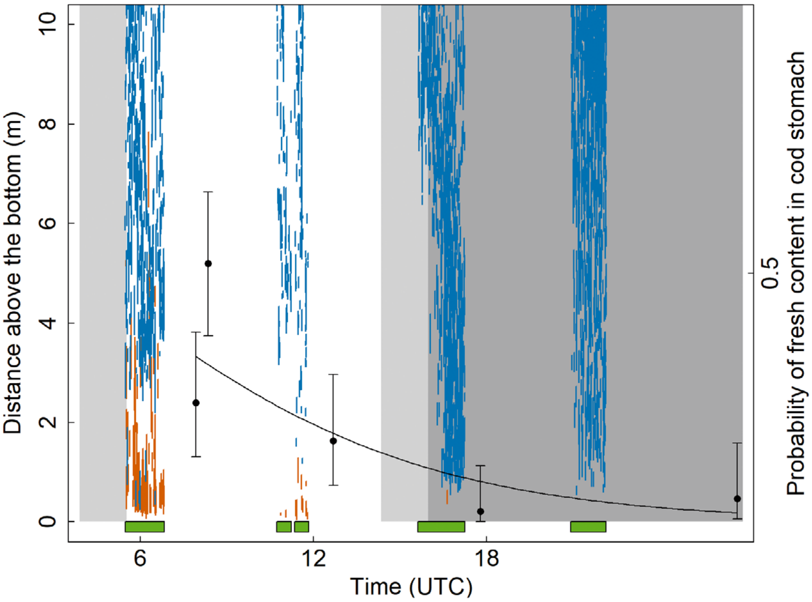

Fig. 4. Overview of acoustic tracks of pelagic fish (blue) and cod (brown) within 10 m from the detected seabed, based on the probe data (the periods of probe deployment are marked in green like in Fig. 3a). The length of the vertical lines corresponds to the vertical range of a given fish track. The tracks are extracted from a 120 kHz broadband echo sounder mounted on a probe submerged to 120 m above the bottom. The black dots denote observed probability of finding fresh content in cod stomachs at a given time of the day with 95 % confidence bands, and the black curve denotes the fit of a generalized linear model (Model 1 in Table 1). The model predicts probability of newly swallowed prey (binomial) as a function of hours past dawn with a binomial distribution of the error term

cod stomach declined significantly with hours since dawn also when including station as a random factor ($\beta = -0.18$, SE = 0.06, $p = 0.0029$, intercept not significantly different from 0). Neither cod length nor stomach fullness were significant variables (Table 1).

Table 1. Summary of the logistic regression of the probability of finding newly eaten pelagic fish in a cod stomach with Akaike information criterion (AIC) and residual deviance. The sample size is 239. All models include a random effect of station to account for dependency between cod caught in the same demersal trawl haul. Stomach fullness was calculated as the total prey mass (excluding newly eaten pelagic fish) weighted by cod mass. Significant variables are marked with an asterisk

Model	Variables	AIC	Residual deviance
1	Hours since dawn*	210.0	204.0
2	Hours since dawn* + cod length	211.3	203.3
3	Hours since dawn* + stomach fullness	209.2	201.2
4	Hours since dawn* + cod length + stomach fullness	210.5	200.5

The pelagic trawl samples were dominated by capelin >15 cm in length, whereas most of the polar cod caught were <13 cm in length (see Fig. S2 in Supplement 2 for details on length compositions). Overall, 2.2 times more capelin than polar cod were caught in the pelagic hauls, but the true ratio of the 2 species in the area could not be determined due to potential differences in catchability between the species.

Of the 239 cod stomachs analysed, 14 % were empty. Of the stomachs containing food, 79 % contained pelagic fish and/or unidentified fish, 65 % contained identified pelagic fish, and only 5 % included fish other than pelagic fish (see Fig. S1 in Supplement 2 for more details on the cod diet). Of the 99 capelin stomachs analysed, 52 % were empty. Of the stomachs containing food, 48 % contained prey that could be identified as krill, while the others mostly contained highly digested food that could be identified as crustaceans, but could be any crustacean species. All 29 polar cod stomachs contained food, mostly krill and unidentified crustaceans (see Fig. S2 in Supplement 2 for more details on the diet of pelagic fish).

The evacuation rate of the cod stomachs over time is shown in Fig. 5. Digestion is slow at these low temperatures, and it would take about 45 h for a median-sized cod to digest half of a median-sized meal given a median composition of prey. There was a very large spread in stomach fullness; the stomach content weight varied from 0–35 % of total body mass, with a median value of 3 % (including empty stomachs).

4. DISCUSSION

Through fine-scale monitoring on an oceanic bank area in the Barents Sea, we show that the spatial associations and interactions between cod, pelagic fish and krill were dynamic and closely followed the diel cycle. Cod were hardly visible acoustically for long periods, likely residing in the acoustic dead zone since they were captured with the demersal trawl. Using a submersible probe and broadband acoustics with high vertical resolution intermittently over the diel cycle, cod tracks were detected close to the sea-

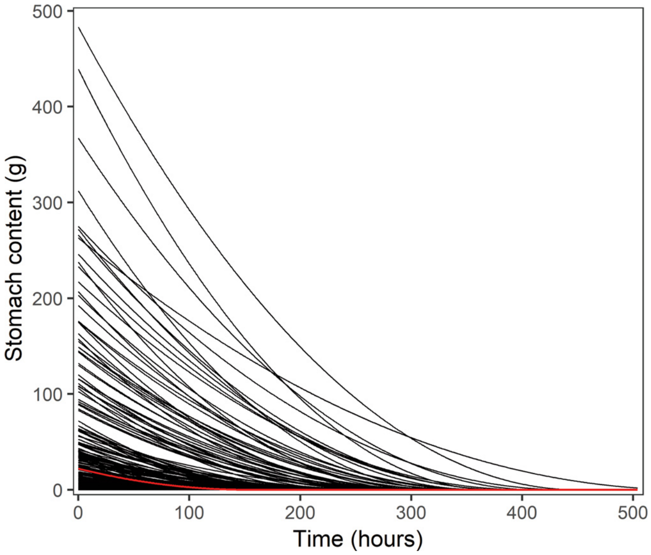

Fig. 5. Time required to fully evacuate a cod stomach at the bottom temperature (1.5°C) in our study area. Each line represents a stomach sample (non-empty stomachs of cod >25 cm, n = 204). The red line denotes evacuation of a stomach with median content

bed barely lifting from the bottom. The tracks observed were normally few, but during the early morning hours, substantially more cod were observed, lifting a few metres from the bottom, indicating feeding behaviour. The acoustic observations coincided with the results from the stomach samples showing that cod had more fresh prey in the stomachs in the morning. Krill stayed close to the bottom during daytime sharing habitat with the cod, but dispersed and overlapped spatially with pelagic fish during night. The pelagic fish avoided light intensities above 0.001 µmol photons m^{-2} s^{-1} when ascending around dusk and descending around dawn. They responded to daylight by aggregating in pelagic schools while they only dispersed during night time, probably strategies to reduce predation risk from cod.

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

The pelagic fish showed a strong diel vertical migration and adjusted their position in the water column to depths where low light levels may inhibit efficient prey detection by visual predators (Warrant & Johnsen 2013). When light levels were sufficient to permit visual prey search all the way down to the seabed, the pelagic fish responded by aggregating and forming schools higher up in the water column — a common anti-predator strategy (Pitcher & Parrish 1993). Both diel vertical migration and schooling in the pelagic come at the cost of lost feeding opportunities on krill, which resided among the cod close to the seabed during daytime. We did not distinguish between fresh and digested prey in pelagic stomachs, but for capelin, the majority of the guts examined were empty, suggesting that they assessed predation risk as too high to engage in foraging.

Krill is the key organism for understanding spatial distributions in this tri-trophic game, since it attracts the pelagic fish to enter the preferred habitat for cod. It is not clear how beneficial the situation is for krill on the banks at this time of year. On the one hand, the shallow depths of the bank areas limit krill from undertaking vertical migrations out of the zone where they are visible to predators (Kaartvedt et al. 1996, Onsrud et al. 2004, Zhou & Dorland 2004). Light penetrates down to the bottom during daytime and krill are blocked from descending further down to escape the threats of visual predation (Aarflot et al. 2019). On the other hand, bottom association appears to effectively reduce the predation risk for krill in our system, since the pelagic fish are schooling and aggregate at a safe distance from the sea floor that is occupied by cod. The cod is known to be a potential predator on krill, but prefer pelagic fish, and paradoxically krill may therefore gain safety by hiding among the cod.

Our investigation must be viewed as an effort to gain insight into processes and mechanisms which cannot easily be obtained from regular monitoring surveys. Inevitably when combining different sampling efforts, there will be gaps in the different data layers due to practical limitations. Also, we investigated a specific situation and location over a short period, and given that cod have very flexible feeding behaviour (Meager et al. 2018), the representativeness of our observations should be tested in further studies. Nonetheless, bank areas like the one studied here are the areas with highest densities of cod and where the main interactions with capelin occur both in the Barents Sea and in other boreal systems (Fahrig et al. 1993, Fall et al. 2018). We demonstrate that the spatial interplay between key species spanning a wide size range in a Barents Sea open ocean bank system can be observed efficiently using a combination of conventional trawl sampling and hydroacoustic techniques. In particular, broadband acoustics open up new possibilities for unobtrusive *in situ* investigations of predator–prey interactions. Our observations indicated that krill is likely a key organism for understanding some of the most important predator–prey dynamics in the Barents Sea. Restricted by the seabed to migrate below the range for being detected visually by predators, krill reside in the habitat of the cod, attracting pelagic fish that are hunting for food. Cod seem to be the 'winner' in this interplay, by gaining access to food with a minimum of effort.

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