

## RESEARCH ARTICLE

# Fine-scale diet data reveal spatial variation in predator–prey interactions in Norwegian fjords

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**Abstract**

1. Predator–prey interactions in time and space determine stock productivity, making them an important consideration when managing marine resources, rebuilding stocks or considering reopening a fishery.
2. We analysed fine-scale diet data from surveys conducted in 2009–2010 and 2018–2019 in three fjords in northern Norway with geostatistical models investigating how predation varied in space, time and between predator species. Our focus prey species was northern shrimp (*Pandalus borealis*), valuable both as a commercial resource and a major food source for other important species like Atlantic cod (*Gadus morhua*).
3. Diet composition of fish predators differed clearly between fjords. While predator species and size were good predictors of shrimp predation, the relationships with bathymetry, prey density and geospatial variables were complex.
4. Our study indicates that predation of forage species, such as shrimp, varies spatially in heterogeneous fjord ecosystems. Shrimp consumption was not highest in the fjord with highest predator density, indicating a higher dependency of cod on shrimp in specific areas.
5. Realized predation is a complex combination of predator and prey densities and predator ecology that differed in each of the three fjords.
6. *Synthesis and applications.* Ignoring spatial variations in predator–prey interactions may lead to an inaccurate perception of stock productivity, suboptimal management and possibly unsustainable management targets. We recommend spatially explicit assessment and management for fish stocks where predator–prey interactions vary substantially in space, such as fjords and reefs.

**KEYWORDS**

Atlantic cod, diet data, fisheries management, heterogeneous ecosystems, northern shrimp, predator–prey interactions, spatial variation

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## 1 | INTRODUCTION

Ecosystem approaches to fisheries management are common policy objectives, yet trophic interactions or spatial structure are rarely included in stock assessments and fisheries management (Skern-Mauritzen et al., 2016). Harvested species are mostly assessed and managed as single homogenous units, although they are part of food webs with complex trophic interactions that vary in time and space with predators and prey abundances (Berryman, 1992). Marine organisms grow many orders of magnitude in size from early life to adult stages, transitioning through multiple trophic levels and ecological niches. The variation in predator size, combined with site-specific biotic and abiotic characteristics, determines the type of available prey and the degree of experienced predation (Weitz & Levin, 2006).

Predator pressure can exert top-down regulation on prey behaviour, demography and population density (Creel & Christianson, 2008; Krivan & Eisner, 2003). Predation response may impose significant effects on prey demographics (Sinclair et al., 2003), foraging efficiency and growth (Creel & Christianson, 2008), habitat use (Fortin et al., 2005), reproductive success (Magnhagen, 1991; Preisser et al., 2005) and consequently survival. Conversely, prey dynamics exert bottom-up control on predator productivity and distribution in marine (Ware & Thomson, 2005) and terrestrial ecosystems (Eide et al., 2012). Thus, predator–prey relationships constitute complex feedback dynamics determined by internal and external factors.

Smaller and usually highly productive forage species such as small fish and crustaceans (e.g. capelin (*Mallotus villosus*) and shrimp) constitute substantial parts of marine ecosystems' biomass and crucial bottlenecks for energy flow to higher trophic levels. Forage species experience particularly high predation throughout ontogenesis (Richards & Jacobson, 2016) and high population fluctuations due to shorter life span, varying availability of food and predation pressure (Pikitch et al., 2014). Additionally, forage species represent crucial marine resources as directly harvested species and food source for valuable higher trophic species.

For management, trophic interactions matter because they determine productivity, sustainable yields and resilience to anthropogenic stressors. Fishing not only impacts abundance and species composition directly but also ecosystem functioning, indirectly modifying species abundances (Plaganyi et al., 2022). Thus, assessing predation pressures is important for sustainable harvesting, especially for forage species (Pope et al., 2021; Trijoulet et al., 2019). Although predation is often assumed to increase with prey or predator density (Rindorf et al., 2010), predation dynamics are not necessarily simple functions of predator–prey ratios but are affected by density-dependent prey and predator behaviour such as prey schooling (Siders et al., 2020) or seeking refuge in complex habitat (Savino & Stein, 1989). Fishing can alter predator–prey dynamics by changing abundances (Durante et al., 2020), especially for heavily predated species or predators with a strong dependence on specific prey. Considering these interactions in management may prevent

unsustainable harvest strategies for both target species as well as other ecosystem components (DeMaster et al., 2001; Plaganyi et al., 2022).

Diet data are key in understanding trophic interactions and energy flow in ecosystems (Nielsen et al., 2017) and important in ecosystem modelling to quantify trophic interactions (Tarnecki et al., 2016). Fine-scale diet data can inform about predation dynamics over time and space (Boyd, 1996) to uncover spatio-temporal variation in prey mortality (Grüss et al., 2020), identify drivers of variation, produce prey biomass indices (Ng et al., 2021) and aid in understanding changes in production (Gaichas et al., 2010) and ecosystem dynamics to inform resource management (Grüss et al., 2020). Accounting for spatial dynamics may be particularly important for finely structured and often vulnerable ecosystems such as coasts, fjords, reefs or seamounts.

We explored the diet composition of higher trophic demersal fish in three large fjord ecosystems in northern Norway, using spatially and taxonomically highly resolved data and geostatistical modelling. Our focus was on northern shrimp (*Pandalus borealis*), a key forage species for demersal fish (Parsons, 2005a) and target of a relevant inshore trawl fishery. Bottom trawling has been banned for 50 years in two study fjords, but reopening of shrimp trawling is presently considered, increasing the need for studying trophic dependencies of other species on shrimp and potential ecosystem effects of fishing. This is a unique case where fine-scale diet data may provide insights on spatial predator–prey dynamics in fjords under different fishing pressure (ongoing shrimp trawling vs. zero trawling), under the hypothesis that shrimp biomass and predatory consumption is lower in the fjord where shrimp trawling occurs. Our aims were to (i) compare diet composition among fish predators and fjords, (ii) determine the abiotic, biotic and geospatial variables explaining variation in shrimp predation and (iii) estimate fjord-specific shrimp consumption by Atlantic cod (*Gadus morhua*). Finally, we discuss the implications of spatial variation in shrimp predation and demersal fish abundance for stock assessment and management.

## 2 | MATERIALS AND METHODS

Surveys with stratified random sampling using a demersal trawl were conducted in three fjords in northern Norway in 2009–2010 and 2018–2019 (Figure 1). All organisms caught were identified and registered. Individual measurements were taken for subsamples of all fish and crustacean species, including stomach contents from important predator species. Stomach contents were identified to lowest taxonomic level possible and weighed to determine diet composition. Statistical analyses focused on prevalence and biomass of shrimp in predator diets. Additionally, we modelled shrimp (prey) and predator densities in space to explore their relationship with predation rates. Lastly, we estimated shrimp consumption by Atlantic cod per fjord from density and predation models. All analyses were conducted in R version 4.2.2 (R Core Team, 2022) with sdmTMB (Anderson et al., 2022) for statistical modelling.

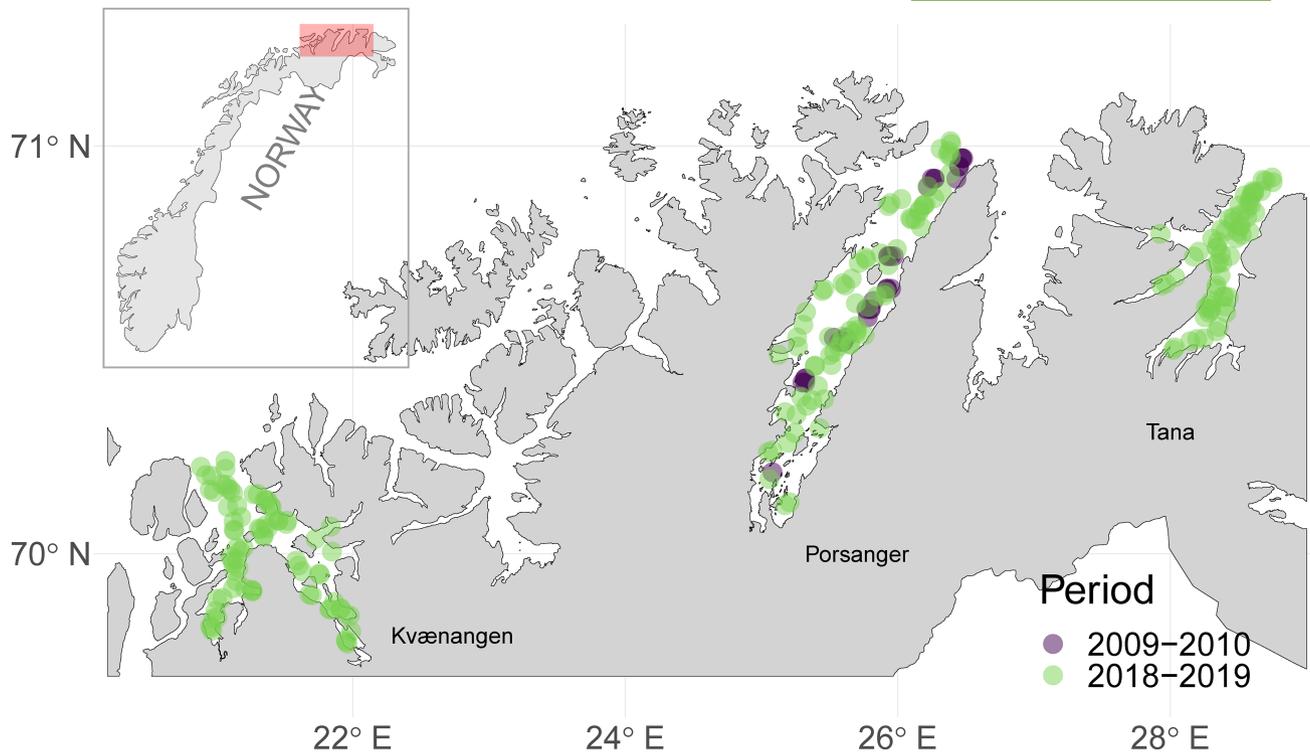


FIGURE 1 Study area and sampling locations in the three fjords in northern Norway in 2009–2010 (purple) and 2018–2019 (green).

The conducted trawling survey was an exemption from the Directorate of Fisheries while no ethical approval was needed for the stomach analysis.

## 2.1 | Study area

The three study fjords in northern Norway (Kvænangen, Porsanger and Tana) (Figure 1) are 60–120 km long, with complex bathymetries and maximum depths varying from around 300 to 450 m. The fjord systems are influenced by inflow of freshwater from rivers and coastal currents. Inner parts of Kvænangen and Porsanger fjords are separated from outer parts by sills (beds of sediment and rock). The inner Porsanger basin is separated from the outer fjord by a shallow sill and characterized by cold bottom water (around 0°C).

Porsanger and Tana were closed for shrimp trawling in the early 1970s because of high bycatches of overfished demersal fish. The neighbouring fjord Kvænangen has had an active shrimp trawl fishery since the 1930s (Hjort & Ruud, 1938) with annual landings in 2010–2020 of 100–200 tonnes, and was included in the study as comparison. Demersal fish are caught in all three fjords with longlines and gillnets.

While coastal Atlantic cod is assessed and managed as separate stock (north of 67° N), shrimp and other demersal fish in the study area are managed together with larger offshore management units or not assessed at all. Shrimp populations in the three fjords are part of one management unit for shrimp north of 62° N dominated

by the Barents Sea, despite different genetic structures (Hansen et al., 2021). Regulations of the shrimp fishery (licences, compulsory sorting grid, temporary spatial closures and no trawling shallower than 170 m depth) mainly aim at reducing fish bycatch.

## 2.2 | Data

### 2.2.1 | 2009–2010

In 2009 and 2010, the Porsanger ecosystem was comprehensively surveyed (see Pedersen et al., 2018). Stomach data from these investigations were included to assess potential temporal changes in cod diets. Stratified random surveys were conducted in February, April/May and August in 2009 and 2010 (in total 53 trawl stations). Demersal trawling was performed using a *Super Campelen* 1400 mesh shrimp trawl with an 8 mm net inside the codend for 30 min at approximately three knots. A total of 607 cod stomachs from 40 stations were analysed (see Appendix S1, Tables S1 and S2).

### 2.2.2 | 2018–2019

The fjords Kvænangen, Porsanger and Tana were surveyed in 2018–2019 to evaluate the reopening of areas closed for shrimp trawling (Søvik et al., 2020). Surveys were conducted in 2018 (autumn) and 2019 (autumn and spring) with a commercial trawler (LK7560,

14.95 m vessel length), using a 1600-mesh shrimp trawl with 15 mm mesh size in the codend and without sorting grid (dispensation given by the Norwegian Directorate of Fisheries). Trawling time was 15 min at 1.5–1.7 knots. Across fjords, 220 trawl stations were placed in a random-stratified design within areas considered accessible to demersal trawling based on bathymetry and bottom sediment. Samples were collected from an average of 22 stations per fjord and survey season (Figure 1; Table S1). Up to 10 stomachs per haul from each relevant predator species were analysed (3490 stomachs in total) (Tables S1 and S2).

### 2.2.3 | Stomach content analysis

Standard protocols were used for stomach content analysis (details in Appendices S1 and S2) of Atlantic cod in both periods, and in 2018–2019 of saithe (*Pollachius virens*), haddock (*Melanogrammus aeglefinus*), golden redfish (*Sebastes norvegicus*), shorthorn sculpin (*Myoxocephalus scorpius*) and whiting (*Merlangius merlangus*). Haddock and cod were commonly caught, while other species had comparatively low sampling sizes (Table S2). Prey species were

weighed and categorized into major groups based on taxonomic and ecological criteria (Figure 2; Figures S1 and S2).

### 2.3 | Statistical analysis

We analysed the data with generalized additive mixed models. Because there was no continuous time series and coverage was more limited in 2009–2010 compared to 2018–2019, we included period as categorical variable. To account for underlying spatial processes, we added Gaussian Markov random fields estimated through stochastic partial differential equation approximation (Lindgren et al., 2011) using sdmTMB (Anderson et al., 2022).

Based on distance between sampling locations and expected range of spatial correlation, spatial meshes were created with R-INLA (Bakka et al., 2018), using maximum and minimum distances between vertices of 30 and 10 km, respectively. Meshes were constrained with nonconvex boundaries for each fjord, separating fjords (Figure M1). For all models, backward model selection using AIC was applied to sets of response-specific fixed effects. Model performance was evaluated through simulated residual distributions using

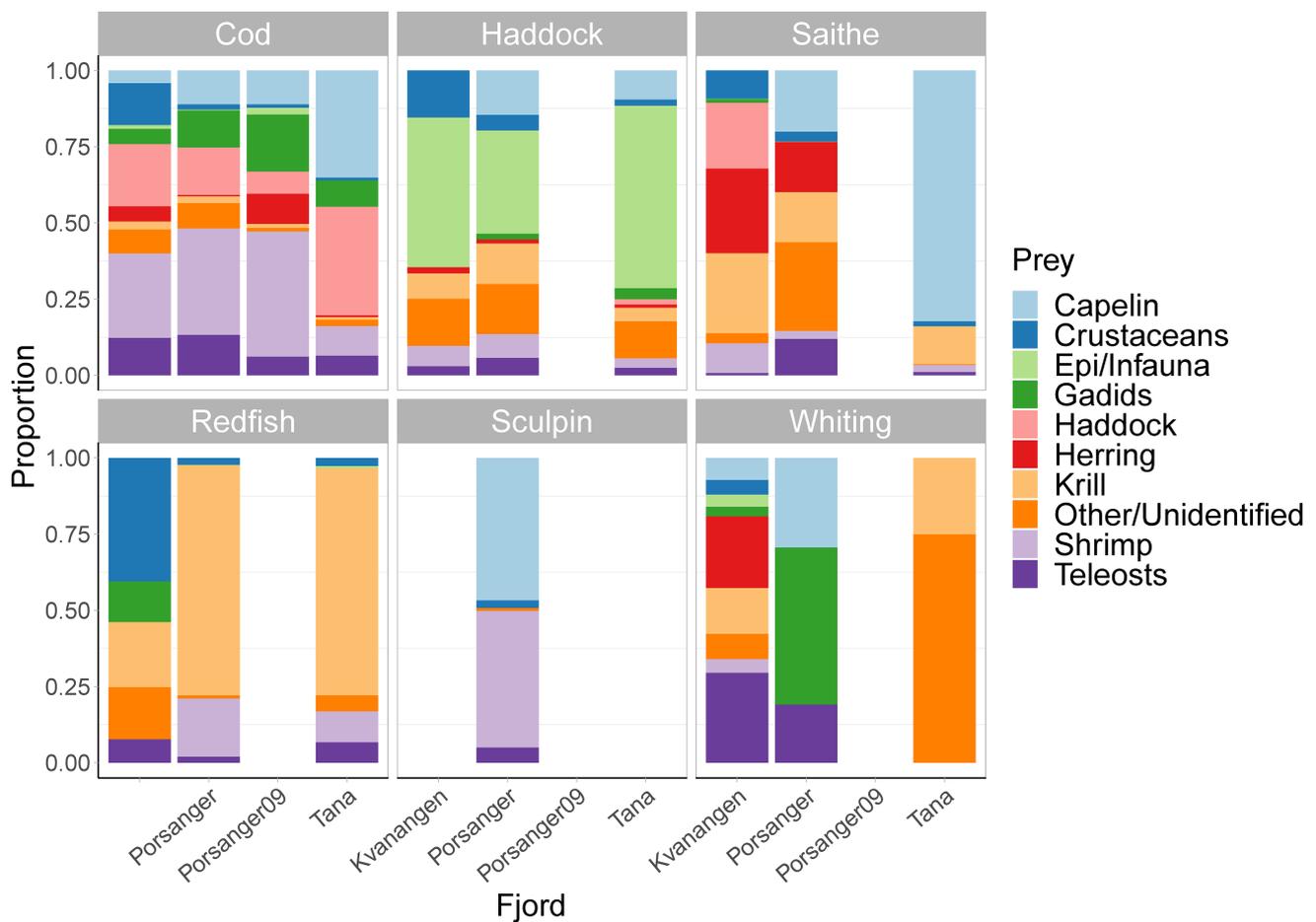


FIGURE 2 Total proportion of prey groups (total prey weight/total stomach content weight) across all stomachs per predator species and fjord for the period 2018–2019. The 2009–2010 period for cod in Porsanger is shown as Porsanger09. Light purple (shrimp) represents Pandalid shrimp (almost exclusively northern shrimp).

the DHARMA package (Hartig, 2021). In-depth model information can be found in Appendix S2.

### 2.3.1 | Models

Models used in the present study were defined as:

$$E[Y_{i,a}] = \mu_{i,a},$$

$$\mu_{i,a} = f\left(X_{i,a}^{\text{cat}}\beta + s\left(X_{i,a}^{\text{cont}}\right) + \omega_i + \alpha_g\right),$$

With mean  $\mu$  for expected values of  $E[Y_{i,a}]$ ,  $y_{i,a}$  representing the response data for station  $i$  in fjord  $a$ ;  $f$  a link function;  $X_{i,a}$  represents a vector of predictors for station in fjord (either categorical or continuous);  $\beta$  represents a vector of fixed-effect coefficients;  $s$  denotes smoothing splines;  $\omega_i$  a spatial random field; and  $\alpha_g$  random intercepts by group. The spatial random field was modelled as spatially correlated random effects  $\omega_i$  with a Matérn covariance matrix  $\Sigma_k \omega_i = f(x_i, y_i) \sim \text{GF}(0, \Sigma_\omega)$ . Response variables and corresponding link functions were: (i) predation probability represented by presence/absence of shrimp in predator stomach as logit-link binomial distribution,  $\text{Binomial}(N, \mu)$ ; (ii) predator consumption as biomass of shrimp in stomach; and (iii) density (biomass per trawl distance) of all predators, cod and shrimp as Tweedie distribution (Poisson–Gamma compound distribution) with log-link:  $\text{Tweedie}(\mu, p, \phi)$  (power parameter  $p$  was restricted to  $1 < p < 2$  for continuously distributed positive values and positive mass at 0). The distribution was selected because the data contained several zero observations combined with continuous positive catch weights.

All analyses (see Appendix S2, model information) included random effects and fixed effects. Possible explanatory variables were selected based on initial investigation and data availability, with fjord and period (2009–2010 or 2018–2019) as categorical fixed effects in all models, and bottom depth (m), predator lengths (cm), shrimp densities (kg/nmi) and predator biomass (kg) as continuous fixed effects. In addition, season (spring, summer, autumn and winter) was included in all models as random intercepts  $\alpha_{(\text{variable})} \sim N(0, \sigma_\alpha^2)$ , as was predator species for predation models. Continuous fixed effects were standardized using z-score normalization to facilitate model convergence and effect size comparison. Thin plate regression splines ('mgvc' R package; Anderson, 2019) restricted to three knots were applied to all continuous effects.

Equally spaced interpolation grids with grid cells of 0.5 km<sup>2</sup> were used to predict the estimated quantities in space. For all prediction points, bottom depth was based on GEBCO bathymetric data (download.gebco.net). Prey and predator densities were predicted from final models derived in the present study. All other continuous effects were set to their average, while categorical effects were included with all levels. Random intercepts for predator species and season were set to 0 (population-level prediction)

or included with specific factor levels (e.g. cod in autumn) where relevant.

### 2.3.2 | Consumption

We applied the evacuation model from dos Santos and Jobling (1992) as adapted in Bogstad and Gjøvsæter (1994) to estimate shrimp consumption by cod (excluding inner Porsanger due to the absence of cod). Estimates were derived from model predictions across the interpolation grid of stomach content, shrimp density and cod density. The latter two were scaled to grid cell area using different swept widths depending on species and gear: for shrimp, 11.7 and 18 m for 2009–2010 and 2018–2019, respectively, and for cod 20 and 25 m, respectively. Bogstad and Gjøvsæter (1994) defined consumption as:

$$C_{\text{Fjord}} = \frac{W_{\text{tot}} \times \ln 2 \times e^{c \cdot T} \times r \times D}{H \cdot r^z},$$

where  $W_{\text{tot}}$  is total cod biomass (tonnes),  $T$  mean temperature (°C),  $r$  is the ratio  $S/W$ , where  $S$  = average stomach content of shrimp,  $D$  = days of overlap between cod and shrimp, the half-life of a same-sized meal as the fish body weight in days  $H = 20.75$  (dos Santos & Jobling, 1992) and  $c = 0.11$  and  $z = 0.54$  are species-independent temperature and shape parameters, respectively. For overlapping days, we used 90 to represent a temporal range comparable to a survey period.

To derive stomach content ratio  $r$ , we converted average cod length to weight by estimating the allometric length–weight relationship for cod from all individual measurements:  $W = a \cdot L^b$  where  $W$  is body weight (g),  $L$  is length (cm) and  $a$  and  $b$  are the allometric coefficient and exponent, respectively. Estimated parameters were  $a = 0.006$  and  $b = 3.093$  using a linear model after log-transforming length and weight.

To propagate uncertainty from each model predicting stomach content, shrimp biomass, cod biomass, length–weight relationship and consumption, we applied a bootstrap process with 500 iterations. Each iteration consisted of simulated predictions drawn per grid cell or area (length–weight) from means and standard errors of all models, resampled individual cod length from observed data and parameter distributions ( $H$ , temperature).

## 3 | RESULTS

The six demersal fish predators displayed a diverse diet, including epi-/infauna, pelagic and demersal crustaceans, and forage fish species (Figure 2; Figures S1 and S2). The diet varied between species and within species among fjords. Shrimp was a common dietary component for most predators, especially for cod and in Porsanger (Figure 2). Similarly, sculpin showed a preference for shrimp and capelin (Figure 2; Figure S1), but samples were limited to the inner

Porsanger basin where other predators were absent. Haddock favoured benthic epi-/infauna (Figure 2; Figure S1). In Tana, cod primarily consumed capelin and gadids (mostly haddock). Sample sizes of redfish, saithe and whiting were small with large inter-fjord variation (Table S2).

### 3.1 | Density

Cod and other demersal predators exhibited highest densities in Kvænangen and Tana (Figure 3) and were prevalent throughout the fjords, particularly in shallower regions (Figures S3 and S4). The higher density in shallower areas was driven by substantial nearshore catches of juvenile haddock. In contrast, Porsanger showed lower predator densities, with cod noticeably absent in the innermost basin. This pattern remained consistent across time periods (Figure S3), indicating that the inner Porsanger area is unfavourable for cod. Seasonally, density of cod was higher in autumn and winter compared to spring and summer, a trend observed for all predators (Tables M1–M4). Most variation in predator and cod density was attributed to observed shrimp density and bathymetry (only cod) (Table M1), with spatial random fields capturing minimal additional spatial variation (Figures M3 and M5).

Shrimp density was similar between fjords (Figure 3) but varied substantially within fjords (Zimmermann et al., 2023). Shrimp density depended strongly on depth (Table M5), with highest shrimp densities in the deeper fjord basins, while the spatial random field captured clusters of high densities in shallower areas (mostly inner

Porsanger) (Figure M7). Shrimp distribution remained consistent between 2009–2010 and 2018–2019 (Figure 3; Figure S5), showing a slight, non-significant decrease between these periods (Table M6). Seasonal impact on shrimp density was low, and cod biomass was irrelevant and excluded from the final model.

### 3.2 | Consumption of shrimp

Substantial intra- and inter-fjord variation in consumption of shrimp by cod was found. Shrimp was more important in cod diet in Porsanger compared to Kvænangen and Tana (Figures 4, 5, and 7). In Porsanger, consumed biomass of shrimp by cod was high in both time periods (Figures 6 and 7; Figure S8), whereas shrimp occurred more frequently in cod stomachs in 2009–2010 (Figure 4; Figures S2 and S9). Seasonal variation was low (Figure S10; Table M9), instead probability of shrimp in cod diet was mostly explained by shrimp density and cod length, with probability of consumption peaking at intermediate predator sizes. Cod biomass was irrelevant, and depth had only a marginal improvement on model performance and was excluded from the selected model (Tables M7 and M8). Fixed effects explained most of the observed variation, with the spatial random field contributing only minimally, primarily in Porsanger, with short Matérn correlation range (Figure M9; Table M8).

Shrimp biomass per predator stomach varied spatially between and within fjords but was highest in Porsanger (Figures 5 and 6). Predator length and spatial random field were the most relevant

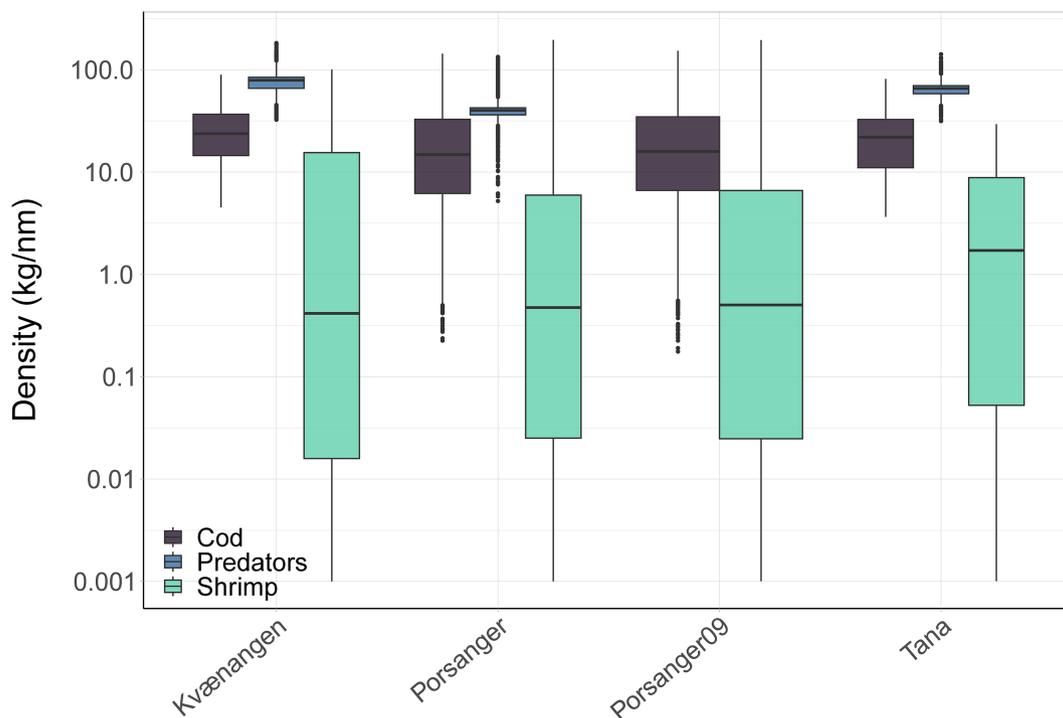
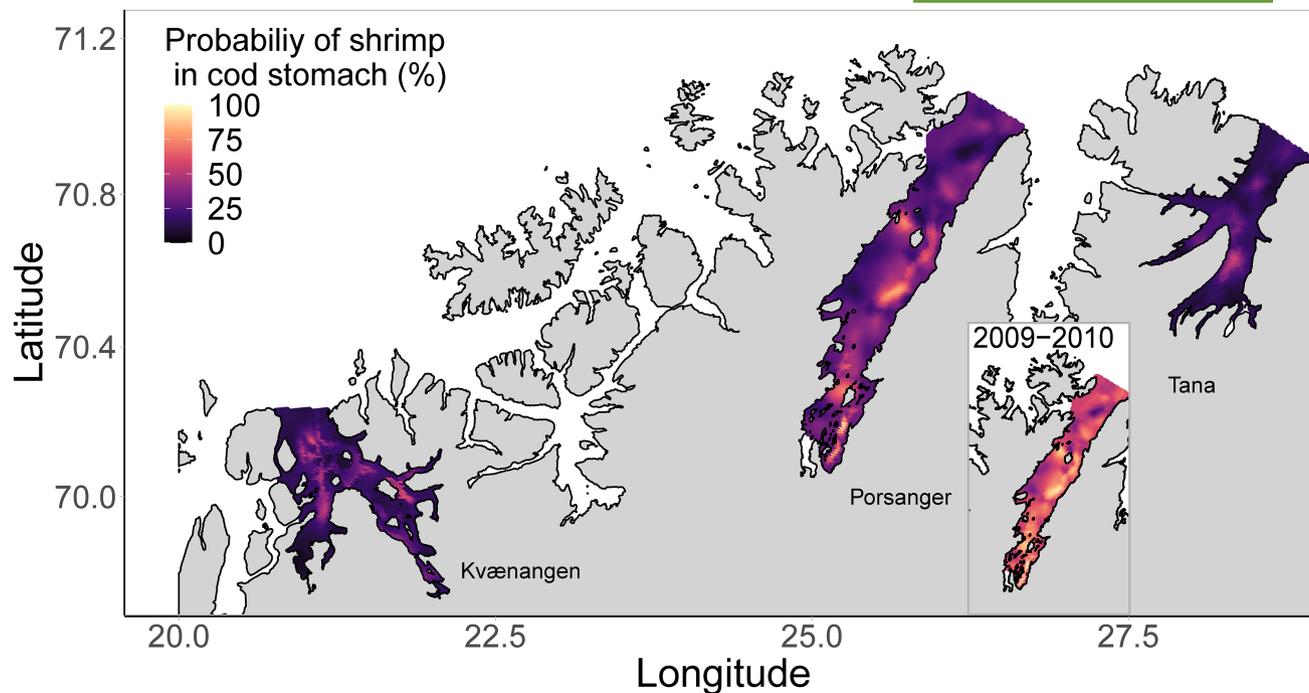


FIGURE 3 The boxplot shows predicted estimates of density (kg/nm) on log-scale from the models, summarized per fjord and when relevant for period, for cod (black), all demersal predators (dark blue) and shrimp (turquoise). Shown are medians (black lines), 25th and 75th percentiles (boxes), 1.5 interquartile ranges (whiskers) and outliers (dots).



**FIGURE 4** Probability of shrimp occurrence in cod stomachs (%) for the periods 2009–2010 (inset map) and 2018–2019 as predicted by the selected model (fjord, period, season, shrimp density and cod length). Information on shrimp density was included for all integration points. Season and length were set to the global means for the predictions shown here.

predictors of consumed shrimp biomass, followed by depth and shrimp density (Table M9). The fixed effects were good predictors for deeper areas of the fjords, while the spatial random field explained the variation in shallower regions of the fjords, particularly for Porsanger (Figure M11). In contrast to a clear, nearly linear increase of shrimp prevalence in cod stomachs with increasing shrimp density (Figure S6A), consumed shrimp biomass in predator stomachs slightly declined after peaking around 75 kg/nm shrimp density (Figure 5b). The slight decline was driven by few sculpin stomach samples from Inner Porsanger where shrimp densities were highest, and cod absent.

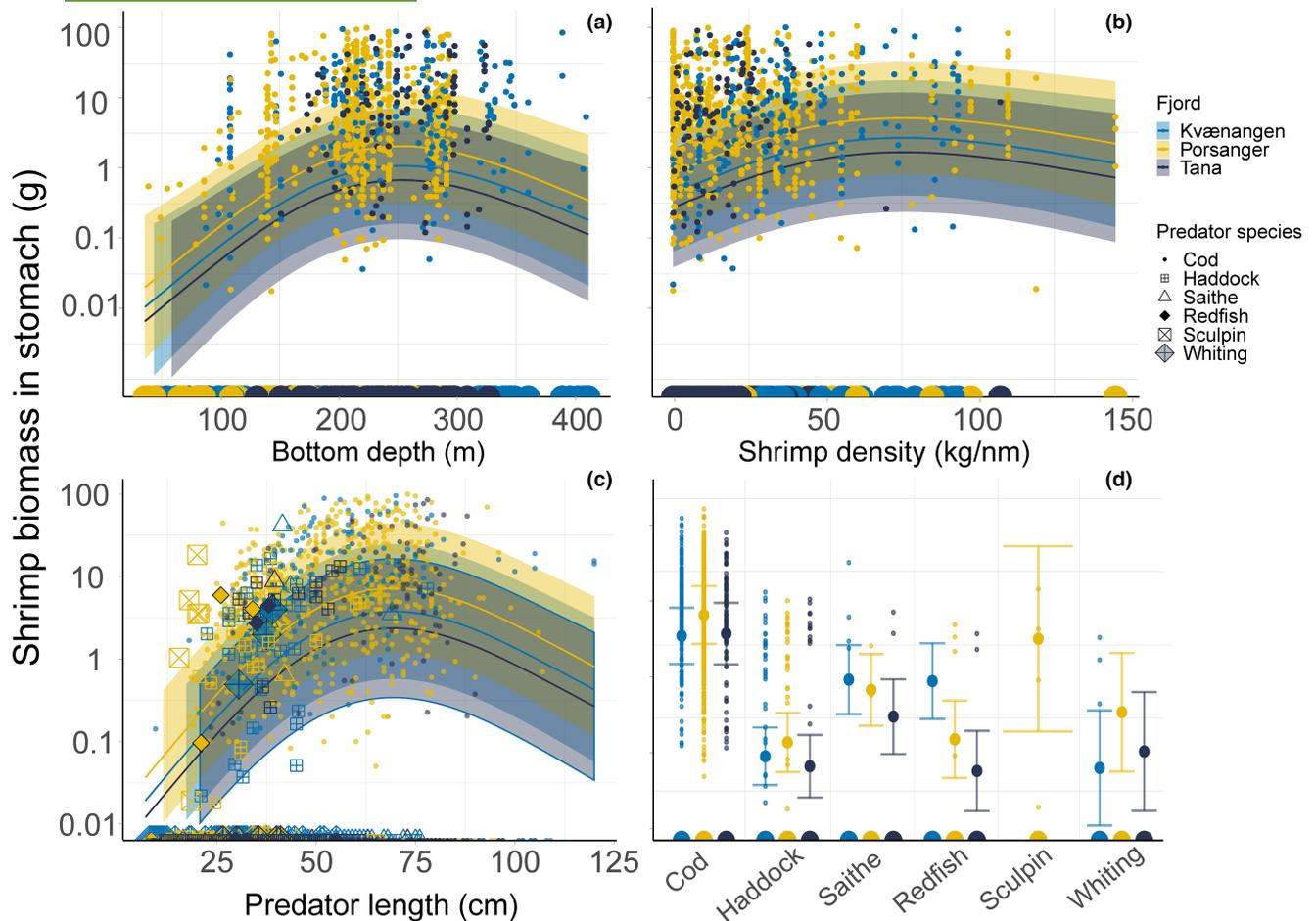
The biomass and proportion of consumed shrimp differed between predators but increased strongly with predator size until predators reached lengths of around 70 cm (Figure 5c). Despite few samples of larger predators, cod up to ~120 cm in length consumed shrimp. Cod was the main predator across all three fjords but consumed the highest biomass of shrimp in Porsanger (Figure 5d; Figure M10). Sculpin consumed a disproportionately high biomass of shrimp given their small size compared to the other predators (Figure 5d; Figure S7; Table M10), while shrimp consumption was minor and uncertain for saithe, redfish and whiting due to small sample sizes (Figures 2 and 5d).

Estimated total shrimp consumption by cod by fjord and shrimp consumed relative both to its own biomass and cod biomass were highest in Porsanger (median of 145 t, ratios of 0.25 and 0.08 in 2018–2019, Figure 7). The consumption ratios (consumed shrimp biomass by cod either relative to shrimp biomass or to cod biomass) were consistent across time periods despite absolute shrimp, cod

and consumption of shrimp biomass levels scaling higher in 2009–2010. Consumption ratio per unit of shrimp biomass was lowest in Kvænangen (0.08). Whereas the low shrimp biomass relative to a large cod biomass in Tana led to a higher consumption ratio (0.19), despite relatively low importance of shrimp in cod diet (Figures 2 and 5). In Kvænangen and Tana, consumption ratios per unit of cod biomass were equally low (0.04) due to a low overall consumption compared to the cod biomass (Figure 7, right panel).

## 4 | DISCUSSION

Our study shows substantial spatial variation in diet composition of predatory demersal fish and predation on a key forage species, northern shrimp, in fjord ecosystems in northern Norway. A high consumption of shrimp by Atlantic cod indicates a strong association between cod and shrimp in fjords closed to shrimp trawling. Particularly in Porsanger, we found highest consumption ratios even though it held the lowest shrimp density. Whereas in Tana, a large discrepancy between cod and shrimp biomass, despite a comparatively low share of shrimp in cod diet, indicated a high consumption ratio relative to shrimp biomass. Despite contrasting causes, shrimp populations in these two fjords experience in the absence of fishing much higher predation pressure than the shrimp population in the fjord with ongoing trawling, Kvænangen. While predator species and size were good predictors of shrimp predation, the relationships with bathymetry, prey density and geospatial variables (random spatial effects) were complex. The

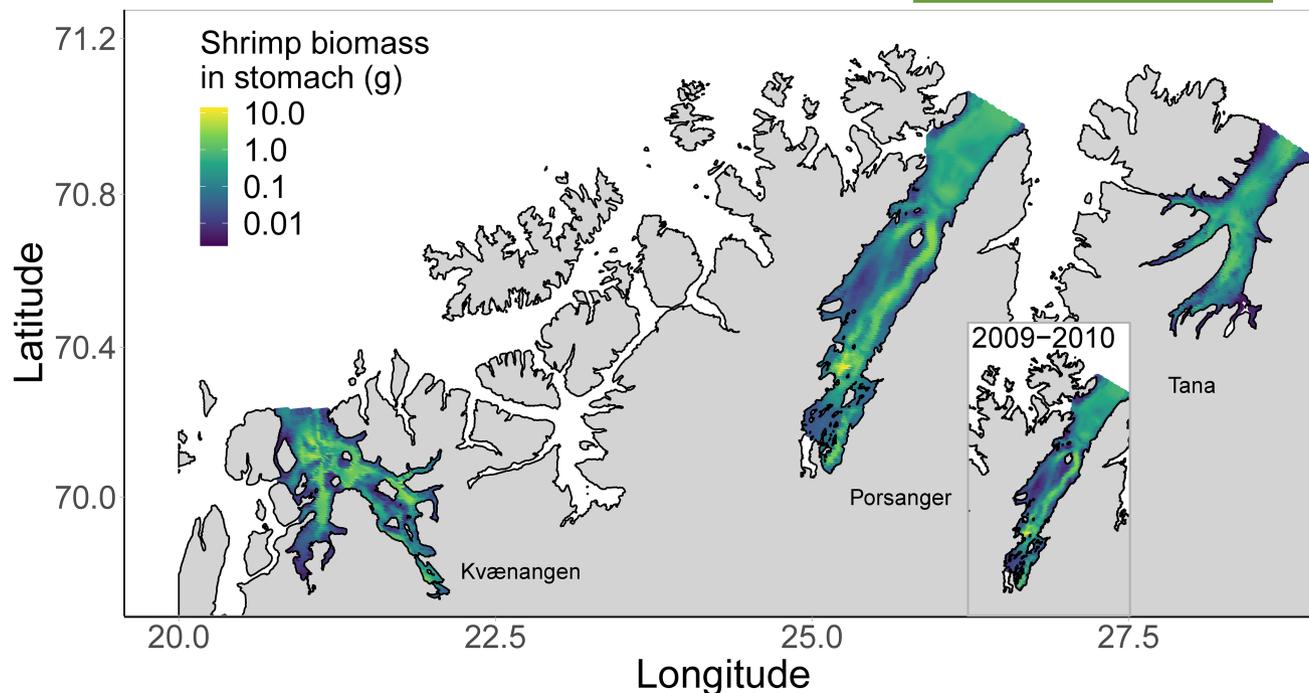


**FIGURE 5** Conditional effects of bottom depth (a), shrimp density (b), predator length (c) and predator species (random intercept, including fjord-specific mean length per species) (d) on shrimp biomass in stomachs estimated in the selected model. Estimates are shown as mean and 95% confidence intervals (large dots and error bars) of joint predictions of categorical fjord effects, period 2018–2019 and respective fixed effect. Other random and fixed effects were set to their mean. Small dots represent individual data points (shrimp biomass in individual stomachs of predators). Sculpin results are uncertain due to sample size, reflected by the large confidence interval. Fjords are differentiated by colour.

results indicate distinctly different food web dynamics between these fjords that may be partly shaped by differences in fishing activities.

Predator–prey dynamics shape food web structures (Preisser et al., 2005; Sinclair et al., 2003; Worm & Myers, 2003). Historically, predator populations, and notably cod, often fluctuate with prey abundance such as shrimp (Parsons, 2005a), simultaneously predation mortality is a key regulator of shrimp population dynamics (Link & Idoine, 2009; Parsons, 2005b; Worm & Myers, 2003). Our findings revealed shrimp density to be an important factor for predator dynamics, while predator biomass was not relevant for shrimp density, emphasizing the role of prey availability as a key factor for the consumed amount of shrimp by cod. Based on the survey data from 2009 to 2010 used here, Pedersen et al. (2018) found shrimp to be the most important prey for local cod in Porsanger, consistent with our analysis. High spatial variability in species densities and diets within and among fjords underlines the complexity of highly structured coastal ecosystems such as fjords. Fjords can act as nursery areas for juvenile

demersal fish, and shrimp was mainly consumed by small to mid-sized cod, suggesting that younger cod might feed in these fjords before switching to their preferred prey, capelin, when they reach bigger sizes (Holt et al., 2019). Consequently, predation is likely to vary spatiotemporally in heterogeneous or partially confined ecosystems (e.g. coasts, fjords or reefs) (Siple et al., 2021). Intra-fjord variation was highest in Porsanger, where in the absence of most predators except for sculpin, shrimp occur in very high densities in the partially separated, cold inner basin. This indicates predation release altering shrimp dynamics in the inner basin in comparison to the rest of the fjord where high predation pressure and comparatively low shrimp densities were found, suggesting that more contrast in cod densities is needed to detect a statistically relevant effect on shrimp density. Despite ongoing shrimp fishing in Kvænangen, shrimp and cod densities in the three fjords were not different (Zimmermann et al., 2023). Trawling in Kvænangen represents top-down mortality for shrimp, potentially substituting predation pressure and disturbing the bottom substrate, possibly enhancing food availability for shrimp. Top-down pressure from



**FIGURE 6** Shrimp biomass in predator stomach (g) on log-scale modelled for the periods 2009–2010 (inset map) and 2018–2019 with fixed (fjord, period, season, depth, predator length, shrimp density and predator species) and random effects. Information on shrimp was included for all integration points. Season and length were set to the population mean for the predictions shown here.

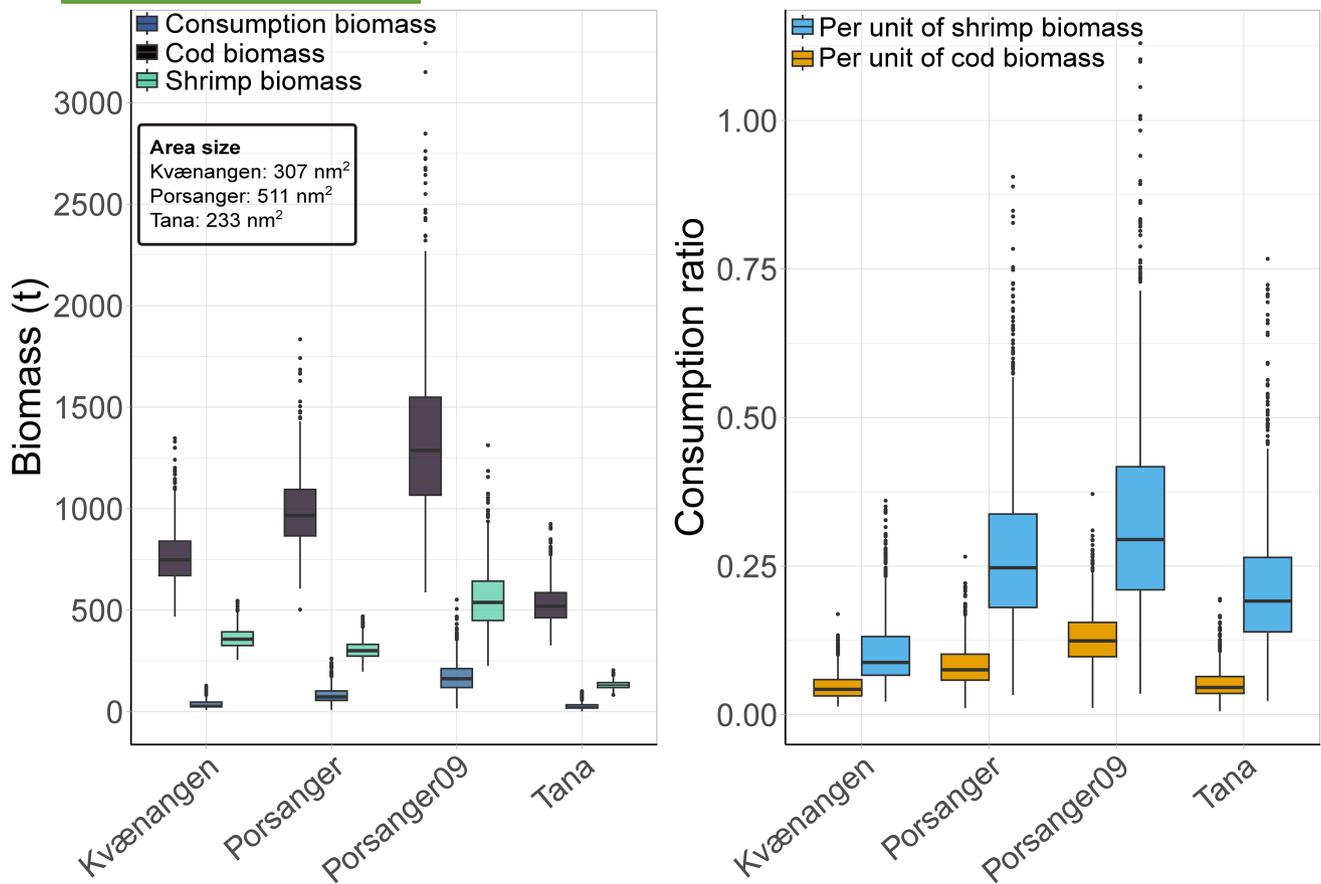
cod consumption in Porsanger and Tana may play a similar role as exerted by harvesting in Kvænangen.

Successful resource management requires knowledge of predator–prey dynamics in space and time, shaped by food web dynamics, environmental cues, behaviour and spatial overlap (Tromeur & Loeuille, 2017; Yodzis, 1994). A main source of error in stock assessment and management advice is limited information on key biological processes, notably predation mortality as main component of natural mortality (Pope et al., 2021). While consumption from major predators has been used as indices for temporal variation in natural mortality, spatial variation in predation mortality has rarely been considered, reflecting the general lack of spatial structure in fisheries management (Cardinale et al., 2023). Our findings show spatial variation of consumption ratios in line with natural mortality rates of shrimp in these fjords estimated from length frequencies (Båtevik, 2020). Comparing diet data from areas with contrasting trawling regimes presents a unique case to determine potential feedbacks between predation and fishing pressure, as both can exert top-down control. The substantial spatial differences revealed by our analysis suggest that spatial variation in consumption should be explored and, if relevant, included in stock assessments, especially when there is genetic or other stock structure that supports different dynamics between subpopulations. Geospatial modelling of consumption indices from diet information can aid in revealing spatio-temporal predator–prey dynamics. Even though stomach data are only snapshots in time and space, they can serve as indicators of prey abundance or predation mortality in management strategies (Siple et al., 2021) and provide additional insight into model performance (Gaichas et al., 2010). Introducing spatially explicit

consumption indices could help to scale sustainable fishing pressure appropriately across subpopulations often found in coastal ecosystems.

Demersal trawls sample larger organisms near the sea floor where most of the species diversity is found, underrepresenting species in other layers or with low catchability. For instance, saithe, an abundant top predator with a similar trophic niche as cod, tends to swim too fast to be caught in demersal trawls. Because of low sample size, it remains unclear whether saithe is a relevant shrimp predator in the study area. Similarly, we did not assess bottom-up productivity as driver of ecosystem dynamics and differences thereof. Fjord-specific hydrographic features affect water circulation, nutrient inflow and possibly overall trophic energy flow. Finally, survey designs and gear differed between 2009–2010 and 2018–2019, which complicates comparing absolute consumption temporally. However, diet composition and density of key species were largely similar during the two survey periods.

Fjords are not closed systems but partially open to the ocean, allowing for migratory movement (e.g. cod and capelin), causing substantial fluctuations in biomass that may alter trophic dynamics intra- and inter-annually. The large cod stock in the Barents Sea ('skrei'), genetically different from coastal cod (Breistein et al., 2022; Johansen et al., 2020) and managed as separate stocks (Howell et al., 2023; ICES, 2023), makes annual spawning migrations to the Norwegian coast and into the fjords (Berg et al., 2016). Extrapolating the estimated shrimp consumption by cod to a whole year could be problematic as annual cod biomass fluctuates strongly due to skrei migrations and population dynamics. Contrary to highly migratory Barents Sea cod, Norwegian coastal



**FIGURE 7** Consumption over a season (90 days) of shrimp by cod in biomass (tonnes) per fjord (in dark blue) in comparison to cod biomass (black) and shrimp biomass (turquoise) (left panel). Consumption ratio of shrimp biomass by cod shown per unit of cod biomass (orange) or per unit of shrimp biomass (blue) (right panel). Box plots are based on bootstrapped biomass and consumption estimates (500 repetitions), showing median (black lines), 25th and 75th percentiles (boxes), 1.5 interquartile range (whiskers) and outliers (dots). Excluding inner basin of Porsanger.

cod is more stationary (Pedersen et al., 2008), and based on otoliths, cod caught on the surveys in 2018–2019 were mainly coastal cod (Søvik et al., 2020). The study area constitutes a relevant part of the coastal cod distribution north of 67° N (ICES, 2023), although the estimated biomass here corresponds to only a few percent of the current spawning stock biomass. However, survey and assessment estimates are often difficult to compare. Because population and cod–shrimp dynamics likely differ substantially between fjords, biomass, consumption indices and mortality should ideally be estimated at fjord level in stock assessment to determine potential differences in dynamics. Additionally, prey switching linked to prey abundance and individual size has been observed in cod (Holt et al., 2019); thus, the role of other relevant prey species should be further explored. Here, however, we did not find a relevant effect of other prey such as capelin and gadids on shrimp consumption.

## 5 | CONCLUSIONS

We found clear intra- and inter-fjord differences in diet composition of demersal fish and predation on shrimp as a key prey species, with

implications for population dynamics of both prey and predators. In the two fjords closed to trawling, reopening for shrimp trawling after 50 years might therefore decrease foraging opportunities for cod in these fjords and undermine ongoing rebuilding efforts of local fjord subpopulations, particularly in Porsanger. Fjord-level stock structure of coastal cod is supported by genetic investigations that revealed genetic differentiation among coastal cod sampled from different fjords (Breistein et al., 2022).

Neglecting spatiotemporal patterns and differing predation pressures may lead to an inaccurate perception of stock productivity (Goethel et al., 2023; Trijoulet et al., 2019). Especially in highly structured or partially confined ecosystems, it could result in biased estimates of sustainable catch of cod and shrimp. Predation is rarely included in stock assessments and advice, with exceptions such as multiple stocks in the North Sea, Barents Sea capelin, cod, and haddock (ICES, 2022). Similarly, spatial structure is considered in stock assessments of few commercial fish stocks in the Northeast Atlantic Ocean (e.g. shrimp in the Norwegian Deep and Skagerrak, North Sea cod), and has typically no management implications (Cardinale et al., 2023). Spatially differing predation levels and stronger reliance of cod on shrimp indicate the need to either (a) consider spatial dynamics of predators when assessing

prey species to avoid unsustainable management of predators and prey or (b) implement spatial regulation of shrimp fishing in important feeding areas to support rebuilding of local cod stocks and avoid that combined mortality from fisheries and predation cause prey stock decline (Overholtz et al., 2000). Area-specific consumption ratios, as presented here, may serve as spatial indices to scale predation mortality in future assessments. Explicit analysis of spatiotemporal patterns in trophic interactions and their implications for predation mortality can add a multispecies aspect to single-species stock assessments as an important step toward an ecosystem-based approach.

## AUTHOR CONTRIBUTIONS

Guldborg Søvik, Ulf Lindstrøm, Torstein Pedersen, Hans Kristian Strand, Mette Strand and Fabian Zimmermann collected data. Mette Strand did the intensive stomach content analysis. Fabian Zimmermann, Katja Enberg and Jessica Tengvall conceived the ideas. Jessica Tengvall and Fabian Zimmermann performed formal analysis and led the writing. All authors contributed critically to the draft and gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

No authors have any conflict of interest.

## DATA AVAILABILITY STATEMENT

Data available via the Brage Institute of Marine Research (IMR), <https://hdl.handle.net/11250/3113938> (Tengvall et al., 2024). The data contain the input data for the statistical models as four files, consisting of: (1) shrimp density, (2) predator fish density, (3) Atlantic cod density and (4) shrimp consumed by predators. The cod density was separated as we also explored another time series for cod that was not available for the other predators.

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## REFERENCES

- Anderson, S. C. (2019). *A reproducible data synopsis for over 100 species of British Columbia groundfish*. Canadian Science Advisory Secretariat (CSAS).
- Anderson, S. C., Ward, E. J., English, P. A., & Barnett, L. A. K. (2022). sdmTMB: An R package for fast, flexible, and user-friendly generalized linear mixed effects models with spatial and spatiotemporal random fields. *BioRxiv*, 2022.03.24.485545. <https://doi.org/10.1101/2022.03.24.485545>
- Bakka, H., Rue, H., Fuglstad, G. A., Riebler, A., Bolin, D., Illian, J., Krainski, E., Simpson, D., & Lindgren, F. (2018). Spatial modeling with R-INLA: A review. *WIREs Computational Statistics*, 10, e1443. <https://doi.org/10.1002/wics.1443>
- Båtevik, T. (2020). *Estimating natural mortality rates for northern shrimp (Pandalus borealis) from a wide range of its latitudinal distribution in the Northeast Atlantic* [Master thesis, University of Bergen].
- Berg, P. R., Star, B., Pampoulie, C., Sodeland, M., Barth, J. M. I., Knutsen, H., Jakobsen, K. S., & Jentoft, S. (2016). Three chromosomal rearrangements promote genomic divergence between migratory and stationary ecotypes of Atlantic cod. *Scientific Reports*, 6, 1–12. <https://doi.org/10.1038/srep23246>
- Berryman, A. A. (1992). The origins and evolution of predator-prey theory. *Ecology*, 73(5), 1530–1535. <https://doi.org/10.2307/1940005>
- Bogstad, B., & Gjøsaeter, H. (1994). A method for estimating the consumption of capelin by cod in the barents sea. *ICES Journal of Marine Science*, 51(3), 273–280. <https://doi.org/10.1006/jmsc.1994.1028>
- Boyd, I. L. (1996). Temporal scales of foraging in a marine predator. *Ecology*, 77(2), 426–434. <https://www.jstor.org/stable/2265619>
- Breistein, B., Dahle, G., Johansen, T., Besnier, F., Quintela, M., Jorde, P. E., Knutsen, H., Westgaard, J.-I., Nedreaas, K., Farestveit, E., & Glover, K. A. (2022). Geographic variation in gene flow from a genetically distinct migratory ecotype drives population genetic structure of coastal Atlantic cod (*Gadus morhua* L.). *Evolutionary Applications*, 15(7), 1162–1176. <https://doi.org/10.1111/eva.13422>
- Cardinale, M., Zimmermann, F., Søvik, G., Griffiths, C., Nord, M., & Winker, H. (2023). Spatially explicit stock assessment uncovers sequential depletion of northern shrimp stock components in the North Sea. *ICES Journal of Marine Science*, 80, 1868–1880. <https://doi.org/10.1093/icesjms/fsad111>
- Creel, S., & Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends in Ecology & Evolution*, 23(4), 194–201. <https://doi.org/10.1016/j.tree.2007.12.004>
- DeMaster, D. P., Fowler, C. W., Perry, S. L., & Richlen, M. F. (2001). Predation and competition: The impact of fisheries on marine-mammal populations over the next one hundred years. *Journal of Mammalogy*, 82(3), 641–651. [https://doi.org/10.1644/1545-1542\(2001\)082<0641:PACTIO>2.0.CO;2](https://doi.org/10.1644/1545-1542(2001)082<0641:PACTIO>2.0.CO;2)
- dos Santos, J., & Jobling, M. (1992). A model to describe gastric evacuation in cod (*Gadus morhua* L.) fed natural prey. *ICES Journal of Marine Science*, 49(2), 145–154. <https://doi.org/10.1093/icesjms/49.2.145>
- Durante, L. M., Beentjes, M. P., & Wing, S. R. (2020). Shifting trophic architecture of marine fisheries in New Zealand: Implications for guiding effective ecosystem-based management. *Fish and Fisheries*, 21(4), 813–830. <https://doi.org/10.1111/faf.12463>
- Eide, N. E., Stien, A., Prestrud, P., Yoccoz, N. G., & Fuglei, E. (2012). Reproductive responses to spatial and temporal prey availability in a coastal Arctic fox population. *Journal of Animal Ecology*, 81(3), 640–648. <https://doi.org/10.1111/j.1365-2656.2011.01936.x>
- Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., & Mao, J. S. (2005). Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, 86(5), 1320–1330. <https://doi.org/10.1890/04-0953>
- Gaichas, S. K., Aydin, K. Y., & Francis, R. C. (2010). Using food web model results to inform stock assessment estimates of mortality and production for ecosystem-based fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences*, 67(9), 1490–1506. <https://doi.org/10.1139/F10-071>
- Goethel, D. R., Berger, A. M., & Cadrin, S. X. (2023). Spatial awareness: Good practices and pragmatic recommendations for developing spatially structured stock assessments. *Fisheries Research*, 264, 106703. <https://doi.org/10.1016/j.fishres.2023.106703>
- Grüss, A., Thorson, J. T., Carroll, G., Ng, E. L., Holsman, K. K., Aydin, K., Kotwicki, S., Morzaria-Luna, H. N., Ainsworth, C. H., & Thompson, K. A. (2020). Spatio-temporal analyses of marine predator diets

- from data-rich and data-limited systems. *Fish and Fisheries*, 21(4), 718–739. <https://doi.org/10.1111/faf.12457>
- Hansen, A., Westgaard, J. I., Søvik, G., Hanebrette, T., Nilssen, E. M., Jorde, P. E., Albreten, J., & Johansen, T. (2021). Genetic differentiation between inshore and offshore populations of northern shrimp (*Pandalus borealis*). *ICES Journal of Marine Science*, 78(9), 3135–3146. <https://doi.org/10.1093/icesjms/fsab181>
- Hartig, F. (2021). DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R package Version 0.4.1. R package. <https://cran.r-project.org/package=DHARMA>
- Hjort, J., & Ruud, J. T. (1938). *Rekefisker som naturhistorie og samfunns-sak*. Fiskeridirektoratets Skrifter, Serie Havundersøkelser, V(No. 4 Bergen), 158.
- Holt, R. E., Bogstad, B., Durant, J. M., Dolgov, A. V., & Ottersen, G. (2019). Barents Sea cod (*Gadus morhua*) diet composition: Long-term interannual, seasonal, and ontogenetic patterns. *ICES Journal of Marine Science*, 76(6), 1641–1652. <https://doi.org/10.1093/icesjms/fsz082>
- Howell, D., Bogstad, B., Chetyrkin, A., Fall, J., Filin, A., Hallfredsson, E. H., Höffle, H., Johannesen, E., Kovalev, Y., Mikhailov, A., Russkikh, A., Stesko, A., Vasilyev, A., Vihtakari, M., Windsland, K., & Yragina, N. (2023). *Report of the Joint Russian-Norwegian Working Group on Arctic Fisheries (JRN-AFWG) 2023*. IMR-PINRO joint report series 2023-7. <https://www.hi.no/hi/nettrapporter/imr-pinro-en-2023-7>
- ICES. (2022). *Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK)*. ICES scientific reports, 4(43), 1367. <https://doi.org/10.17895/ices.pub.19786285>
- ICES. (2023). *Cod (Gadus morhua) in Subareas 1 and 2, North of 67°N (Norwegian Sea and Barents Sea), Northern Norwegian Coastal Cod*. In report. <https://doi.org/10.17895/ices.advice.21828306>
- Johansen, T., Besnier, F., Quintela, M., Jorde, P. E., Glover, K. A., Westgaard, J. I., Dahle, G., Lien, S., & Kent, M. P. (2020). Genomic analysis reveals neutral and adaptive patterns that challenge the current management regime for East Atlantic cod *Gadus morhua* L. *Evolutionary Applications*, 13(10), 2673–2688. <https://doi.org/10.1111/eva.13070>
- Křivan, V., & Eisner, J. (2003). Optimal foraging and predator-prey dynamics III. *Theoretical Population Biology*, 63(4), 269–279. [https://doi.org/10.1016/S0040-5809\(03\)00012-1](https://doi.org/10.1016/S0040-5809(03)00012-1)
- Lindgren, F., Rue, H., & Lindström, J. (2011). An explicit link between gaussian fields and Gaussian Markov random fields: The stochastic partial differential equation approach. *Journal of the Royal Statistical Society, Series B: Statistical Methodology*, 73(4), 423–498. <https://doi.org/10.1111/j.1467-9868.2011.00777.x>
- Link, J. S., & Idoine, J. S. (2009). Estimates of predator consumption of the northern shrimp *Pandalus borealis* with implications for estimates of population biomass in the Gulf of Maine. *North American Journal of Fisheries Management*, 29(6), 1567–1583. <https://doi.org/10.1577/M08-233.1>
- Magnhagen, C. (1991). Predation risk as a cost of reproduction. *Trends in Ecology & Evolution*, 6(6), 183–186. [https://doi.org/10.1016/0169-5347\(91\)90210-O](https://doi.org/10.1016/0169-5347(91)90210-O)
- Ng, E. L., Deroba, J. J., Essington, T. E., Grüss, A., Smith, B. E., & Thorson, J. T. (2021). Predator stomach contents can provide accurate indices of prey biomass. *ICES Journal of Marine Science*, 78(3), 1146–1159. <https://doi.org/10.1093/icesjms/fsab026>
- Nielsen, J. M., Clare, E. L., Hayden, B., Brett, M. T., & Kratina, P. (2017). Diet tracing in ecology: Method comparison and selection. *Methods in Ecology and Evolution*, 9(2), 278–291. <https://doi.org/10.1111/2041-210X.12869>
- Overholtz, W. J., Link, J. S., & Suslowicz, L. E. (2000). Consumption of important pelagic fish and squid by predatory fish in the northeastern USA shelf ecosystem with some fishery comparisons. *ICES Journal of Marine Science*, 57(4), 1147–1159. <https://doi.org/10.1006/jmsc.2000.0802>
- Parsons, D. G. (2005a). Interactions between northern shrimp, *Pandalus borealis* (Pandalidae), and its key predators within the eastern Newfoundland and Labrador marine ecosystem. *Marine Biology Research*, 1(1), 59–67. <https://doi.org/10.1080/17451000510019060>
- Parsons, D. G. (2005b). Predators of northern shrimp, *Pandalus borealis* (Pandalidae), throughout the North Atlantic. *Marine Biology Research*, 1(1), 48–58. <https://doi.org/10.1080/17451000510018944>
- Pedersen, T., Fuhrmann, M. M., Lindstrøm, U., Nilssen, E. M., Ivarjord, T., Ramasco, V., Jørgensen, L. L., Sundet, J. H., Sivertsen, K., Källgren, E., Hjelset, A. M., Michaelsen, C., Systad, G., Norrbinn, F., Svenning, M.-A., Bjørge, A., Steen, H., & Nilssen, K. T. (2018). Effects of the invasive red king crab on food web structure and ecosystem properties in an Atlantic fjord. *Marine Ecology Progress Series*, 596, 13–31. <https://doi.org/10.3354/meps12548>
- Pedersen, T., Cuveliers, E. L., & Berg, E. (2008). Spatial scales of movement in Northeast Atlantic coastal cod. *Reviews in Fisheries Science*, 16(1–3), 348–356. <https://doi.org/10.1080/10641260701678462>
- Pikitch, E. K., Rountos, K. J., Essington, T. E., Santora, C., Pauly, D., Watson, R., Sumaila, U. R., Dee Boersma, P., Boyd, I. L., Conover, D. O., Cury, P., Heppell, S. S., Houde, E. D., Mangel, M., Plagányi, É., Sainsbury, K., Steneck, R. S., Geers, T. M., Gownaris, N., & Munch, S. B. (2014). The global contribution of forage fish to marine fisheries and ecosystems. *Fish and Fisheries*, 15(1), 43–64. <https://doi.org/10.1111/faf.12004>
- Plaganyi, E. E., Blamey, L. K., Rogers, J., & Tulloch, V. J. D. (2022). Playing the detective: Using multispecies approaches to estimate natural mortality rates. *Fisheries Research*, 249, 106229. <https://doi.org/10.1016/j.fishres.2022.106229>
- Pope, J. G., Gislason, H., Rice, J. C., & Daan, N. (2021). Scrabbling around for understanding of natural mortality. *Fisheries Research*, 240(April), 105952. <https://doi.org/10.1016/j.fishres.2021.105952>
- Preisser, E. L., Bolnick, D. I., & Benard, M. F. (2005). Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, 86(2), 501–509. <https://doi.org/10.1890/04-0719>
- R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.r-project.org/>
- Richards, R. A., & Jacobson, L. D. (2016). A simple predation pressure index for modeling changes in natural mortality: Application to gulf of Maine northern shrimp stock assessment. *Fisheries Research*, 179, 224–236. <https://doi.org/10.1016/j.fishres.2016.03.003>
- Rindorf, A., Andersen, N. G., & Vinther, M. (2010). Spatial differences in natural mortality of North Sea gadoids. *ICES CM*, 100, 18.
- Savino, J. F., & Stein, R. A. (1989). Behavioural interactions between fish predators and their prey: Effects of plant density. *Animal Behaviour*, 37, 311–321. [https://doi.org/10.1016/0003-3472\(89\)90120-6](https://doi.org/10.1016/0003-3472(89)90120-6)
- Siders, Z. A., Ahrens, R. N. M., Allen, M. S., & Walters, C. J. (2020). Density-dependent prey behaviours and mutable predator foraging modes induce Allee effects and over-predation of prey mortality rates. *Freshwater Biology*, 65(10), 1752–1764. <https://doi.org/10.1111/fwb.13577>
- Sinclair, A. R. E., Mduma, S., & Brashares, J. S. (2003). Patterns of predation in a diverse predator-prey system. *Nature*, 425(6955), 288–290. <https://doi.org/10.1038/nature01934>
- Siple, M. C., Koehn, L. E., Johnson, K. F., Punt, A. E., Canales, T. M., Carpi, P., de Moor, C. L., De Oliveira, J. A. A., Gao, J., Jacobsen, N. S., Lam, M. E., Licandeo, R., Lindegren, M., Ma, S., Óskarsson, G. J., Sanchez-Marroño, S., Smoliński, S., Surma, S., Tian, Y., ... Zimmermann, F. (2021). Considerations for management strategy evaluation for small pelagic fishes. *Fish and Fisheries*, 22(6), 1167–1186. <https://doi.org/10.1111/faf.12579>
- Skern-Mauritzen, M., Ottersen, G., Handegard, N. O., Huse, G., Dingsør, G. E., Stenseth, N. C., & Kjesbu, O. S. (2016). Ecosystem processes are

- rarely included in tactical fisheries management. *Metroeconomica*, 67(3), 165–175. <https://doi.org/10.1111/faf.12111>
- Søvik, G., Nedreaas, K., Zimmermann, F., Berengere, H., Strand, H. K., Jørgensen, L. L., Strand, M., Thangstad, T. H., Hansen, A., Båtevik, T., Albretsen, J., & Staby, A. (2020). *Mapping of the fjord ecosystems in the tana and Porsanger fjords*. Rapport Fra Havforskningen, 39, 1–140.
- Tarnecki, J. H., Wallace, A. A., Simons, J. D., & Ainsworth, C. H. (2016). Progression of a Gulf of Mexico food web supporting Atlantis ecosystem model development. *Fisheries Research*, 179, 237–250. <https://doi.org/10.1016/j.fishres.2016.02.023>
- Tengvall, J., Søvik, G., Enberg, K., Lindstrøm, U., Strand, M., Pedersen, T., Strand, H. K., & Zimmermann, F. (2024). *Data from: Fine-scale diet data reveals spatial variation in predator-prey interactions in Norwegian fjords*. Brage IMR. <https://hdl.handle.net/11250/3113938>
- Trijoulet, V., Fay, G., & Miller, T. J. (2019). Performance of a state-space multispecies model: What are the consequences of ignoring predation and process errors in stock assessments? *Journal of Applied Ecology*, 57(1), 121–135. <https://doi.org/10.1111/1365-2664.13515>
- Tromeur, E., & Loeuille, N. (2017). *Balancing yield with resilience and conservation objectives in harvested predator–Prey communities*. (May), 1780–1789. <https://doi.org/10.1111/oik.03985>
- Ware, D. M., & Thomson, R. E. (2005). Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. *Science*, 308(5726), 1280–1284. <https://doi.org/10.1126/science.1109049>
- Weitz, J. S., & Levin, S. A. (2006). Size and scaling of predator-prey dynamics. *Ecology Letters*, 9(5), 548–557. <https://doi.org/10.1111/j.1461-0248.2006.00900.x>
- Worm, B., & Myers, R. A. (2003). Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. *Ecology*, 84(1), 162–173. [https://doi.org/10.1890/0012-9658\(2003\)084\[0162:MAOCSI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0162:MAOCSI]2.0.CO;2)
- Yodzis, P. (1994). Predator-prey theory and Management of Multispecies Fisheries. *Ecological Applications*, 4, 51–58. <https://doi.org/10.2307/1942114>
- Zimmermann, F., Tengvall, J., Strand, H. K., Nedreaas, K., Thangstad, T. H., Husson, B., & Søvik, G. (2023). Fine-scale spatial variation of northern shrimp and Atlantic cod across three Norwegian fjord systems and implications for management. *Estuarine, Coastal and Shelf Science*, 292(July), 108435. <https://doi.org/10.1016/j.ecss.2023.108435>

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Fine-scale diet data reveals spatial variation in predator-prey interactions in Norwegian fjords.

**Appendix S2.** Model information.

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