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Research

Predator–prey overlap in three dimensions: cod benefit from capelin coming near the seafloor

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Spatial overlap between predator and prey is a prerequisite for predation, but the degree of overlap is not necessarily proportional to prey consumption. This is because many of the behavioural processes that precede ingestion are non-linear and depend on local prey densities. In aquatic environments, predators and prey distribute not only across a surface, but also vertically in the water column, adding another dimension to the interaction. Integrating and simplifying behavioural processes across space and time can lead to systematic biases in our inference about interaction strength. To recognise situations when this may occur, we must first understand processes underlying variation in prey consumption by individuals. Here we analysed the diet of a major predator in the Barents Sea, the Atlantic cod *Gadus morhua*, aiming to understand drivers of variation in cod's feeding on its main prey capelin *Mallotus villosus*. Cod and capelin only partly share habitats, as cod mainly reside near the seafloor and capelin inhabit the free water masses. We used data on stomach contents from ~2000 cod individuals and their surrounding environment collected over 12 years, testing hypotheses on biological and physical drivers of variation in cod's consumption of capelin, using generalized additive models. Specifically, effects of capelin abundance, capelin depth distribution, bottom depth and cod abundance on capelin consumption were evaluated at a resolution scale of 2 km. We found no indication of food competition as cod abundance had no effect on capelin consumption. Capelin abundance had small effects on consumption, while capelin depth distribution was important. Cod fed more intensively on capelin when capelin came close to the seafloor, especially at shallow banks and bank edges. Spatial overlap as an indicator for interaction strength needs to be evaluated in three dimensions instead of the conventional two when species are partly separated in the water column.

Keywords: functional response, *Gadus morhua*, *Mallotus villosus*, predator–prey, predatory fish, spatial overlap, stomach contents, vertical distribution



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Introduction

Predation structures natural ecosystems (Schmitz et al. 2017). At the scale of populations, the intensity of predation is often characterised by the average predator's consumption of prey in relation to prey density, or the functional response (Holling 1959). Functional response models typically assume that all individuals in a predator population respond uniformly to changes in prey density (but see Abrams 1984, Bjørnstad and Hansen 1994, Bolnick et al. 2011). However, variation in diet exists on several spatial and temporal scales, and combining or averaging diets across these scales without accounting for the variation may result in biased estimates of interaction strength (Bergström et al. 2006, Melbourne and Chesson 2006, Hunsicker et al. 2011, Deroba 2018). To understand effects of lower-scale variation on the population-level functional response and potential biases introduced by aggregating across time and space, we must first identify the scales, patterns and drivers of variation in the feeding of individual predators (Englund and Cooper 2003, Railsback et al. 2020).

Foraging in predatory fish depends on a wide range of intrinsic and extrinsic factors such as light, temperature, bathymetry, local prey density and predator size that act on different spatial and temporal scales (Stefansson and Pálsson 1997, Johannesen et al. 2012, Lopez-Lopez et al. 2015, Deroba 2018). At the scale of geographical regions or seasons, large-scale fluctuations in environmental conditions or prey availability influence predator–prey distributions and overlap. Within regions at the scale of local habitats, feeding opportunity is affected by local bathymetries, water temperatures or fronts that either act directly on predator physiology or indirectly through effects on prey distributions (Sims et al. 2003, Genin 2004, Ciannelli and Bailey 2005, Skern-Mauritzen et al. 2011). At scales relevant to individual foraging behaviour, short-term spatio-temporal dynamics in prey availability and detectability influence feeding success. For example, light is crucial for prey detection in visual predators (Aksnes and Utne 1997), and diel vertical migrations and schooling in the prey can alter prey encounter rates (Clark and Levy 1988, Pitcher and Parrish 1993). The particular feeding strategy of a predator is also influenced by its size or age (Pettorelli et al. 2015), its competitive ability (Svanbäck and Bolnick 2007), and other phenotypic traits affecting foraging behaviour (Sih et al. 2012, Parsons et al. 2016). Disentangling the effects of these diverse sources of variability at different spatial and temporal scales is a major challenge in the study of predator–prey interactions (Hunsicker et al. 2011, Fouzai et al. 2019).

Atlantic cod *Gadus morhua* (hereafter 'cod') is a key generalist predator in the North Atlantic Ocean, whose population-level diet reflects seasonal and geographical prey availability (Meager et al. 2017). In many ecosystems, cod and other species in the Gadidae family feed on pelagic fish prey, such as capelin, herring or sprat, that often are distributed outside their immediate near-bottom habitat (O'Driscoll et al. 2000, Rindorf et al. 2006, Moustahfid et al. 2010, Andersen et al. 2017). Demersal predators (fish living near the seafloor like

cod) encounter pelagic prey either through vertical ascents into the pelagic habitat, or by exploiting vertical prey migrations (Mauchline and Gordon 1991). Our empirical knowledge of vertical interactions between demersal predators and pelagic prey is limited, as data with high spatial and temporal resolution is often needed to understand them (Heffernan et al. 2004). Such data are costly and time-consuming to collect in the open ocean and is therefore rarely available for the larger areas and longer time frames needed to generalise the patterns observed. For this reason, studies in the vertical dimension are limited to smaller areas, where predator–prey dynamics are monitored over a few diel cycles (Schabetsberger et al. 2000, Sims et al. 2006, Harrison et al. 2013, Andersen et al. 2017, Skaret et al. 2020, but see Solberg et al. 2012). Today many fish monitoring surveys use state-of-the-art echosounders that collect data on vertical species distributions. While the data resolution is often coarser than in small-scale process studies, fish monitoring data usually extend over larger areas. So far, this type of data has been sparingly used to study vertical predator–prey dynamics.

In the Barents Sea, a North Atlantic shelf sea bordering the Arctic Ocean, cod is an important predator on the pelagic schooling fish capelin *Mallotus villosus*. While capelin is the most profitable prey for cod in this region (Fall and Fiksen 2020), the population-level diet also includes many other prey species (Holt et al. 2019). Cod diet changes with size (Dolgov et al. 2011, Holt et al. 2019), but the influence of other biological and physical factors on diet variation has not been quantified. This cod population is currently thriving under reduced fishing pressure in a warming sea (Kjesbu et al. 2014), where it has expanded into areas previously dominated by small-bodied Arctic species (Fossheim et al. 2015, Kortsch et al. 2015). In this situation, it is urgent to understand how ecological mechanisms influence feeding interactions to accurately reflect them in stock assessments, ecosystem models and other evaluations of trophic responses to environmental change.

Here we ask, what really drives predator–prey interactions between demersal and pelagic fish in large marine ecosystems? What is the relative role of three-dimensional space, predator–prey overlap and environmental conditions on cod consumption? To answer these questions, we formulate hypotheses that we test against data on the environment and individual-level cod diets collected in the 2004–2015 summer feeding season. This rich dataset allows us to study local (km-scale) drivers of individual diet variation in a demersal predator, including horizontal and vertical overlap with pelagic prey. We hypothesise that cod's consumption of capelin 1) increases with capelin density to a point of saturation, 2) decreases with increasing cod density, 3) decreases with increasing bottom depth and 4) is higher in areas where capelin is distributed closer to the seafloor, as detailed below.

1. Capelin consumption increases with increasing capelin density to a point of saturation

As prey density increases, a predator's consumption rate may reach a plateau where further increases in prey density no

longer affect consumption (type I with saturation or a type II functional response). This is attributed to limitations on the number of prey a predator can handle (pursue, capture and ingest) or digest per time unit (Jeschke et al. 2002). In predatory fish, prey handling times are often negligible compared to digestion times, and digestion therefore limits feeding rate at high prey density (Breck 1993). A previous study found increased cod feeding success, measured as total energy intake per day and unit of cod mass, with increasing capelin density, but with large variation at the highest densities (Johannesen et al. 2012). Any saturation of the functional response may have been masked by applying mathematical transformations to consumption and prey density (i.e. a log-linear relationship is non-linear at raw scale), or by averaging consumption across individuals in a sample. Due to the slow digestion times in the cold waters of the Barents Sea (Fall and Fiksen 2020), we hypothesise that the functional response fitted to individual-level data reaches saturation at high capelin density.

II. Capelin consumption decreases with increasing cod density

The density of the predator itself can also affect feeding levels. Intraspecific collaborative feeding strategies, which imply positive effects of predator density on individual intake rates, has not been demonstrated in fishes beyond simple group formation (Brosnan et al. 2010) and changes in predator school size and density during prey search and feeding (DeBlois and Rose 1995). Conversely, numerous mechanisms can result in lower intake rate for individual predators at high predator density (Ward et al. 2006). For instance, competition may take the form of physical interference. Juvenile cod living in complex environments may defend territories against conspecifics, but it is unknown whether aggressive behaviour occurs in the Barents Sea cod population outside of the spawning season (Meager et al. 2017). In cannibalistic species like cod, high densities can increase predation risk for younger conspecifics that may respond with reduced feeding activity (Biro et al. 2003). High predator density can also reduce per-capita prey consumption through exploitative competition (Svanbäck and Bolnick 2007). Based on any of these mechanisms, we hypothesise that cod's consumption of capelin decreases with increasing cod density.

III. Capelin consumption decreases with increasing bottom depth

Cod energy intake rate decreases with depth (Johannesen et al. 2012). As capelin density has a positive effect on energy intake, we expect that the consumption of capelin also decreases with depth. Since cod use vision to hunt pelagic prey (Brawn 1969) and light is attenuated rapidly with depth in the water column (Lorenzen 1972), reduced consumption of capelin with depth may be related to decreasing light levels that reduce capelin detectability. Cod densities are highest at the relatively shallow banks and bank edges of the central

Barents Sea where cod also overlaps with capelin (150–200 m depth, Fall et al. 2018). If the spatial consumption pattern reflects cod's association with banks, the depth effect may be non-linear, i.e. consumption is lower in areas shallower and deeper than the banks.

IV. Capelin consumption is higher when capelin is distributed closer to the seafloor

Adult cod mainly occupy near-bottom habitats, but vertical movements are not unusual (Strand and Huse 2007). Cod can regulate the volume of its swim bladder to achieve neutral buoyancy at depth, but gas resorption is slow and cod rely on compensatory swimming to regulate buoyancy during rapid vertical movements (van der Kooij et al. 2007). Both swim bladder regulation and compensatory swimming come with an energetic cost (Strand et al. 2005). The proximity of the pelagic capelin to the seafloor may therefore be important for the availability of capelin to cod and the energetic benefit of feeding on this prey.

Material and methods

Area of interest and data collection

We used data collected by Norwegian vessels participating in the Norwegian–Russian Barents Sea Ecosystem Survey in 2004–2015 (Eriksen et al. 2017). The survey covers the entire ice-free Barents Sea in August–October each year and follows a regular grid design with sampling stations spaced approximately 65 km apart, collecting data on environmental conditions, species composition and abundance for several trophic levels. We selected stations from areas where cod and capelin overlap spatially (Fall et al. 2018), i.e. stations where both species were observed (Fig. 1). At each station, a CTD (conductivity–temperature–depth) probe is lowered to measure depth-specific temperature, a Campelen 1800 demersal shrimp trawl is used for near-bottom sampling over a distance of 1.4 km (0.75 nautical miles, nmi), and a pelagic trawl ('Harstad trawl', Godø et al. 1993) samples the upper approximately 60 m of the water column. Continuously during the survey, Simrad EK60 echo sounders with 18, 38, 120 and 200 kHz split beam transducers (on some vessels Simrad EK500 during the first years) record fish echoes along the survey tracks. The acoustic backscatter at 38 kHz is manually allocated to target groups based on species-specific acoustic signatures and the catch composition in pelagic and bottom trawls, then stored at a horizontal resolution of 1.9 km (1 nmi) and a vertical resolution of 10 m. One individual cod from each 5-cm length group present in the bottom trawl catch is randomly chosen for sampling of age, sex, mass, length, maturity stage and stomach contents. The stomachs are frozen on board, and the contents identified to the lowest possible taxonomic level in a laboratory on land. Prey items are assigned a qualitative digestion stage from 1 to 5, where 1 corresponds to undigested prey and 5 to prey that is

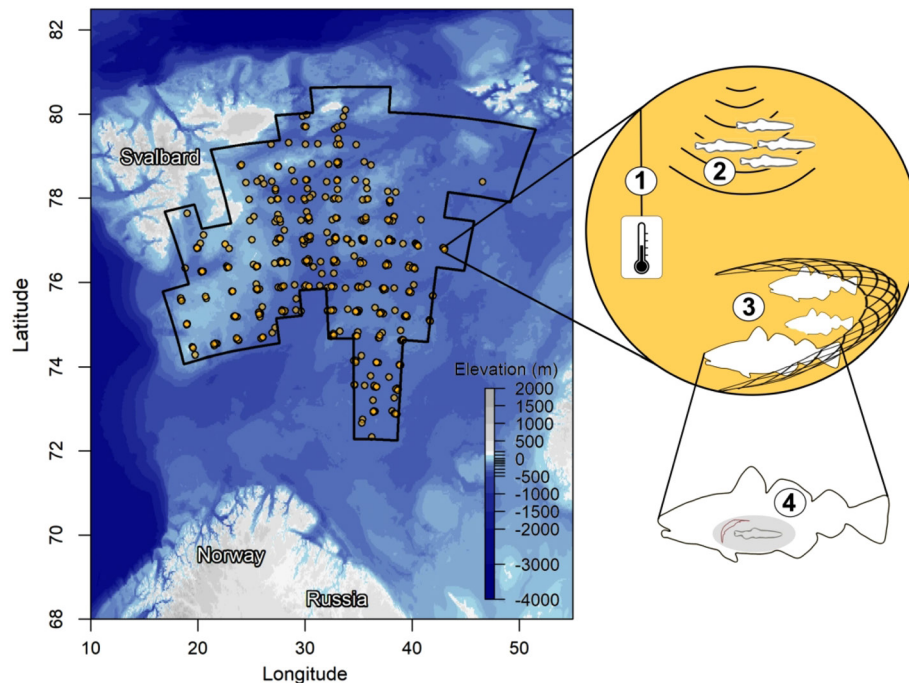


Figure 1. Study area in the Barents Sea, with bathymetric features (elevation) and sampling methods. The colour scale for elevation (GEBCO Compilation Group 2020) is compressed at shallow depths to better show depth variations on the shelf. The cod–capelin overlap area is marked with black borders (Fall et al. 2018), and the yellow circles show the location of the sampling stations selected for the present study. At each station, a CTD was lowered to measure depth-specific temperature (1), densities of pelagic species were measured acoustically (2) and demersal trawling for cod was performed (3). Cod stomach contents were frozen on board and analysed in a laboratory on land (4).

so heavily digested that it is unidentifiable by visual inspection. Prey categories are weighed (wet mass) and, if possible, counted and length measured. For further details on survey design and stomach sampling procedures (Dolgov et al. 2007, Michalsen et al. 2011).

We selected stomach data from cod in the size range 30–70 cm, since capelin is less important as prey for smaller and larger cod (Dolgov et al. 2011). We did not differentiate between females and males; cod of this size is mainly immature (ICES 2020) and previous studies have found no difference in diets (Michalsen et al. 2008) or growth rates (Pedersen and Jobling 1989) between males and females in the summer season studied here. Empty stomachs (9.2%) were excluded from the analyses, leaving 1944 stomachs from 455 stations across the 12 years.

To describe the local conditions at each station, we used the following covariates: capelin density, capelin weighted median depth, cod density, cod length (for each individual within the station) and bottom depth (measured by the vessel-mounted echosounder at the start of trawling). The local capelin density (in units of Nautical Area Scattering Coefficient; $m^2 nmi^{-2}$, integrated throughout the water column) was taken from the acoustic segment of 1.9 km length that had the highest temporal overlap with each trawl haul. This included acoustic recordings from before, during and after trawling. We do not expect that trawling will have a large impact on capelin density estimates as the presence of a vessel has little to no influence on volume backscatter

(Jørgensen et al. 2004). For a more intuitive representation of prey density, we converted the acoustic values to number of individuals km^{-2} based on the length distribution in the closest pelagic trawl hauls taken during the survey, and the relationship between capelin length and acoustic target strength (Gjørseter et al. 1998). For capelin weighted depth, we used the same acoustic segment resolved in 10 m depth channels to calculate the weighted median depth of the capelin backscatter at each trawl location. Capelin may dive around 10 m in response to a vessel passing overhead (Jørgensen et al. 2004). However, this is a small distance compared to the range of capelin weighted mean depth in our data, and local avoidance of the vessel or trawl gear should have little impact on the overall depth across the 1.9 km acoustic segment. The local cod density (number of individuals ≥ 30 cm km^{-2}) was estimated from each demersal trawl haul using standard methods for cod swept area calculation in the Barents Sea, which assume that the effective sweep width of the trawl increases with cod size up to 62 cm (Mehl et al. 2014).

Like many pelagic organisms, capelin perform diel vertical migrations (Dalpadado and Mowbray 2013) and is often observed in looser aggregations during night-time than during the day when they form schools, some of which descend deeper into the water column (Fig. 2 and Skaret et al. 2020). However, capelin vertical migrations are diurnal, while it takes days for cod to digest a stomach full of capelin in the cold waters of the Barents Sea (Fall and Fiksen 2020). Hence, we are not able to reliably detect feeding periodicity

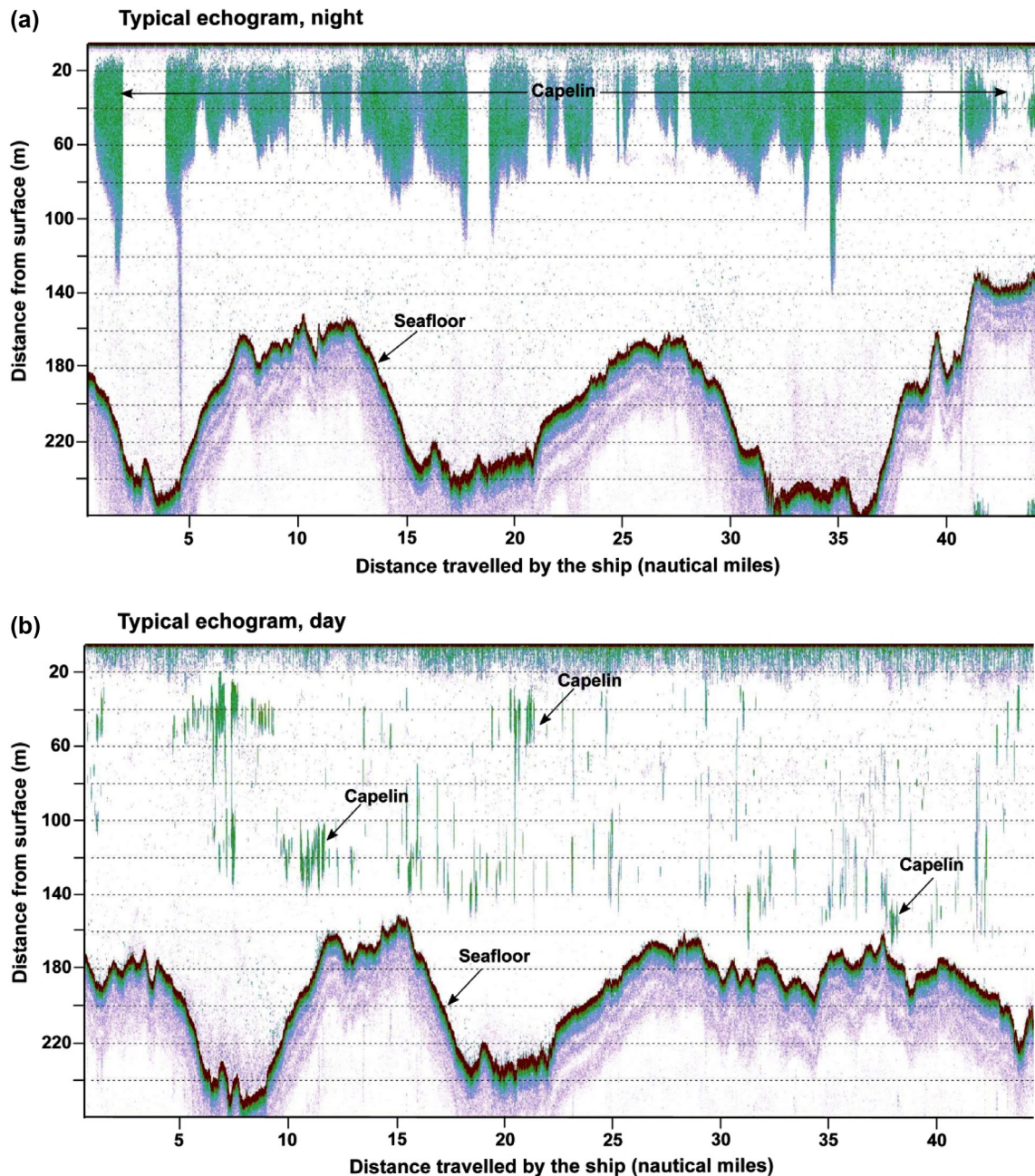


Figure 2. Acoustic registrations of capelin at the Great Bank of the Barents Sea in late September 2015. Data was collected in a small area over the diel cycle and the panels show (a) typical near-surface night distributions of capelin collected over 4.5 h and (b) registrations during the following dawn and daylight hours (6 h), when capelin formed schools further down in the water column. The colour scale reflects the volume acoustic backscattering coefficient (Sv) at 38 kHz, with the strongest echoes in red, coming from the seafloor and surface, and capelin registrations ranging from light purple to green with increasing density. 1 nautical mile = 1.85 km.

by analysing stomach contents. In the analysis we therefore standardise capelin depth with respect to light level to reduce high-frequency variation that may mask relationships with other variables (Standardisation of capelin vertical distribution below, and Supporting information). The standardised capelin depth reflects how capelin's distance to the seafloor varies throughout the study area at a given light level. If cod

consumes more capelin when capelin come closer to the seafloor, we expect consumption to be higher in areas where the standardised capelin depth is closer to the seafloor.

Other factors such as densities of prey other than capelin may also influence capelin consumption, but analyses of the full prey community are outside the scope of this paper.

Data analysis

The statistical approach applied here builds on previous work using generalised additive (mixed) models (GAM/GAMM) to analyse individual-level stomach data in relation to the environment (Stefansson and Pálsson 1997, Buchheister and Latour 2015, Deroba 2018), extending it to include a larger suite of ecologically relevant covariates including horizontal and vertical prey distribution. Predator–prey interactions typically contain non-linear processes, making GAM an appropriate statistical tool as it does not require a priori assumptions about the shape of response–covariate relationships (Wood 2017). Instead of the two-step delta-GAM approach commonly applied to zero-inflated data, we applied the Tweedie distribution to allow inclusion of both zeroes and positive values in a single model (Tweedie 1984, Shono 2008). We fit GAMs in the R library *mgcv*, using R ver. 4.0.2 (<www.r-project.org>). The library *itsadug* (van Rij et al. 2016) was used to illustrate the results.

Standardisation of capelin vertical distribution

To standardise capelin depth distribution in the survey area, we fit capelin weighted median depth as the response variable against solar elevation angle, bottom depth and a variable coefficient term (Ciannelli et al. 2012) of geographical location by sampling day in a GAM with gamma distribution and log-link. The variable coefficient term was included to account for variations in survey timing and coverage, which created strong residual patterns. Solar elevation angle, a proxy for surface light, was calculated from the day of the year, geographical position and time of trawling. It was adjusted by subtracting the angle at sunrise to account for the rapidly changing light regime during the sampling period. The standardised capelin depth at each sampling station was predicted from the model using the observed bottom depth and geographical location and constant (median) values for solar elevation angle and survey day (details in the Supporting information). We used the predicted median depth as a covariate in the main model rather than capelin's distance from the seafloor, as the latter was strongly correlated with bottom depth (Supporting information) and we had hypotheses regarding both variables.

Analysis of factors affecting cod's consumption of capelin

Daily capelin consumption rate was used as the response variable. We estimated capelin consumption rate for each individual cod (C_i , g \times day⁻¹) from an experimentally derived stomach evacuation model for Atlantic cod (Eq. 1), where evacuation rate depends on the wet mass of capelin found in the stomach (δ_i), the natural exponential function of surrounding temperature (T , bottom temperature from nearest CTD probe), cod mass (m_i) and an evacuation parameter specific to capelin prey ($\rho = 0.00749$) (Temming and Herrmann 2003):

$$C_i = 24\rho m_i^{0.305} e^{0.117T} \delta_i^{0.5} \quad (1)$$

Consumption rate was standardised by dividing by cod body mass and multiplying by 100, i.e. expressed as a percentage of cod body weight per day. Cod length was nevertheless included as a covariate to account for any differences in consumption rate with size that are not directly related to the predator's physical ability to consume more capelin as it grows (e.g. changes in feeding behaviour).

The covariates were standardised to z-scores, ensuring that effects could be evaluated on a comparable scale. Before standardization, we log₁₀-transformed cod- and capelin density to reduce the leverage of points at the ends of highly skewed distributions. The data come from cluster sampling, i.e. several cod are caught at each sampling station (Fig. 1). These cod are more likely to be similar to each other than cod sampled at different stations, which may result in statistical relationships appearing more significant than they are (Nelson 2014). To account for this dependency, we included a random effect of station in the analyses, specified using the 're' basis in the smooth function.

We included a two-dimensional smooth term of geographical location to account for any spatial patterns in consumption that were not captured by the other covariates. The geographical coordinates were expressed as distance from 75 N and 35 E (middle of the Barents Sea) in km. We also included a variable coefficient term (Ciannelli et al. 2012) of geographical location by sampling day as explained for the capelin depth model above. Year was included as a factor variable to account for overall differences in the magnitude of capelin consumption between years. To avoid overfitting the smooth functions, we constrained their level of wiggleness by limiting the maximum number of basis dimensions to five for one-dimensional terms and 30 for the two-dimensional term of geographical location. Variance inflation factors were calculated to evaluate collinearity between the covariates. Capelin weighted depth had the highest collinearity, which was not unexpected as it was predicted from a model including some of the same covariates as the main model. With a variance inflation factor of 3.8, it was somewhat higher than the limit of three given by Zuur et al. (2010) but lower than the limit of 10 from Montgomery et al. (2012). We consider this level of collinearity acceptable given that it was necessary to standardise capelin depth.

Two-way interactions were evaluated for all combinations of the covariates capelin depth, bottom depth and capelin density to be able to separate effects of horizontal and vertical predator–prey overlap. A three-way interaction of these covariates was also evaluated. All interactions were specified as tensor product smooths ('ti'-terms) in the GAMs.

Since the analysis contained a random effect, we started with a model that included all covariates and interactions in order to give as much explanatory power to the fixed effects as possible (Zuur et al. 2009). Models were fitted with maximum likelihood estimation so that the Akaike information criterion (AIC) could be used to compare models with different fixed effects. Model selection was performed by sequentially removing non-significant ($p > 0.05$) covariates using the approximate p-values given in the summary call to the

GAM object. We identified the final model as the one with lowest AIC, choosing a model with simplest structure (fewest covariates) if AICs differed less than four.

Model validation was done by examining residuals and by inspecting the output of the function *gam.check*. Direct calculation of effect sizes is not implemented for GAMs, but we used the partial effect plots to visually inspect response–covariate relationships and compare the relative strength of effects. We then tested the predictive capacities of models with and without important effects by performing a cross-validation with 500 iterations. In each iteration, models were fit with a random sample representing 90% of the data and thereafter used to predict consumption rate for the remaining out-of-sample observations. The genuine cross-validation score (gCV) was calculated for each model as the mean square prediction error of the 500 iterations. In this test, the random station effect was excluded to speed up fitting.

Results

Out of the 1944 stomachs analysed, 22% contained capelin only, 16% contained capelin and other prey and the remaining 62% contained other prey only. Summed across stomachs, capelin nevertheless made up 59% of the total prey mass consumed by cod. In cod that had fed on capelin, the median capelin mass in stomachs was 22 g, and the median consumption rate was 0.73% of cod body mass per day (range 0.04–2.6%). Most of the capelin in cod stomachs were assigned digestion stage 3, ‘half digested’. Undetermined fish (included in ‘other prey’) made up 14% of the total stomach content by mass and likely contained some heavily digested capelin.

Standardisation of capelin vertical distribution

The capelin depth distribution model explained 31% of the deviance. All covariates were significant predictors of capelin weighted median depth; bottom depth (edf=2.79, $p < 0.001$), solar elevation angle (edf=2.91, $p < 0.001$) and the spatially variant effect of sampling day (edf=9.29, $p < 0.001$). Capelin distributed deeper with increasing bottom depth down to 150 m bottom depth, but in deeper areas there was no clear trend (Supporting information). Capelin also distributed deeper with increasing solar elevation angle (increasing light level), with a stronger trend going from night to dawn than after sunrise (Supporting information). The standardised capelin depth predicted for each sampling location resulted in a smaller range of capelin depths while preserving the pattern of shallower distributions in shallower areas (Fig. 3).

Factors affecting cod’s consumption of capelin

The final model for consumption rate explained 40% of the deviance and retained all covariates except cod density (Supporting information). Significant interactions were found

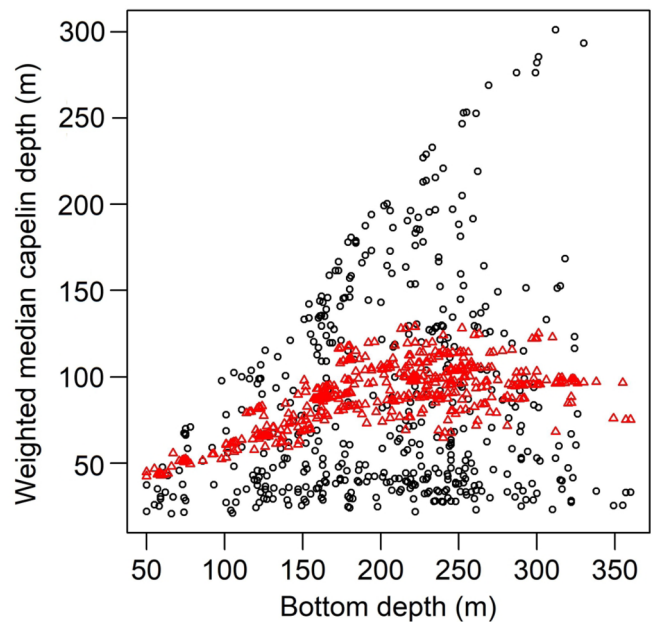


Figure 3. Observed (black circles) and standardised (red triangles) capelin weighted median depth versus bottom depth for each sampling location.

between capelin depth and bottom depth, between capelin density and capelin depth, and between capelin density and bottom depth. Consumption rate (% of cod body mass per day) increased sharply with capelin density before levelling off (Fig. 4a), decreased with depth (Fig. 4b), increased with capelin weighted median depth (Fig. 4c) and was slightly higher in 40–50 cm cod (Fig. 4d). Consumption increased from the south to the north of the study area (Fig. 4e), and the later in the sampling season the area was surveyed, the lower was the consumption observed in the west and the higher it was in the east (Fig. 4f). The main increase in capelin consumption with capelin density occurred below median density (Fig. 5). There was no additional effect of capelin density on consumption when capelin was distributed close to the seafloor (Supporting information). Capelin was distributed closest to the seafloor in bank areas (Fig. 6a), and the highest consumption rates were observed on banks in the eastern part of the study area (Fig. 6b). In all areas with bottom depth larger than approximately 80 m, cod’s consumption rate was higher when capelin was distributed closer to the seafloor (Fig. 6c). In areas with bottom depths between 150 and 200 m, consumption rate was relatively high for all capelin depths observed (Fig. 6c).

Sampling day was identified as an important covariate as it accounted for the changing light regime (lower solar elevation angles towards the winter and polar night) and more northern locations sampled later in the season. As such, including sampling day in the model removed the confounding effect it had on the other response–covariate relationships. To validate the model, we compared the prediction error of our final model with models without 1) sampling day, 2) capelin weighted median depth, 3) capelin density interactions

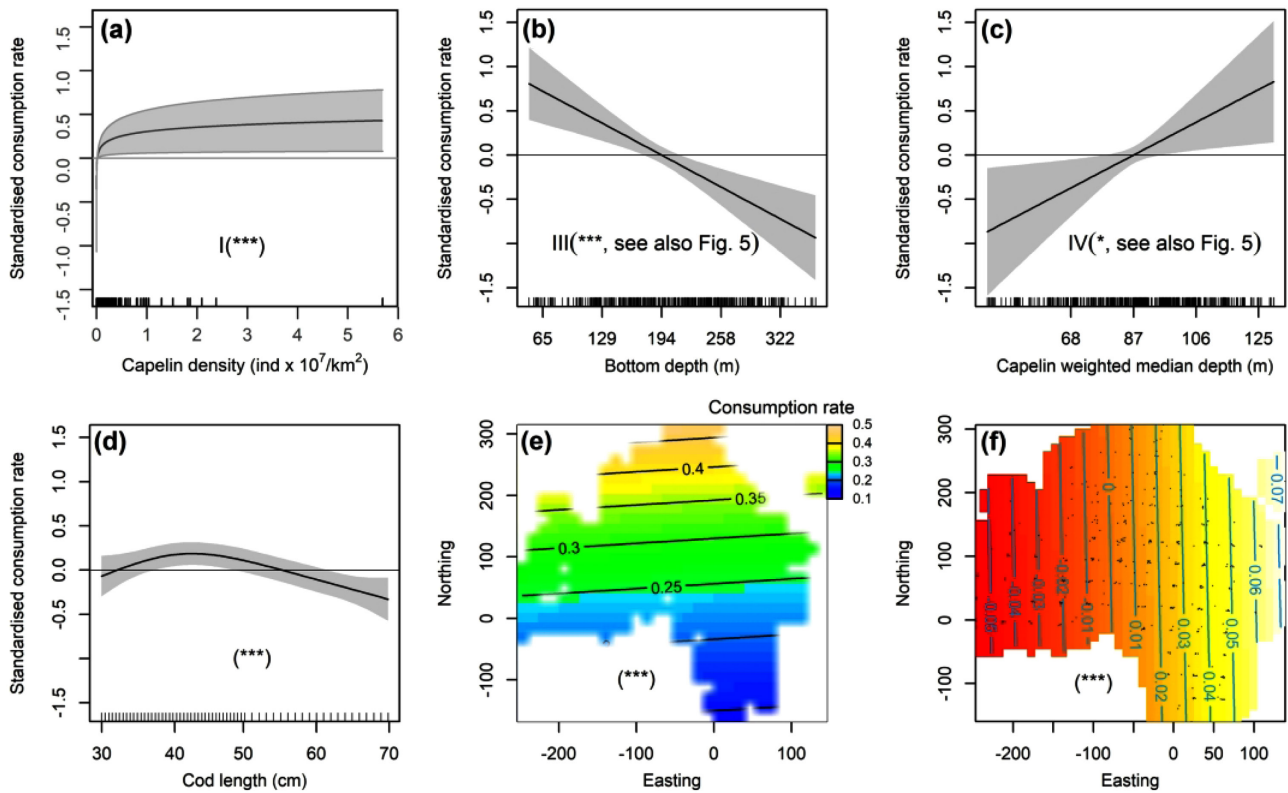


Figure 4. Partial effects of covariates on cod's consumption rate of capelin (percentage of cod body weight per day) from the generalised additive model. Only effects retained in the model are shown. In (a–d), the y-axis represents deviation from mean predicted consumption rate for changing values of the covariate (x-axis) on the scale of the linear predictor, i.e. on the log link scale used here, a value of 0.5 corresponds to a 65% increase in consumption rate. The roman numerals refer to the predictions (methods) and p-values are indicated in brackets, * $p \leq 0.05$, ** $p < 0.01$, *** $p < 0.001$. The shaded areas represent ± 2 SE around the smooth estimate. Rugs along the x-axis in each plot show the distribution of covariate values in the raw data. The capelin density covariate was back-transformed from log density. (e) Surface color illustrates the geographical pattern in consumption rate. Predictions are only shown for covariate combinations close to observed data. (f) Shows how the geographical pattern in consumption varies with sampling date. The numbers on the isolines are estimated slopes in local linear regressions between consumption rate and sampling day.

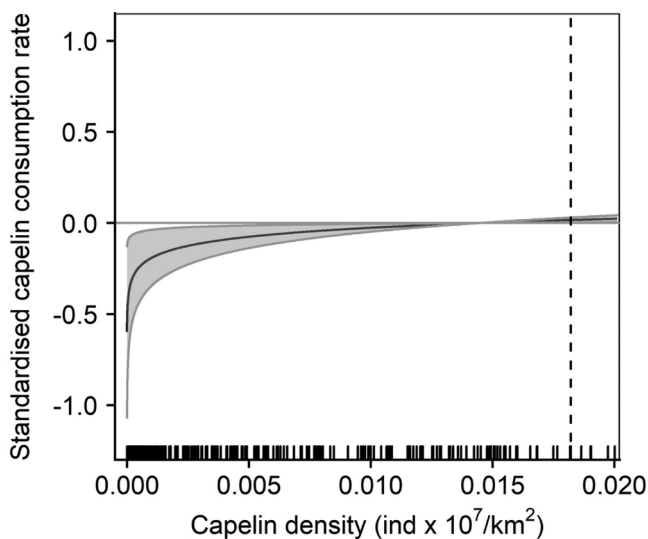


Figure 5. Smooth function of consumption rate versus capelin density, zoomed in from Fig. 4a. Median observed capelin density is indicated by the dashed vertical line.

and 4) all interactions. The gCV score (mean square prediction error) was lowest for the model without capelin density interactions, i.e. it was best at predicting observations not included in the model (Supporting information). These interactions are therefore shown in the Supporting information only. Removing sampling day gave highest prediction error, while models 2 and 4 had similar prediction errors as our final model. In each case, a non-linear depth effect captured the consumption peak at intermediate depths where cod and capelin overlapped vertically (Supporting information).

Predictions

Based on the statistical models, three of the four predictions on drivers of variation in cod feeding were supported in the data (Table 1).

Discussion

In this study, we formulated hypotheses on drivers of variation in a demersal predator's consumption of a pelagic prey

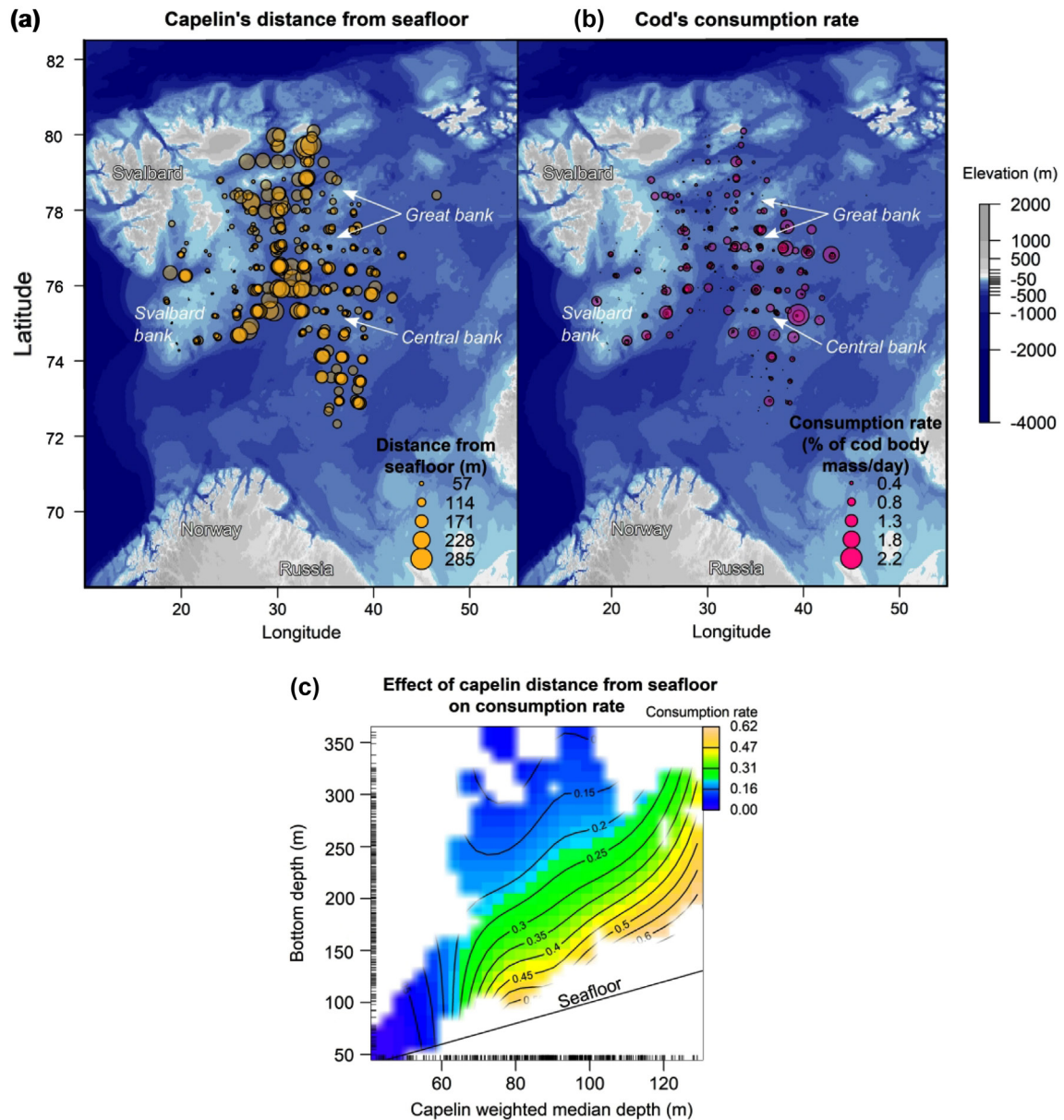


Figure 6. (a) Spatial distribution of capelin's distance to the seafloor calculated as the difference between the bottom depth and the standardized weighted median depth of capelin. (b) Spatial distribution of cod's consumption rate calculated as averages for each sampling station. (c) Interaction between capelin weighted median depth and bottom depth from the generalised additive model ($edf = 3.3$, $p < 0.001$). The surface colour, ranging from blue to orange, indicate the predicted consumption rate. Predictions are only shown for covariate combinations close to observed data. Rugs along the axes show the distribution of covariate values in the raw data.

Table 1. Summary of the results in relation to the hypothesised drivers of cod feeding presented in the methods section. The statistical significances of the respective response–covariate relationships are presented in Fig. 4, 6 and in the Supporting information.

Prediction	Supported by the data
I. Capelin consumption increases with increasing capelin density to a point of saturation.	yes (Fig. 4a)
II. Capelin consumption decreases with increasing cod density.	no (Supporting information)
III. Capelin consumption decreases with increasing depth, possibly non-linearly if the spatial consumption pattern reflects cod's association with banks.	yes (Fig. 4b) (consumption decreases non-linearly with depth, Fig. 6c)
IV. Capelin consumption is higher when capelin is distributed closer to the seafloor.	yes – except at the shallowest depths (Fig. 6c)

and tested predictions on a large dataset on predator stomach contents and environmental variables. Nearly two thirds of the total prey mass consumed by cod was capelin, but only every third cod had capelin in the stomach. This variation was weakly related to prey density, but there was a clear association between cod consumption and capelin distance from the seafloor, with the most favourable conditions occurring at depths corresponding to the Great and Central banks of the Barents Sea (150–200 m). Consumption was low in shallower areas, and in deeper areas only the deepest capelin distributions were associated with higher consumption. Thus, feeding was strongly dependent on vertical predator–prey overlap, while variations in horizontal overlap across the study area was less important. These results are discussed in more detail below.

Drivers of variation in cod feeding

Prey and predator densities

Neither capelin nor cod densities had large effects on the amount of capelin consumed by cod. The main increase in capelin consumption with capelin density occurred at very low capelin densities. Even when capelin was distributed close to the seafloor where cod resides, we found no additional effect of capelin density on consumption. The mass of capelin found in cod stomachs generally exceeded the amount that cod can digest in a day (Supporting information), suggesting that once capelin is available, the feeding rate is limited by digestive capacity (Fall and Fiksen 2020). The weak effect of capelin density on feeding may explain the weak aggregative response of cod to capelin (Fall et al. 2018), and the lack of influence of cod density on consumption.

However, time lags between feeding and stomach sampling can lead to a mismatch between the measured prey density at the time of capture and that experienced by the predator during feeding (Rindorf and Gislason 2005). To evaluate possible effects of such time lags, we must know the time since ingestion. The digestion stages used are qualitative and cannot directly be translated to time since ingestion, but a rough approximation can be done using the stomach evacuation model we use to estimate consumption rate. Cod that had fed on capelin had a median mass of 22 g capelin of digestion stage 3, ‘half digested’ in their stomachs. If we take ‘half digested’ to mean an initial meal size of 44 g, it would have taken around 54 h to digest the meal to the median mass observed (for cod with body mass 1300 g at 0.7°C). In some cases, stomach contents may therefore reflect feeding events that took place a few days before the cod was caught. This may explain the high variability in consumption rate within stations (Supporting information). We consider it unlikely, however, that differences in capelin density between the area of ingestion and the area of capture would lead to the pattern observed, as that would require systematic movement of cod to areas of lower capelin density after feeding. The slow digestion rate also implies saturation of the functional response at capelin densities similar to those observed here (Fall and Fiksen 2020).

Synergies between bottom depth and vertical prey distribution

Cod in the Barents Sea aggregate on the banks (Fall et al. 2018), and we found that this is also where they consume most capelin, particularly when capelin is distributed close to the seafloor. In the ocean, banks and other shallow bathymetries often attract high abundances of fish, which is exploited in commercial fisheries. One reason for this, which we have demonstrated here, is that prey may be more available for predators in shallower habitats. A small-scale study from the Great Bank, an area that is also included in the present study, revealed that cod remains in close association with the bottom throughout the day (Skaret et al. 2020). In Newfoundland, cod’s consumption of capelin decreased with depth (Fahrig et al. 1993), suggesting that higher vertical overlap and encounter rates in shallow water is important for feeding success. The strong effect of capelin depth distribution on cod feeding identified here alludes to a sit-and-pursue strategy, where cod rely on diel prey migrations to bring abundant food closer to the sea floor rather than searching for it higher in the water column.

For capelin, too, banks are profitable feeding grounds since their zooplankton prey gets transported onto the banks by currents and the shallow depth prevent them from descending into darker areas where they can hide from visual predation (Isaacs and Schwartzlose 1965, Aarflot et al. 2020). Despite higher feeding success over the banks (Aarflot et al. 2020), capelin is not strongly associated with these depths (Fall et al. 2018). This may reflect a tradeoff between feeding opportunity and predation risk – while large zooplankton prey like krill are caught in broad daylight near the bottom in daytime (Aarflot et al. 2018), foraging near the bottom comes with a risk of encountering the cod predator. Capelin off Newfoundland distributed farther from the seafloor when cod density increased (Mowbray 2002), which may result from avoidance behaviour or direct consumption, while in the Barents Sea, some capelin appears to take the risk of descending into the cod habitat to feed (Skaret et al. 2020).

Shallow water implies better light conditions for visual predators (Mazur and Beauchamp 2006). In the Barents Sea, feeding on the Great Bank occurred in the hours after dawn (Skaret et al. 2020), while in the Baltic Sea, cod feeding on sprat *Sprattus sprattus* were most active around dawn and dusk (Andersen et al. 2017). Generally, feeding periodicity is highly variable in cod between and within populations, between seasons, and even within individuals (Meager et al. 2017). We were not able to study feeding periodicity with available data, but given the difference in capelin depth distribution between day and night (Fig. 2 and the Supporting information), it is likely that capelin is not equally available to cod throughout the diel cycle.

The topography of the Barents Sea is a rugged landscape of shallow banks and deep troughs, and this appears to structure ecological interactions in space – from zooplankton to top predators. Aarflot et al. (2018, 2020) showed that capelin feed more effectively over the banks where plankton are unable to hide in the deep and dark during the day. Here we show that cod predation on capelin is also most intense

when capelin come down close to the bottom, pointing at a tradeoff between foraging and predation risk for capelin. The rugged underwater landscape may therefore create ideal habitats for both planktivore and piscivore fish and explain why some of the richest fisheries in the world are found here.

Spatial overlap in three dimensions

Recently, a thorough review article summarised 10 different spatial overlap indices and their ecological interpretation, many of which are assumed to reflect predation pressure (Carroll et al. 2019). In marine science, spatial overlap is almost always evaluated in the horizontal dimension using either vertically integrated species densities (e.g. from hydroacoustics) or data sampled at specific depths (e.g. by bottom trawling). At the same time, there is broad recognition of vertical migration behaviours in aquatic organisms, e.g. plankton (Hutchinson 1967), fish larvae and juveniles (Jensen et al. 2011), and adult pelagic (Huse and Korneliussen 2000) and demersal fish (Konstantinov 1958, Ono et al. 2018), and the resulting effect these behaviours may have on predation risk, predation rates and feeding periodicity (Clark and Levy 1988, Pearre 2003, Hrabik et al. 2006, Hansen et al. 2013, Langbehn et al. 2019). Based on their widespread use, one would think that spatial overlap indices evaluated in the horizontal dimension correlate well with consumption estimates or other measures of interaction. However, as emphasised by Grüss et al. (2020), how we use spatial overlap indices to predict predator–prey interactions remains a pressing question in ecology. Here we show that horizontal overlap alone has low predictive ability for species that are partly separated in the vertical dimension. It is likely that interactions between horizontal, vertical and temporal overlaps all need consideration to increase predictive power of predator–prey models.

Concluding remarks

We found strong spatial and temporal variation in the feeding of the generalist cod predator on its capelin prey in the Arctic Barents Sea. Prey consumption was highest in bank areas, reinforcing the view of bathymetric features as important hotspots of species interactions in large marine ecosystems. For the demersal cod, the vertical distance of the pelagic prey to the seafloor was a more important predictor of consumption than integrated prey density. In marine systems, the vertical dimension has strong gradients in light and other environmental factors that vary in diel and seasonal cycles, and spatial and temporal overlap along this dimension is key to quantify predator–prey interactions.

Data availability statement

Data will be archived in Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.4j0zpc89q>> (Fall et al. 2021).

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Author contributions

Johanna Fall: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Methodology (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Edda Johannesen:** Conceptualization (equal); Data curation (equal); Funding acquisition (lead); Methodology (supporting); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (supporting). **Göran Englund:** Conceptualization (equal); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Geir O. Johansen:** Conceptualization (equal); Methodology (supporting); Supervision (supporting); Writing – original draft (supporting). **Øyvind Fiksen:** Conceptualization (equal); Methodology (supporting); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (supporting).

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