Weak effects of local prey density and spatial overlap on predation intensity in a temperate marine ecosystem

Max Lindmark[1,*], Christopher A. Griffiths[1], Valerio Bartolino[1], Viktor Thunell[1], Federico Maioli[2], Sean C. Anderson[3], Andrea Belgrano[1], Michele Casini[1,4], Katarzyna Nadolna-Ałtyn[5], Joanna Pawlak[5], Marzenna Pachur[5], Marcin Rakowski[5], Karolina Wikström[1], Murray S. A. Thompson[6], Mayya Gogina[7], Didzis Ustups[8†], and Nis S. Jacobsen[2]

[1]Swedish University of Agricultural Sciences, Department of Aquatic Resources, Sweden
[2]Technical University of Denmark, National Institute of Aquatic Resources, Denmark
[3]Pacific Biological Station, Fisheries and Oceans Canada, Nanaimo, BC, Canada
[4]University of Bologna, Department of Biological, Geological and Environmental Sciences (BiGeA), Bologna, Italy
[5]National Marine Fisheries Research Institute, Gdynia, Poland
[6]Centre for Environment, Fisheries and Aquaculture Science (Cefas), Lowestoft, UK
[7]Leibniz Institute for Baltic Sea Research, Rostock, Germany
[8]Fish Resources Research Department, Institute of Food Safety, Animal Health and Environment BIOR, Riga, Latvia

Corresponding author: max.lindmark@slu.se

†Deceased author

Running head: Predator-prey overlap weakly linked to predation

Abstract

Quantifying the impact of lower trophic level species abundance on higher trophic level predators (and vice versa) is critical for understanding marine ecosystem dynamics and for implementing ecosystem-based management. Trophic ecosystem models generally predict a tight coupling between prey and fish predators, such that higher abundance of lower trophic species results in abundance of higher trophic level predators. This assumes that predator feeding rates to some degree are limited by prey availability. Despite being a key component of predator-prey interactions and multi-species fisheries management, relatively few studies have assessed the impacts of prey availability on predation patterns of mobile, generalist fish predators using spatiotemporal models and local-scale stomach content, predator, and prey data. In this study, we explore the association between local density of key prey and predator stomach contents, and predator-prey spatiotemporal overlap and predation indices, using the Baltic Sea as a case study. We use three decades of spatially resolved biomass and stomach content data on Atlantic cod (*Gadus morhua*), and biomass data on three of its key prey: herring (*Clupea harengus*), the isopod *Saduria entomon*, and sprat (*Sprattus sprattus*). Using geostatistical Generalized Linear Mixed Effects Models fitted to relative biomass density and prey-weight-per-predator-weight, we estimate spatiotemporal trends and annual indices of biomass weighted and area-expanded per-capita and population-level predation, predator-prey overlap, and the correlation between these indices. Range shifts have resulted in reduced predator-prey overlap over time, which is now the lowest in three decades. For *Saduria*, we find an association between prey availability and stomach contents, but not for herring or sprat. Similarly, only in *Saduria* do we find a positive correlation between population-level predation indices and the spatiotemporal overlap. Although behavioral interactions with pelagic prey are challenging to infer from stomach content and acoustic data due to high mobility, leading to fine-scale spatiotemporal mismatch, the weak connection between local-scale availability, and low correlation between population-level predation- and spatial overlap, could imply weaker coupling between pelagic prey and cod than previously thought. These findings provide key information on the strength of species interactions, which is crucial for the development of multi-species models and ecosystem-based fisheries management.

Keywords: predator-prey dynamics, diet, spatiotemporal mixed models, species distribution modelling, Atlantic cod, Baltic Sea, stomach data, ecosystem-based fisheries management

Introduction

Temperate marine ecosystems are shaped by complex combinations of bottom-up and top-down processes (Lynam *et al.* 2017). In coastal or upwelling systems, these two processes can be linked at intermediate trophic levels by small pelagic planktivorous fish, which can control lower trophic levels with top down effects and upper trophic levels via bottom up effects — also referred to as wasp-waist control (Cury *et al.* 2000, Bakun 2006). Ecological theory generally suggests a tight coupling between prey and predators (Poggiale 1998) such that higher prey densities benefit predator populations. This positive link between prey abundance and predator performance has been supported by a range of trophic ecosystem models (Smith *et al.* 2011, Pikitch *et al.* 2014, Chagaris *et al.* 2020), although this may vary depending on structural model assumptions (Walters *et al.* 2016). Such findings have led in some circumstances to management strategies that aim to reducing fishing pressure on lower trophic level fish to avoid negative impacts on higher trophic levels (Cury *et al.* 2011, Pikitch *et al.* 2012, Chagaris *et al.* 2020).

Empirical support for this form of bottom-up or "donor effect" (i.e., positive effects of prey on the predator but no clear negative effects of predators on prey, *sensu* Jennings and Kaiser 1998) from intermediate to upper trophic levels is, however, fairly limited (Jensen *et al.* 2012). This could be because marine predatory fish are typically mobile generalists, with diets changing through their ontogeny, which implies many but weak trophic links (Jennings and Kaiser 1998, Strong 1992). Not surprisingly, one of the clearer examples of a donor effect is the decline in productivity of Atlantic cod (*Gadus morhua*) in the Barents Sea. This decline occurred because cod had limited ability to switch prey due to low diversity in the intermediate trophic levels, leading to reduced productivity after the main prey species, capelin and herring, collapsed (Mehl and Sunnanå 1991, Hamre 1994, Jensen *et al.* 2012).

Another reason why these effects are difficult to detect relates to spatial dynamics and the scale at which trophic interactions occur (Hunsicker *et al.* 2011). Often trophic interactions are assessed by relating time series of population abundance of predators and prey (Jennings and Kaiser 1998, Overholtz and Link 2007, Hilborn *et al.* 2017), which neglects the important spatial dimension. While there are several examples of the importance of local scale prey availability and donor effects on upper trophic levels, most are for central place foragers (e.g., for seabirds, Crawford 2007, Cury *et al.* 2011, Robinson *et al.* 2015, Hentati-Sundberg *et al.* 2021), and few involve commercially

exploited mobile fish predators (Hilborn *et al.* 2017, Pikitch *et al.* 2018) (but see Fall *et al.* 2021). Recent studies have illustrated the potential of spatiotemporal modelling of predator and prey density and stomach content data to quantify fine-scale spatial and temporal variability in diet, and to derive model-based indices of consumption (Grüss *et al.* 2020, Goodman *et al.* 2022, Gartland and Latour 2024). For example, Gartland and Latour (2024) related model-based consumption-indices derived from spatiotemporal models to stock-level biomass of prey and found positive associations. In a similar study, Goodman *et al.* (2022) correlated annual spatial overlap and predation indices, and found that the support for such correlations varied across species. These studies did not, however, include spatially explicit prey covariates, which may be important, because local prey densities can be high and sufficient for predators even though total prey population abundance is low (Hilborn *et al.* 2017), and because the spatial overlap between predators and their prey can vary in the studied time period.

In this study, we investigated the relationship between local prey availability and the relative weight of prey in predator stomachs, as well as the relationship between spatial overlap and predation at a population level, using the Baltic Sea as a case study. We used three decades of biomass and stomach content data from surveys for the predator Atlantic cod (*Gadus morhua*), and biomass data for some of its main prey, sprat (*Sprattus sprattus*), herring (*Clupea harengus*), and the benthic isopod *Saduria entomon* (henceforth only *Saduria*). The central Baltic Sea ecosystem is an interesting case study for several reasons. It is a species-poor ecosystem where sprat and herring make up more than 75% of the diet by weight in cod around than 35 cm, and there is no alternative pelagic prey for cod present in the system (Kulatska *et al.* 2019, Lindmark *et al.* 2025). Moreover, within this time period, the feeding rates on sprat and *Saduria*, as well as the growth, condition and size-at-maturity of cod have declined substantially (Neuenfeldt *et al.* 2020, Mion *et al.* 2021, Lindmark *et al.* 2023, Svedäng *et al.* 2024). Together with an increased natural mortality (ICES 2022a, Eero *et al.* 2023), this has severely impacted the conservation status of cod, to the degree that even in the absence of a commercial targeted fishery (by EU countries), the stock is expected to remain below its biological limit reference point in the near future (ICES 2021). Hence, it is critically important to understand the drivers behind these changes in the physiological performance of cod in the Baltic Sea. Reduced feeding opportunities on benthic and pelagic prey have been proposed as two of the possible underlying causes (Casini *et al.* 2016, Neuenfeldt *et al.* 2020). Reduced feeding on benthic

prey is thought to be due to increased competition for dwindling benthic prey resources mainly linked to the deterioration of the benthic habitats (Neuenfeldt *et al.* 2020), while reduced feeding on pelagic prey has been hypothesized to be due to a reduction of the prey in the main areas of cod occurrence (Casini *et al.* 2016, ICES 2023). This has led to suggestions that pelagic fisheries should be limited in the current main distribution area of cod to improve growth (Eero *et al.* 2012, ICES 2015, Casini *et al.* 2016). However, it is largely unknown how the overall local-scale overlap and encounter rates have changed over time, and how the local prey availability affects feeding opportunities for cod.

Here we aim to answer the following research questions: 1) Is the relative weight of sprat, herring, and *Saduria* in cod stomachs related to the local availability of these prey? 2) Have the relative weights of, and predation on, these prey in the diet changed over space and time? 3) Has the spatial overlap between cod and its prey changed over time? and 4) Do spatial overlap indices correlate with population-level predation indices over time?

Methods

Data

Stomach data

Stomach content data for Baltic cod have been collected by national institutes (opportunistically or within designated programs) over the past decades. In this study, we use mainly data collated in EU funded projects (Huwer *et al.* 2014, Jacobsen *et al.* 2023) that are available at the newly updated International Council for the Exploration of the Sea (ICES) stomach content database (`https://www.ices.dk/data/data-portals/Pages/Stomach-content.aspx`). We complement these data with data collated in Lindmark *et al.* (2025), and historical data (Huwer *et al.* 2014). We used 31 years (1993–2023) of data, mainly collected on the bi-annual Baltic International Trawl Survey (BITS) conducted in the first and fourth quarter of the year, but also from other cruises conducted in other times of the year (see Huwer *et al.* (2014) and Jacobsen *et al.* (2023) for a detailed description of the data sources). Therefore, the spatial coverage of stomach sampling has varied over time (see Fig. 1 for the spatiotemporal distribution of data).

We removed regurgitated and empty stomachs since they have not been treated in the same way over time, which can affect the proportion of empty stomachs (Neuenfeldt *et al.* 2020). For each cod predator, we calculated the total weight of sprat, herring and *Saduria* in the stomachs. In cases where individual prey length but not prey weight was available, we estimated weight using species specific condition factors and weight-length exponents. The condition factor and exponent for *Saduria* are means for isopods in Robinson *et al.* (2010), and for fish prey (herring and sprat) they were retrieved from FishBase (Froese *et al.* 2010). These individual-level prey weights were used to calculate prey-weight-per-predator-weight — hereafter referred to as "relative prey weight". The size distribution of cod, and the distribution of relative prey weights can be seen in Figs. S1, S2. Similarly, cod weight was estimated from cod length if missing in the data. Because the length-weight relationship in Baltic cod has varied substantially over the time period, affecting the relative prey weight, we estimated annual values of the condition factor from the trawl survey BITS (see section *Biomass density models*). After data processing, 33,243 cod stomachs were available for analysis.

Prey data

ICES rectangle-level (Fig. 1) biomass estimates for sprat and herring were acquired from the ICES Baltic International Fish Survey Working Group (WGBIFS) database for the Baltic International Acoustic Survey (BIAS) (`https://www.ices.dk/community/groups/pages/WGBIFS.aspx`). As in Lindmark *et al.* (2023), biomass density of *Saduria* was extracted from a habitat distribution model coupled with modelled hydrographical data from the regional coupled ocean biogeochemical model ERGOM (Gogina *et al.* 2020, Neumann *et al.* 2021). The model was trained to the time period 1981–2019 and predicted for the time period 1993–2019 (but note that this prediction is constant over time and therefore represents the core *Saduria* habitat).

Predator biomass density

To calculate spatially explicit, weighted predation metrics and predator-prey overlap metrics (Fig. 2), we modelled the spatiotemporal distribution of cod using catch per unit effort data (CPUE, numbers/hour) by length class from the fishery-independent Baltic International Trawl Survey (BITS) conducted in the first and fourth quarter between 1993–2023 in the ICES subdivisions 24–28. We

used data from the ICES trawl survey database DATRAS (https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx). CPUE data were standardized based on gear dimensions and towing speed (TVL trawl with 75 m sweeps at 3 knots) to units of kg/km², following Orio *et al.* (2017) and Lindmark *et al.* (2023), using length-weight relationships fitted by year to convert from numbers-at-length to weight.

Environmental data

We included dissolved sea bottom oxygen concentration (ml/l), sea bottom temperature (°C), and sea bottom salinity (‰) from the Copernicus Marine Service Baltic Monitoring and Forecasting Centre (BAL MFC) as covariates in our biomass density models. Dissolved oxygen values at the sea floor stem from the Baltic Sea biogeochemical model (https://doi.org/10.48670/moi-00009), which is based on ERGOM (Ecological Regional Ocean Model, https://ergom.net/) (Neumann *et al.* 2021), coupled with the NEMO ocean model (Madec *et al.* 2023). Sea floor temperature and salinity stem from the Baltic Sea Physical Reanalysis (https://doi.org/10.48670/moi-00013), based on simulations from the NEMO 3D ocean-ice model version 4.0 (Gurvan *et al.* 2019). These variables were matched to the survey catch data on a monthly resolution. We also included depth (m) in the model, which was was extracted from the EMODnet Bathymetry project (https://emodnet.ec.europa.eu/en/bathymetry) (EMODnet Bathymetry Consortium 2022).

Spatiotemporal modelling framework

Model description

We used spatiotemporal GLMMs (Generalized Linear Mixed Effects Models) to model stomach contents and biomass density of cod. Per-capita and population-level predation, and predator-prey overlap, were calculated from predictions onto a 3×3 km spatiotemporal grid. Fig. 2 illustrates the workflow and how the models and data come together. The full model can be written as follows,

but note that the biomass density and diet models do not contain all these terms:

$$\mathbb{E}[y_{\boldsymbol{s},t}] = \mu_{\boldsymbol{s},t}, \tag{1}$$

$$\mu_{\boldsymbol{s},t} = f^{-1}\left(\boldsymbol{X}^{\text{main}}_{\boldsymbol{s},t}\boldsymbol{\beta} + \alpha_g + \boldsymbol{X}^{\text{tvc}}_{\boldsymbol{s},t}\boldsymbol{\gamma}_t + \boldsymbol{X}^{\text{svc}}_{\boldsymbol{s},t}\boldsymbol{\zeta}_{\boldsymbol{s}} + \omega_{\boldsymbol{s}} + \epsilon_{\boldsymbol{s},t}\right), \tag{2}$$

$$\zeta_{\boldsymbol{s}} \sim \text{MVN}(\boldsymbol{0}, \Sigma_\zeta), \tag{3}$$

$$\omega_{\boldsymbol{s}} \sim \text{MVN}(\boldsymbol{0}, \Sigma_\omega), \tag{4}$$

$$\epsilon_{\boldsymbol{s},t} \sim \text{MVN}(\boldsymbol{0}, \Sigma_\epsilon), \tag{5}$$

where $y_{\boldsymbol{s},t}$ is the response variable (relative prey weight or cod biomass density) in location $\boldsymbol{s}$ at time t, μ is the mean, f^{-1} is the inverse link function, $\boldsymbol{X}^{\text{main}}$, $\boldsymbol{X}^{\text{tvc}}$, and $\boldsymbol{X}^{\text{svc}}$ are design matrices for fixed effects, time-varying coefficients, and spatially varying coefficients, respectively. Their corresponding coefficient vectors are $\boldsymbol{\beta}$, $\boldsymbol{\gamma}_t$, and $\boldsymbol{\zeta}_{\boldsymbol{s}}$. All fixed effect covariates were standardized by subtracting their mean and dividing by their standard deviation. The parameter α_g represents a random intercept for month. The spatially-varying coefficients ($\zeta_{\boldsymbol{s}}$), spatial ($\omega_{\boldsymbol{s}}$), and spatiotemporal random effects ($\epsilon_{\boldsymbol{s},t}$), are assumed drawn from Gaussian Markov random fields (GMRFs) with covariance matrices (i.e., inverse precision matrices) Σ_ζ, Σ_ω, and Σ_ϵ constrained by Matérn covariance functions (Rue *et al.* 2009, Lindgren *et al.* 2011). The spatially varying coefficients $\zeta_{\boldsymbol{s}}$ are included in the biomass density model to allow the distribution of cod to vary between quarters in addition to the variation given by changes in dynamic covariates, while $\omega_{\boldsymbol{s}}$ and $\epsilon_{\boldsymbol{s},t}$ reflect spatially correlated latent effects that are constant through time and that vary through time, respectively. The Stochastic Partial Differential Equation (SPDE) approach (Lindgren *et al.* 2011), which links continuous Gaussian random fields with discretely indexed GMRFs, requires piece-wise linear basis functions defined by a triangulated mesh. We defined this mesh using triangles with a cutoff distance (minimum distance between vertices) of 8 km and 10 km for diet and biomass models, respectively, and kept all other arguments in `fm_rcdt_2d_inla()` (`fmesher` R package; Lindgren 2023) at their defaults (Figs. S3–S4). Across all models, the cutoff distance was between 2.5–10 times smaller than the estimated Matérn range, which is defined as the distance where spatial correlation effectively disappears (≈ 0.13, Lindgren *et al.* 2011).

To propagate uncertainty in both stomach content predictions and cod density predictions when calculating predation and overlap indices (see sections *Predation indices* and *Spatiotemporal*

overlap indices), we simulated 500 draws from the joint parameter precision matrix to make model predictions on the grid. For each draw, we calculated overlap or predation metrics and we present the median, mean, or coefficient of variation of these draws. We predict from the model for a cod length of 33 cm, which is the mean in the diet data.

Diet models

The relative prey weight models were fit to each prey species separately. Since these response variables are positive continuous and contain zeroes, we modelled them with either a Tweedie distribution (herring and sprat) or as a "Poisson-link" delta model (Thorson 2018) (*Saduria*), which has the flexibility of a classic delta or hurdle model (Aitchison 1955), but enables a simpler interpretation of covariates due to log links on both linear predictors (Thorson 2018, Anderson *et al.* 2024). The model family (delta or Tweedie) was chosen based on convergence diagnostics. We included a linear depth effect on all prey, as it has been shown previously to affect cod diets (Pachur and Horbowy 2013). Month was included as a random effect in the *Saduria* model, but not the herring and sprat models because the standard deviation of the month random effect was estimated near zero. We included a linear effect of predator length, reflecting the underlying ontogenetic diet shift cod undergo. To be able to interpolate across a missing year (2011), we modelled the intercept as a time-varying coefficient following an AR(1) process:

$$\gamma_{t=1} \sim \mathrm{N}(0, \sigma_\gamma^2), \tag{6}$$

$$\gamma_{t>1} \sim \mathrm{N}(\rho_\gamma \gamma_{t-1}, \sqrt{1-\rho_\gamma^2}\sigma_\gamma^2), \tag{7}$$

where ρ is the correlation between subsequent years and σ^2 is the variance. We included spatially correlated latent effects ($\omega_{\boldsymbol{s}}$) that are constant over time and that vary independently each year ($\epsilon_{\boldsymbol{s}}$). Lastly, we included prey biomass or biomass densities as covariates. For the sprat and herring models, this was the estimated biomass per ICES rectangle for ages 1–8+, while for *Saduria*, we extracted rasterized local biomass densities. For each prey, we explored three models: a breakpoint (hockey-stick) function (corresponding to a type I functional response with saturation or a type II functional response), a linear effect, and one without prey availability as covariate. In the break-

point term, prey $\times$ b_0 is the effect below the threshold, and $b_0 \times b_1$ is the value at the asymptote. We compared the models using the (marginal) Akaike information criterion (AIC; Akaike 1973).

Biomass density models

We modelled cod biomass density as a Poisson-link delta model (Thorson 2018) and included year and quarter as factors, where the latter was in addition modelled as a spatially varying effect, linear effects of salinity, temperature and temperature squared, as well as a breakpoint effect of oxygen, to reflect that dissolved oxygen tends to correlate with biomass density up to a certain point (Essington *et al.* 2022). We also included a time-varying effect of depth and depth squared following a random walk. This to allow the unimodal depth-preferences to change over time (English *et al.* 2022), in line with the shallowing that has been observed for eastern Baltic cod (Orio *et al.* 2019, Lindmark *et al.* 2023).

$$\gamma_{t=1} \sim \mathrm{N}(0, \sigma_\gamma^2), \tag{8}$$

$$\gamma_{t>1} \sim \mathrm{N}(\gamma_{t-1}, \sigma_\gamma^2), \tag{9}$$

Lastly we included both spatial random effects that are constant in time (ω_s) and spatial random effects that are independent each year ($\epsilon_{s,t}$).

Model fitting

We fit the spatiotemporal models with the R version 4.3.2 (R Core Team 2024) package `sdmTMB` (Anderson *et al.* 2024), version 0.6.0.9023. `sdmTMB` uses automatic differentiation and the Laplace approximation from the R package `TMB` (Kristensen *et al.* 2016) and sparse matrix structures to set up the SPDE-based Gaussian Markov random fields from the R package `fmesher` (Lindgren 2023). We estimated parameters via maximum marginal likelihood using the non-linear minimizer `nlminb` (R Core Team 2024). We confirmed that the optimization was consistent with convergence by checking that the Hessian matrix was positive definite and the maximum absolute log-likelihood gradient with respect to fixed effects was <0.001. We evaluated consistency of the models with the data by calculating simulation-based randomized quantile residuals (Dunn and Smyth 1996, Hartig 2022) (Figs. S5–S6). When calculating expected values for the purposes of

residual calculation, we took a single draw of the random effects from their multivariate normal distribution (Waagepetersen 2006) rather than using the empirical Bayes random effects estimates. This acknowledges that the random effects are estimated from a distribution (Waagepetersen 2006, Thorson and Kristensen 2024, p. 41).

Predation indices

We followed the approach presented in Goodman *et al.* (2022) to calculate density-weighted per-capita and population-level predation intensity based on model-predicted relative prey weights and predator densities across the spatiotemporal grid. Population-level predation intensity, $P_{p,i}$, for year i was calculated as:

$$P_{p,i} = \sum_{j=1}^{n} R_{i,j} \times D_{i,j} \times A_j, \tag{10}$$

where $R_{i,j}$ is the prey-specific relative prey weights (kg/kg) in grid cell j, $D_{i,j}$ is the predicted cod density (kg/km²), and A_j is the area of the grid cell (km²). This represents a spatially explicit, density-weighted measure of predation intensity (an instantaneous "snapshot" of total weight of a prey species in cod stomachs in units of kg) (Goodman *et al.* 2022). Temporal trends in predation intensity in the domain were acquired by summing grid-level predictions by year. Prior to calculating grid-cell level predation, we omitted grid cells with cod biomass density predictions greater than the 99.99th percentile across all simulations, and relative prey weight predictions >1 (less than 0.001% of rows in simulated values of relative sprat weight). We also omitted areas deeper than 130 m in the prediction grid, since trawl surveys are not conducted at those depths.

Since both cod and pelagic species have undergone shifts in their spatial distribution in this time window (Bartolino *et al.* 2017, Orio *et al.* 2019, Lindmark *et al.* 2023, ICES 2023), and the average feeding rate of cod has declined over time (Neuenfeldt *et al.* 2020), we also wanted to disentangle the effect of distribution shifts from changes in mean feeding rates. This was done by dividing the population-level predation ($P_{p,i}$) by the population-level cod biomass in year i (Goodman *et al.* 2022), which yields a weighted average prey biomass per unit predator biomass

(per-capita predation), $P_{c,i}$:

$$P_{c,i} = \frac{\sum_{j=1}^{n} R_{i,j} \times D_{i,j} \times A_j}{\sum_{j=1}^{n} D_{i,j} \times A_j}. \tag{11}$$

Spatiotemporal overlap indices

Predator-prey overlap metrics were calculated from grid-level predictions of cod biomass density, biomass density of *Saduria* and biomass of sprat and herring at the ICES-rectangle level. There are numerous ways to calculate overlap metrics with slightly different interpretations (for a review, see Carroll *et al.* 2019). In this study, we use the "local index of collocation" overlap metric (Pianka 1973), as in Goodman *et al.* (2022):

$$\text{Overlap}_i = \frac{\sum_j^n (\text{pred}_{i,j} \times \text{prey}_{i,j})}{\sqrt{\sum_j^n \text{pred}_{i,j}^2 \times \sum_j^n \text{prey}_{i,j}^2)}}, \tag{12}$$

where overlap in year i is calculated from the proportions of total biomass of cod ($\text{pred}_{i,j}$) and its prey ($\text{prey}_{i,j}$) in grid cell j. We use the same grid as for the stomach content predictions. This metric ranges between 0 and 1 and estimates co-occurrence using correlations between predator and prey densities at the grid-scale, and is suitable for estimating encounter rates (Carroll *et al.* 2019, Goodman *et al.* 2022). When visualizing the overlap in space, we omit the summation across grid cells.

For pelagic prey (sprat and herring), we used only cod predictions in the fourth quarter, since that is when the hydro-acoustic survey (BIAS) takes place. After confirming that the difference between quarters was minimal for overlap with *Saduria* with respect to trends, we presented only results for quarter 4 also for *Saduria*. Given that the spatial predictions of *Saduria* densities are constant over time, changes in overlap with *Saduria* are only driven by changes in the distribution of cod, while in reality, *Saduria* also likely have changed their spatial distribution (Gogina *et al.* 2020).

To quantify how overlap between cod and its prey was related to the predation intensity, we tested the correlation between annual predation intensity (per-capita and population-level) and the annual spatial overlap.

Lastly, to highlight trends over time in per capita and population-level predation, and spatial overlap, we fit Generalized additive models (GAMs) to the annual indices, with prey-specific smooth effects of year. We assumed Gamma-distributed errors and a log link for the predation indices, and Beta-distributed errors and a logit link for the overlap indices. The models were fitted with the R package `brms` (Bürkner 2017). We used default priors, i.e, Student-t$(3, 0, 2.5)$ for the intercept and the standard deviations of spline coefficients, and flat priors for the prey-coefficients. The shape parameter in the Gamma model, and the precision parameter in the Beta model, were given a Gamma(0.01, 0.01) prior. We visualized predictions by summarizing draws from the expectation of the posterior predictive distribution, using the R package `tidybayes` (Kay 2019).

Results

The relative weight of a prey species in cod stomachs was positively related to the local density of that prey for *Saduria*, but not for sprat or herring. For sprat, the model without prey biomass was favored by AIC (Table 1). For herring, the breakpoint model and the model without herring were indistinguishable in terms of AIC (Table 1), and the herring covariate was negatively related to herring in the stomachs of cod. Therefore, further analysis were based on the simpler model without the breakpoint herring covariate. The breakpoint model had the lowest AIC among the *Saduria* models, however, the conditional predictions showed high uncertainty on the total prediction (both model components combined) (Fig. S7; Table. S1).

We found clear spatial patterns in both stomach contents and predation indices (Figs. 3, 4). The relative prey weight of herring in the cod stomachs showed low spatiotemporal variation compared to the other prey apart from very local hotspots from year to year (Fig. 3a, d). Both relative prey weight of, and predation on, *Saduria* were highest in the central parts of the southern Baltic Sea (Figs. 3b, e, 4b, e), which corresponds to the core area of the *Saduria* distribution in this region (Fig. S8b). Both the relative prey weight of sprat (Fig. 3c, f) and the predation on sprat (Fig. 4c, f) occurred throughout the Baltic Sea, although the predation was more limited to the southwestern part in recent years due to the shift in distribution of cod (Fig. 5).

Over time, the area-expanded per-capita predation on herring increased steadily (with a small decline around the mid 2000s), while the population-level predation reached a peak around 2010

after which it declined to levels similar to the early 2000s (Fig. 6a, d). Both per-capita and population-level predation on *Saduria* showed a peak at around 2007, after which it declined steadily to very low levels (Fig. 6b, e). Both per-capita and population-level predation on sprat declined in the early 1990s (Fig. 6c, f). From then, the per-capita predation on sprat varied somewhat cyclically, and showed a weak tendency for an overall increase throughout the time period (Fig. 6c). The population-level predation on sprat instead peaked around 2010, and has declined since (Fig. 6f). The uncertainty around the per-capita and total predation estimates are substantial when accounting for uncertainty in both cod biomass density and relative prey weights, especially for *Saduria* early in the time series and sprat (Fig. 6b, c), and this is largely due to higher uncertainty in the stomach content predictions (Fig. S9).

The overlap between cod and its prey was highest in the central parts of the southern Baltic Sea, and along the southeast coast of Sweden (Fig. 7). Over time, the overlap with herring started to decline around 2005 (Fig. 8a). The spatial overlap with *Saduria* increased slightly between 1993–2009, but since 2010 it has been lower then average, resulting in a weakly negative trend over time (Fig. 8b). The spatial overlap with sprat also declined over time, but in a more cyclic fashion. The current spatial overlap with sprat is the lowest since 2007 (Fig. 8c).

The correlation between annual estimates of per-capita- and population-level predation with spatial overlap was only clearly positive for *Saduria* (Fig. 9b, e). For herring and sprat, the correlation coefficients ranged between −0.39 and −0.12, but the confidence intervals overlapped zero (Fig. 9a,c,d,f).

Discussion

In this study, we quantified the effects of local prey availability on the stomach contents of predators and the relationship between predation and spatial overlap of predator and prey. Our analysis used the Baltic Sea as a case study. However, the spatiotemporal modelling approach used, which scales up local-scale diet data to population-level predation metrics while accounting for range shifts, can be applied generally, and is well suited to improve our understanding of predator-prey interactions in other systems. Our results suggest that the effects of local prey availability are modest and uncertain, and that only in the case of the benthic isopod *Saduria* availability is related to

what is found in the stomachs of cod. Furthermore, only for *Saduria* do we find a correlation between predator-prey spatial overlap and per-capita and population-level predation. Our analysis therefore echoes previous studies on the challenges of linking prey dynamics to predator performance in marine generalist predators (Hilborn *et al.* 2017, Fall *et al.* 2021, Goodman *et al.* 2022), and is at contrast with the strong bottom-up effects present in trophic ecosystem models (Smith *et al.* 2011, Chagaris *et al.* 2020). Our analyses constitute important steps towards understanding the spatial scale of trophic interactions (Amarasekare 2008, Carroll *et al.* 2024), which are needed to support the implementation of ecosystem-based fisheries management.

Effects of prey availability on feeding of generalist predators

It has been suggested that the large abundance fluctuations of many small pelagic fish species would help identifying relationships between forage fish and predators (Hilborn *et al.* 2017) because it results in large contrasts for analysis. This is also the case in our system. The Baltic Sea sprat stock increased 5-fold between 1991–1997 (ICES 2022b), albeit in the entire Baltic Sea, and not necessarily in the entire distributional range of cod. However, we did not detect an effect of sprat availability on the relative weight of sprat in cod stomachs, and the per-capita and population-level predation on sprat by cod correlated negatively (but not significantly) with cod-sprat spatial overlap. One potential reason for this could be that cod are not limited by sprat biomass but by their digestive capacity. This could limit predation even if the population-level prey biomass is low, as long as there is relatively high prey density locally (Hilborn *et al.* 2017, Fall and Fiksen 2020). Alternatively, it may be that the prey availability is not modelled at the appropriate spatial or temporal scale. Prey biomass is aggregated over ICES rectangles and is derived from a hydroacoustic survey conducted in the fourth quarter (while approximately 60% of stomach data are sampled in the fourth quarter). Hence, the spatiotemporal mismatch between data might be too large to accurately reflect predator-prey interactions, given the patchy distribution of schooling prey and the fact that stomach content data reflect consumption over a relatively short time period. Moreover, we measure overlap and pelagic prey availability in two dimensions, which may not accurately reflect encounter rates in a three dimensional environment. In line with this, Fall *et al.* (2021), also found weak effects of prey (capelin, *Mallotus villosus*) abundance on the consumption of capelin by cod. Instead they found that proximity of capelin to the seafloor was a better pre-

dictor of capelin in the cod diet, which illustrates the potential importance of the third dimension (i.e., depth). Future studies could explore whether this is also the case in the Baltic Sea, potentially using high-resolution data on schooling fish in combination with stomach content data to try and determine appropriate scales for analysis.

The spatial and temporal scale is not only relevant for the actual interaction (encounter and predation), but also when it comes to "scaling-up" functional responses or predation metrics from experimental or local scales to scales more relevant for management, e.g., to the stock- or population-level (Hunsicker *et al.* 2011). This is inherently difficult, as the relationship between consumption and prey density can change over spatial scales (Bergström and Englund 2004). Another approach, which overcomes this issue, is to use stock-level estimates when estimating functional responses (Essington and Hansson 2004). However, a limitation is that spatial heterogeneity in feeding dynamics or predator distribution and range shifts would not be accounted for. In the alternative model-based approach used here, we arrive at population-level predation metrics by summing spatially explicit predictions over the heterogeneous domain. This has the benefit that local scale heterogeneity in prey availability and stomach contents are explicitly considered, providing more accurate estimates.

Implications for Baltic Sea cod

Our results on the spatiotemporal dynamics of predation and overlap provide novel insights that both corroborate and contrast previous hypotheses on Baltic cod. Neuenfeldt *et al.* (2020) identified that cod feeding rates on *Saduria* and sprat were substantially higher in the period 1963–1989 than in 1994–2014. Within the second time period, the physiological condition of cod declined rapidly (Mion *et al.* 2021, Eero *et al.* 2023, Lindmark *et al.* 2023). This makes it an important time period to analyze for understanding the relationship between feeding dynamics and predator-prey overlap. We observe that feeding on *Saduria* continued to decline after 2014 to near zero in the most recent years. Although the spatial overlap with *Saduria* also declined slightly, it seems that the loss of predation on *Saduria* is mainly driven by changes in per-capita predation, because trends are similar for per-capita (where the total cod biomass is factored out) and population-level predation rates. This could in turn be due to declining local abundances of *Saduria*, because even though *Saduria* does not seem to have declined substantially over the last 30 years in shallow areas

(Svedäng *et al.* 2022), its area occupied may have declined, since its depth distribution is linked to oxygen dynamics on the sea floor (Karlson *et al.* 2002). This, however, is not currently possible to investigate further due to the low spatiotemporal resolution of *Saduria* biomass data. Increased competition for *Saduria* with flounder (*Platichthys* spp.) could also potentially explain the declines in availability of *Saduria* to cod, as was found in a recent study on a smaller spatial and temporal scale (Lindmark *et al.* 2023).

Previous studies have hypothesized that the decline in feeding rates on sprat is linked to availability and spatial overlap (Eero *et al.* 2012, Casini *et al.* 2016, Neuenfeldt *et al.* 2020), although this has never been tested explicitly. While there is a spatial mismatch in the sense that sprat biomass is highest in the northeast (Fig. S8c) and cod is mainly found in the southern parts, that does not necessarily mean cod are limited by low sprat abundances in the south. In line with Eero *et al.* (2012), our results suggest that predation pressure on sprat is highest in the south. We find fluctuations in the spatial overlap with sprat, with a positive trend for the per-capita predation. Also considering the lack of effect of sprat biomass on the relative weight of sprat in cod stomachs (Table 1), our study does not support the hypothesis that spatial dynamics and spatiotemporal mismatch in overlap explains trends in cod feeding on sprat. The lack of correlation between overlap and predation is also found in herring, and per-capita predation on herring by cod even increased since 2010 when the spatial overlap started to decline.

Limitations and areas of future research

We made several simplifying assumptions that warrant future research. When calculating the predation indices, we used the total cod density in the survey catches, i.e. not resolved by length class. Since cod undergo strong ontogenetic diet shifts (Kulatska *et al.* 2019, Lindmark *et al.* 2025), it may be more appropriate to use the biomass density of cod within specific size groups that mainly feed on a specific prey. However, that may also not have a strong impact, since the correlation between local cod densities of different size groups is quite high (Jacobsen *et al.* 2023), the population size structure is highly truncated, and the main sizes currently in the population feed on a mix of pelagic and benthic prey (Lindmark *et al.* 2025). Moreover, the predation indices calculated here are only for cod of 33 cm (for simplicity, the mean size in the diet data), although they could be predicted for any size since length is a covariate in the models. This simplifying

assumption effectively assumes the entire cod stock is of a specific size, which can be misleading for population-level predation metrics since the size-distribution of the cod population has been truncated over time (Eero *et al.* 2023). However, it does facilitate comparison over time for the per-capita predation metrics. Moreover, the indices are relative since the biomass density of cod is relative (due to unknown survey catchability), and since length is only a fixed effect in the model, predicting for different lengths would just change the relative value of the index identically over time.

The exact values of the predation indices are not directly comparable to mortality rates because the units are different. However, it would be straightforward to expand our work by converting our predation metrics to predation rates using gastric evacuation models (as in e.g., Gartland and Latour 2024). A qualitative comparison between our predation estimates and natural mortality estimates from the Baltic Stochastic Multispecies Model (SMS) model (Lewy and Vinther 2004) suggests that population-level predation intensity and natural mortality both increased from 1993 to until around 2010, after which it declined to levels comparable to around year 2000 (ICES 2019). This implies that the stomach content data, more than model type (spatiotemporal index or multispecies assessment model) drives the result, although more work is needed to identify which processes cause discrepancies between the time series of predation and mortality.

Stomach content sampling is often affected by gaps and inconsistencies in space and time (Fig. 1). This represents a challenge for using stomach data in population dynamic models without some form of standardization, since there are clear spatiotemporal patterns in stomach content data. This is, however, not routinely done (ICES 2019, Neuenfeldt *et al.* 2020). The approach used in this study represents a model-based approach to estimate trophodynamic indices over the spatial domain using spatial and spatiotemporal random effects (Thorson *et al.* 2015, Cao *et al.* 2017, Karp *et al.* 2025). This approach has benefits over design-based indices by being able to include covariates and latent variables, which can improve estimates when the sampling is spatially or temporally unbalanced; however, this relies on the models being specified appropriately (Yalcin *et al.* 2023). We believe there are several possibilities for future work. For instance, this could include further exploration of density dependence, or at which spatiotemporal scale covariates should be included (Fall *et al.* 2021, Lindmark *et al.* 2024). Another area of research could be the co-variation between different prey groups, since they are likely not independent. For instance, if

cod recently fed on herring, they may not feed on benthic prey soon after, or cod may switch to sprat if the abundance of herring declines. Questions such as these could potentially be addressed using dynamic structural equation models including simultaneous or lagged effects (Thorson *et al.* 2024).

Conclusion

Predator-prey interactions play an important role in defining ecosystem functioning and the trophic structure of marine food webs. The relationship between predator feeding dynamics and prey is a crucial aspect of this. Understanding these interactions is critical for supporting the implementation of broader food web considerations in an ecosystem-based approach to fisheries management. Essentially, this means being able to predict the ecological effects on predators that may stem from changes in prey abundance and distribution, fisheries and other anthropogenic pressures. For increases in prey to have a causal impact on predator productivity, there has to be a link between prey availability and predation. We do not find evidence of such positive associations between prey and predator feeding dynamics despite large fluctuations in abundance, local-scale availability, and population-level spatiotemporal overlap. While we do acknowledge that spatiotemporal dynamics of these interactions are complex and scale-dependent and may be difficult to quantify (e.g., Fall *et al.* 2021), our results could mean that the effects of specific prey are weaker than previously thought. However, it is difficult to make general statements given the mixed results in the literature (e.g., Free *et al.* 2021, Goodman *et al.* 2022), and since it may have implications for assessment and management, it should be evaluated case-by-case. In the example of Baltic cod, it could mean that management interventions aimed at increasing the availability of pelagic prey would have limited impacts on the productivity of cod.

Acknowledgments

In memory of our dear friend and colleague Dr. Didzis Ustups, a key contributor to the manuscript, the ICES community, and to fisheries ecology in the Baltic Sea. We thank everyone involved in the collection, processing, and collation of stomach content data over time that led to the creation of the ICES stomach content database, Ivo Šics and everyone else involved in the EASME/EMFF/2018/011

SC10, Olavi Kaljuste for providing pelagic data, Hagen Radtke and Ivan Kuznetsov for assistance in acquiring predictions of *Saduria* densities, and Gemma Carroll for help with spatial overlap metrics. We also thank Robert Thorpe for a review of the paper. This work builds on the findings of the specific contract CINEA/EMFAF/2021/3.1.4-LOT1/SC10/SI2.877930*, requested by the European Climate, Infrastructure and Environment Executive Agency (CINEA), and funded through the European Maritime, Aquaculture and Fisheries Fund (EMFAF). Neither CINEA or the European Commission can guarantee the accuracy of the scientific data/information, the information does not necessarily reflect their official opinion, and they are not to be held accountable for the contents herein.

Author contributions

Conceptualization: M.L., C.A.G., V.B., F.M.; Data curation: V.T., M.L; Methodology: M.L., C.A.G., V.B., F.M., S.C.A; Formal analysis: M.L., V.T., S.C.A; Visualization: M.L., S.C.A; Software: S.C.A; Project administration: N.S.J., M.L., C.A.G., V.B.; Resources: K.N.A., J.P., M.A., M.R., K.W., M.G., I.S., D.U.; Writing – original draft: M.L.; Writing – review & editing: All authors.

Data Availability Statement

Code and data to reproduce the results are available on GitHub (https://github.com/maxlindmark/pred-prey-overlap) and will be deposited on Zenodo upon publication.

Funding

V.T. was supported by a research grant from the Oscar and Lili Lamm Foundation (grant no. FO2023-0037), awarded to M.L. M.G. was supported by grant no. 03F0937A (project MGF Baltic Sea II funded by the German Federal Ministry of Education and Research). MSAT was supported by the Natural Environment Research Council grant NE/V017039/1.

References

Aitchison, J. (1955) On the distribution of a positive random variable having a discrete probability mass at the origin. *Journal of the American Statistical Association* **50**, 901.

Akaike, H. (1973) Information theory as an extension of the maximum likelihood principle. In: *Second International Symposium on Information Theory*. Akademiai Kiado, Budapest, pp. 267–281.

Amarasekare, P. (2008) Spatial Dynamics of Foodwebs. *Annual Review of Ecology, Evolution, and Systematics* **39**, 479–500. URL https://www.annualreviews.org/doi/10.1146/annurev.ecolsys.39.110707.173434.

Anderson, S.C., Ward, E.J., English, P.A., Barnett, L.A.K. and Thorson, J.T. (2024) 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**. URL https://doi.org/10.1101/2022.03.24.485545.

Bakun, A. (2006) Wasp-waist populations and marine ecosystem dynamics: Navigating the "predator pit" topographies. *Progress in Oceanography* **68**, 271–288. URL https://linkinghub.elsevier.com/retrieve/pii/S0079661106000097.

Bartolino, V., Tian, H., Bergström, U., Jounela, P. *et al.* (2017) Spatio-temporal dynamics of a fish predator: Density-dependent and hydrographic effects on Baltic Sea cod population. *PLoS One* **12**, e0172004. URL https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0172004.

Bergström, U. and Englund, G. (2004) Spatial scale, heterogeneity and functional responses. *Journal of Animal Ecology* **73**, 487–493. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/j.0021-8790.2004.00823.x.

Bürkner, P.C. (2017) **brms** : An *R* Package for Bayesian Multilevel Models Using *Stan*. *Journal of Statistical Software* **80**. URL http://www.jstatsoft.org/v80/i01/.

Cao, J., Thorson, J.T., Richards, R.A. and Chen, Y. (2017) Spatiotemporal index standardization improves the stock assessment of northern shrimp in the Gulf of Maine. *Canadian Jour-*

nal of Fisheries and Aquatic Sciences URL https://cdnsciencepub.com/doi/abs/10.1139/cjfas-2016-0137.

Carroll, G., Abrahms, B., Brodie, S. and Cimino, M.A. (2024) Spatial match–mismatch between predators and prey under climate change. *Nature Ecology & Evolution* , 1–9URL https://www.nature.com/articles/s41559-024-02454-0.

Carroll, G., Holsman, K.K., Brodie, S., Thorson, J.T. *et al.* (2019) A review of methods for quantifying spatial predator–prey overlap. *Global Ecology and Biogeography* **28**, 1561–1577. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/geb.12984.

Casini, M., Käll, F., Hansson, M., Plikshs, M. *et al.* (2016) Hypoxic areas, density-dependence and food limitation drive the body condition of a heavily exploited marine fish predator. *Royal Society Open Science* **3**, 160416. URL https://royalsocietypublishing.org/doi/full/10.1098/rsos.160416.

Chagaris, D., Drew, K., Schueller, A., Cieri, M., Brito, J. and Buchheister, A. (2020) Ecological Reference Points for Atlantic Menhaden Established Using an Ecosystem Model of Intermediate Complexity. *Frontiers in Marine Science* **7**. URL https://www.frontiersin.org/journals/marine-science/articles/10.3389/fmars.2020.606417/full. Publisher: Frontiers.

Crawford, R.J.M. (2007) Food, fishing and seabirds in the Benguela upwelling system. *Journal of Ornithology* **148**, 253–260. URL https://doi.org/10.1007/s10336-007-0228-z.

Cury, P., Bakun, A., Crawford, R.J.M., Jarre, A., Quiñones, R.A., Shannon, L.J. and Verheye, H.M. (2000) Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. *ICES Journal of Marine Science* **57**, 603–618. URL https://doi.org/10.1006/jmsc.2000.0712.

Cury, P.M., Boyd, I.L., Bonhommeau, S., Anker-Nilssen, T. *et al.* (2011) Global Seabird Response to Forage Fish Depletion—One-Third for the Birds. *Science* **334**, 1703–1706. URL https://www.science.org/doi/10.1126/science.1212928.

Dunn, P.K. and Smyth, G.K. (1996) Randomized Quantile Residuals. *Journal of Computational and Graphical Statistics* **5**, 236–244. URL https://www.jstor.org/stable/1390802.

Eero, M., Brander, K., Baranova, T., Krumme, U., Radtke, K. and Behrens, J.W. (2023) New insights into the recent collapse of Eastern Baltic cod from historical data on stock health. *PLOS ONE* **18**, e0286247. URL https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0286247.

Eero, M., Vinther, M., Haslob, H., Huwer, B., Casini, M., Storr-Paulsen, M. and Köster, F.W. (2012) Spatial management of marine resources can enhance the recovery of predators and avoid local depletion of forage fish. *Conservation Letters* **5**, 486–492. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1755-263X.2012.00266.x.

EMODnet Bathymetry Consortium (2022) *EMODnet Digital Bathymetry (DTM 2022)*. URL https://doi.org/10.12770/ff3aff8a-cff1-44a3-a2c8-1910bf109f85.

English, P.A., Ward, E.J., Rooper, C.N., Forrest, R.E. *et al.* (2022) Contrasting climate velocity impacts in warm and cool locations show that effects of marine warming are worse in already warmer temperate waters. *Fish and Fisheries* **23**, 239–255. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/faf.12613.

Essington, T.E., Anderson, S.C., Barnett, L.A.K., Berger, H.M., Siedlecki, S.A. and Ward, E.J. (2022) Advancing statistical models to reveal the effect of dissolved oxygen on the spatial distribution of marine taxa using thresholds and a physiologically based index. *Ecography* **2022**, e06249. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/ecog.06249. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/ecog.06249.

Essington, T.E. and Hansson, S. (2004) Predator-dependent functional responses and interaction strengths in a natural food web. *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 2215–2226. URL https://cdnsciencepub.com/doi/abs/10.1139/f04-146.

Fall, J. and Fiksen, Ø. (2020) No room for dessert: A mechanistic model of prey selection in gut-limited predatory fish. *Fish and Fisheries* **21**, 63–79. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/faf.12415.

Fall, J., Johannesen, E., Englund, G., Johansen, G.O. and Fiksen, Ø. (2021) Predator–prey overlap in three dimensions: cod benefit from capelin coming near the seafloor. *Ecography* **44**, 802–815. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/ecog.05473.

Free, C.M., Jensen, O.P. and Hilborn, R. (2021) Evaluating impacts of forage fish abundance on marine predators. *Conservation Biology* **35**, 1540–1551. URL https://conbio.onlinelibrary.wiley.com/doi/10.1111/cobi.13709.

Froese, R., Pauly, D. *et al.* (2010) Fishbase.

Gartland, J. and Latour, R.J. (2024) Disentangling bottom-up and top-down controls on fish consumption of key prey in the Northeast US Shelf ecosystem. *ICES Journal of Marine Science* , fsae115URL https://doi.org/10.1093/icesjms/fsae115.

Gogina, M., Zettler, M.L., Wåhlström, I., Andersson, H., Radtke, H., Kuznetsov, I. and MacKenzie, B.R. (2020) A combination of species distribution and ocean-biogeochemical models suggests that climate change overrides eutrophication as the driver of future distributions of a key benthic crustacean in the estuarine ecosystem of the Baltic Sea. *ICES Journal of Marine Science* **77**, 2089–2105. URL https://academic.oup.com/icesjms/advance-article/doi/10.1093/icesjms/fsaa107/5880824.

Goodman, M.C., Carroll, G., Brodie, S., Grüss, A. *et al.* (2022) Shifting fish distributions impact predation intensity in a sub-Arctic ecosystem. *Ecography* , e06084URL https://onlinelibrary.wiley.com/doi/abs/10.1111/ecog.06084.

Grüss, A., Thorson, J.T., Carroll, G., Ng, E.L. *et al.* (2020) Spatio-temporal analyses of marine predator diets from data-rich and data-limited systems. *Fish and Fisheries* **21**, 718–739. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/faf.12457. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/faf.12457.

Gurvan, M., Bourdallé-Badie, R., Chanut, J., Clementi, E. *et al.* (2019) NEMO ocean engine URL https://zenodo.org/records/3878122. Publisher: Zenodo.

Hamre, J. (1994) Biodiversity and exploitation of the main fish stocks in the Norwegian - Barents Sea ecosystem. *Biodiversity and Conservation* **3**, 473–492. URL http://link.springer.com/10.1007/BF00115154.

Hartig, F. (2022) *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models*. URL https://CRAN.R-project.org/package=DHARMa. R package version 0.4.6.

Hentati-Sundberg, J., Olin, A.B., Evans, T.J., Isaksson, N., Berglund, P.A. and Olsson, O. (2021) A mechanistic framework to inform the spatial management of conflicting fisheries and top predators. *Journal of Applied Ecology* **58**, 125–134. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/1365-2664.13759.

Hilborn, R., Amoroso, R.O., Bogazzi, E., Jensen, O.P., Parma, A.M., Szuwalski, C. and Walters, C.J. (2017) When does fishing forage species affect their predators? *Fisheries Research* **191**, 211–221. URL https://www.sciencedirect.com/science/article/pii/S0165783617300176.

Hunsicker, M.E., Ciannelli, L., Bailey, K.M., Buckel, J.A. *et al.* (2011) Functional responses and scaling in predator-prey interactions of marine fishes: contemporary issues and emerging concepts: Predator-prey interactions in marine systemsis. *Ecology Letters* **14**, 1288–1299. URL https://onlinelibrary.wiley.com/doi/10.1111/j.1461-0248.2011.01696.x.

Huwer, B., Neuenfeldt, S., Rindorf, A., Andreasen, H. *et al.* (2014) Study on stomach content of fish to support the assessment of good environmental status of marine food webs and the prediction of MSY after stock restoration. Technical report, Final report for EU contract No MARE/2012/02. 56 pp.

ICES (2015) ICES advice on fishing opportunities, catch, and effort Baltic Sea ecoregion. Technical Report Book 8.

ICES (2019) Working Group on Multispecies Assessment Methods (WGSAM). ICES Scientific Reports 1:91. 320 pp. URL http://doi.org/10.17895/ices.pub.5758.

ICES (2021) Cod (*Gadus morhua*) in subdivisions 24-32, eastern Baltic stock (eastern Baltic Sea). *In* Report of the ICES Advisory Committee. Technical report. URL https://doi.org/10.17895/ices.advice.7745.

ICES (2022a) Baltic Fisheries Assessment Working Group (WGBFAS). Technical Report 4:44. URL https://doi.org/http%3A//doi.org/10.17895/ices.pub.19793014.

ICES (2022b) Sprat (Sprattus sprattus) in subdivisions 22–32 (Baltic Sea). *In* Report of the ICES Advisory Committee. Technical report. URL https://doi.org/10.17895/ices.advice.19453856.

ICES (2023) Cod (Gadus morhua) in subdivisions 24–32, eastern Baltic stock (eastern Baltic Sea). report, ICES Advice: Recurrent Advice. URL https://ices-library.figshare.com/articles/report/Cod_Gadus_morhua_in_subdivisions_24_32_eastern_Baltic_stock_eastern_Baltic_Sea_/21820497/1.

Jacobsen, N.S., Nadolna-Altyn, K., Ustups, D., Lindmark, M. *et al.* (2023) Study on stomach content of fish to update databases and analyse possible changes in diet or food web interactions : Final report. Technical report, European Commission, Brussels. URL https://library.wur.nl/WebQuery/wurpubs/626273. ISBN: 9789294050328.

Jennings, S. and Kaiser, M.J. (1998) The Effects of Fishing on Marine Ecosystems. In: *Advances in Marine Biology*, volume 34 (eds. J.H.S. Blaxter, A.J. Southward and P.A. Tyler). Academic Press, pp. 201–352. URL https://www.sciencedirect.com/science/article/pii/S0065288108602126.

Jensen, O.P., Branch, T.A. and Hilborn, R. (2012) Marine fisheries as ecological experiments. *Theoretical Ecology* **5**, 3–22. URL https://doi.org/10.1007/s12080-011-0146-9.

Karlson, K., Rosenberg, R. and Bonsdorff, E. (2002) Temporal and spatial large-scale effects of eutrophication and oxygen deficiency on benthic fauna in scandinavian and baltic waters—a review. *Oceanography and Marine Biology: an Annual Review* **40**, 427–489.

Karp, M.A., Cimino, M., Craig, J.K., Crear, D.P. *et al.* (2025) Applications of species distribution modeling and future needs to support marine resource management. *ICES Journal of Marine Science* **82**, fsaf024. URL https://academic.oup.com/icesjms/article/doi/10.1093/icesjms/fsaf024/8052165.

Kay, M. (2019) Tidybayes: Tidy Data and Geoms for Bayesian Models.

Kristensen, K., Nielsen, A., Berg, C.W., Skaug, H. and Bell, B.M. (2016) TMB: Automatic Differentiation and Laplace Approximation. *Journal of Statistical Software* **70**, 1–21. URL https://www.jstatsoft.org/index.php/jss/article/view/v070i05. Number: 1.

Kulatska, N., Neuenfeldt, S., Beier, U., Elvarsson, T, B., Wennhage, H., Stefansson, G. and Bartolino, V. (2019) Understanding ontogenetic and temporal variability of Eastern Baltic cod diet using

a multispecies model and stomach data. *Fisheries Research* **211**, 338–349. URL http://www.sciencedirect.com/science/article/pii/S0165783618303370.

Lewy, P. and Vinther, M. (2004) A stochastic age-length-structured multispecies model applied to North Sea stocks URL https://ices-library.figshare.com/articles/conference_contribution/A_stochastic_age-length-structured_multispecies_model_applied_to_North_Sea_stocks/25349317/1.

Lindgren, F. (2023) *fmesher: Triangle Meshes and Related Geometry Tools*. URL https://CRAN.R-project.org/package=fmesher. R package version 0.1.5.

Lindgren, F., Rue, H. and 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**, 423–498. URL https://rss.onlinelibrary.wiley.com/doi/abs/10.1111/j.1467-9868.2011.00777.x.

Lindmark, M., Anderson, S.C., Gogina, M. and Casini, M. (2023) Evaluating drivers of spatiotemporal variability in individual condition of a bottom-associated marine fish, Atlantic cod (*Gadus morhua*). *ICES Journal of Marine Science* **80**, 1539–1550. URL https://doi.org/10.1093/icesjms/fsad084.

Lindmark, M., Anderson, S.C. and Thorson, J.T. (2024) Estimating scale-dependent covariate responses using two-dimensional diffusion derived from the spde method. *bioRxiv* URL https://www.biorxiv.org/content/10.1101/2024.12.17.628864v1.

Lindmark, M., Maioli, F., Anderson, S.C., Gogina, M. *et al.* (2025) Quantifying competition between two demersal fish species from spatiotemporal stomach content data. *bioRxiv* URL https://www.biorxiv.org/content/10.1101/2024.04.22.590538v2.

Lynam, C.P., Llope, M., Möllmann, C., Helaouët, P., Bayliss-Brown, G.A. and Stenseth, N.C. (2017) Interaction between top-down and bottom-up control in marine food webs. *Proceedings of the National Academy of Sciences* **114**, 1952–1957. URL https://www.pnas.org/doi/abs/10.1073/pnas.1621037114.

Madec, G., Bell, M., Blaker, A., Bricaud, C. *et al.* (2023) Nemo ocean engine reference manual. *Mrežno]. Available: https://zenodo. org/record/8167700* **23**.

Mehl, S. and Sunnanå, K. (1991) Changes in growth of Northeast Arctic cod in relation to food consumption in 1984-1988. *ICES Marine Science Symposia* **193**, 109–112.

Mion, M., Haase, S., Hemmer-Hansen, J., Hilvarsson, A. *et al.* (2021) Multidecadal changes in fish growth rates estimated from tagging data: A case study from the Eastern Baltic cod *Gadus morhua*, Gadidae). *Fish and Fisheries* **22**, 413–427. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/faf.12527.

Neuenfeldt, S., Bartolino, V., Orio, A., Andersen, K.H. *et al.* (2020) Feeding and growth of Atlantic cod (*Gadus morhua* L.) in the eastern Baltic Sea under environmental change. *ICES Journal of Marine Science* **77**, 624–632. URL https://academic.oup.com/icesjms/advance-article/doi/10.1093/icesjms/fsz224/5643855.

Neumann, T., Koponen, S., Attila, J., Brockmann, C. *et al.* (2021) Optical model for the Baltic Sea with an explicit CDOM state variable: a case study with Model ERGOM (version 1.2). *Geoscientific Model Development* **14**, 5049–5062. URL https://gmd.copernicus.org/articles/14/5049/2021/.

Orio, A., Bergström, U., Florin, A.B., Lehmann, A., Šics, I. and Casini, M. (2019) Spatial contraction of demersal fish populations in a large marine ecosystem. *Journal of Biogeography* **46**, 633–645. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/jbi.13510.

Orio, A., Florin, A.B., Bergström, U., Šics, I., Baranova, T. and Casini, M. (2017) Modelling indices of abundance and size-based indicators of cod and flounder stocks in the Baltic Sea using newly standardized trawl survey data. *ICES Journal of Marine Science* **74**, 1322–1333. URL https://academic.oup.com/icesjms/article/74/5/1322/2972205.

Overholtz, W.J. and Link, J.S. (2007) Consumption impacts by marine mammals, fish, and seabirds on the Gulf of Maine–Georges Bank Atlantic herring (Clupea harengus) complex during the years 1977–2002. *ICES Journal of Marine Science* **64**, 83–96. URL https://doi.org/10.1093/icesjms/fsl009.

Pachur, M.E. and Horbowy, J. (2013) Food composition and prey selection of cod, Gadus morhua (Actinopterygii: Gadiformes: Gadidae), in the southern Baltic Sea. *Acta Ichthyologica et Piscatoria* **43**, 109–118. URL https://aiep.pensoft.net/article/26365/.

Pianka, E.R. (1973) The Structure of Lizard Communities. *Annual Review of Ecology and Systematics* **4**, 53–74. URL https://www.jstor.org/stable/2096804.

Pikitch, E., Boersma, P.D., Boyd, I., Conover, D. *et al.* (2018) The strong connection between forage fish and their predators: A response to Hilborn et al. (2017). *Fisheries Research* **198**, 220–223. URL https://hal.science/hal-01826745.

Pikitch, E., Boersma, P.D., Boyd, I.L., Conover, D.O. *et al.* (2012) Little fish, big impact: managing a crucial link in ocean food webs. *Lenfest Ocean Program, Washington, DC* **108**.

Pikitch, E.K., Rountos, K.J., Essington, T.E., Santora, C. *et al.* (2014) The global contribution of forage fish to marine fisheries and ecosystems. *Fish and Fisheries* **15**, 43–64. URL https://onlinelibrary.wiley.com/doi/10.1111/faf.12004.

Poggiale, J. (1998) Emergence of donor control in patchy predator-prey systems. *Bulletin of Mathematical Biology* **60**, 1149–1166. URL http://link.springer.com/10.1016/S0092-8240(98)90006-4.

R Core Team (2024) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Robinson, L.A., Greenstreet, S.P.R., Reiss, H., Callaway, R. *et al.* (2010) Length–weight relationships of 216 North Sea benthic invertebrates and fish. *Journal of the Marine Biological Association of the United Kingdom* **90**, 95–104. URL https://www.cambridge.org/core/journals/journal-of-the-marine-biological-association-of-the-united-kingdom/article/lengthweight-relationships-of-216-north-sea-benthic-invertebrates-and-fish/81302AECC322F20593D541D481DC31A2#.

Robinson, W.M.L., Butterworth, D.S. and Plagányi, É.E. (2015) Quantifying the projected impact of the South African sardine fishery on the Robben Island penguin colony. *ICES Journal of Marine Science* **72**, 1822–1833. URL https://doi.org/10.1093/icesjms/fsv035.

Rue, H., Martino, S. and Chopin, N. (2009) Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* **71**, 319–392. URL https://rss.onlinelibrary.wiley.com/doi/abs/10.1111/j.1467-9868.2008.00700.x.

Smith, A.D.M., Brown, C.J., Bulman, C.M., Fulton, E.A. *et al.* (2011) Impacts of Fishing Low–Trophic Level Species on Marine Ecosystems. *Science* **333**, 1147–1150. URL https://www.science.org/doi/10.1126/science.1209395.

Strong, D.R. (1992) Are Trophic Cascades All Wet? Differentiation and Donor-Control in Speciose Ecosystems. *Ecology* **73**, 747–754. URL https://www.jstor.org/stable/1940154.

Svedäng, H., Hornborg, S. and Grimvall, A. (2024) Centurial Variation in Size at Maturity of Eastern Baltic Cod (Gadus morhua) Mirrors Conditions for Growth. *Ecology and Evolution* **14**, e70382. URL https://onlinelibrary.wiley.com/doi/abs/10.1002/ece3.70382.

Svedäng, H., Savchuk, O., Villnäs, A., Norkko, A., Gustafsson, B.G., Wikström, S.A. and Humborg, C. (2022) Re-thinking the "ecological envelope" of Eastern Baltic cod (*Gadus morhua*): conditions for productivity, reproduction, and feeding over time. *ICES Journal of Marine Science* , fsac017URL https://doi.org/10.1093/icesjms/fsac017.

Thorson, J.T. (2018) Three problems with the conventional delta-model for biomass sampling data, and a computationally efficient alternative. *Canadian Journal of Fisheries and Aquatic Sciences* **75**, 1369–1382. URL https://cdnsciencepub.com/doi/10.1139/cjfas-2017-0266.

Thorson, J.T., Anderson, S.C., Goddard, P. and Rooper, C.N. (2024) tinyVAST: R package with an expressive interface to specify lagged and simultaneous effects in multivariate spatio-temporal models. URL http://arxiv.org/abs/2401.10193.

Thorson, J.T. and Kristensen, K. (2024) *Spatio-Temporal Models for Ecologists.* CRC Press, Boca Raton, FL.

Thorson, J.T., Shelton, A.O., Ward, E.J. and Skaug, H.J. (2015) Geostatistical delta-generalized linear mixed models improve precision for estimated abundance indices for West Coast groundfishes.

ICES Journal of Marine Science **72**, 1297–1310. URL https://academic.oup.com/icesjms/article/72/5/1297/767661.

Waagepetersen, R. (2006) A simulation-based goodness-of-fit test for random effects in generalized linear mixed models. *Scandinavian Journal of Statistics* **33**, 721–731.

Walters, C., Christensen, V., Fulton, B., Smith, A.D. and Hilborn, R. (2016) Predictions from simple predator-prey theory about impacts of harvesting forage fishes. *Ecological Modelling* **337**, 272–280. URL https://linkinghub.elsevier.com/retrieve/pii/S0304380016302587.

Yalcin, S., Anderson, S.C., Regular, P.M. and English, P.A. (2023) Exploring the limits of spatiotemporal and design-based index standardization under reduced survey coverage. *ICES Journal of Marine Science* , fsad155URL https://doi.org/10.1093/icesjms/fsad155.

Tables

Table 1: ΔAIC (marginal AIC for the model relative to the model with the lowest AIC) for all models fitted to stomach content data.

		Δ AIC	
Prey	**Breakpoint**	**Linear**	**No prey covariate**
Herring	0	274	0.09
Saduria	0	38.7	51.5
Sprat	1.78	2616	0

Figures

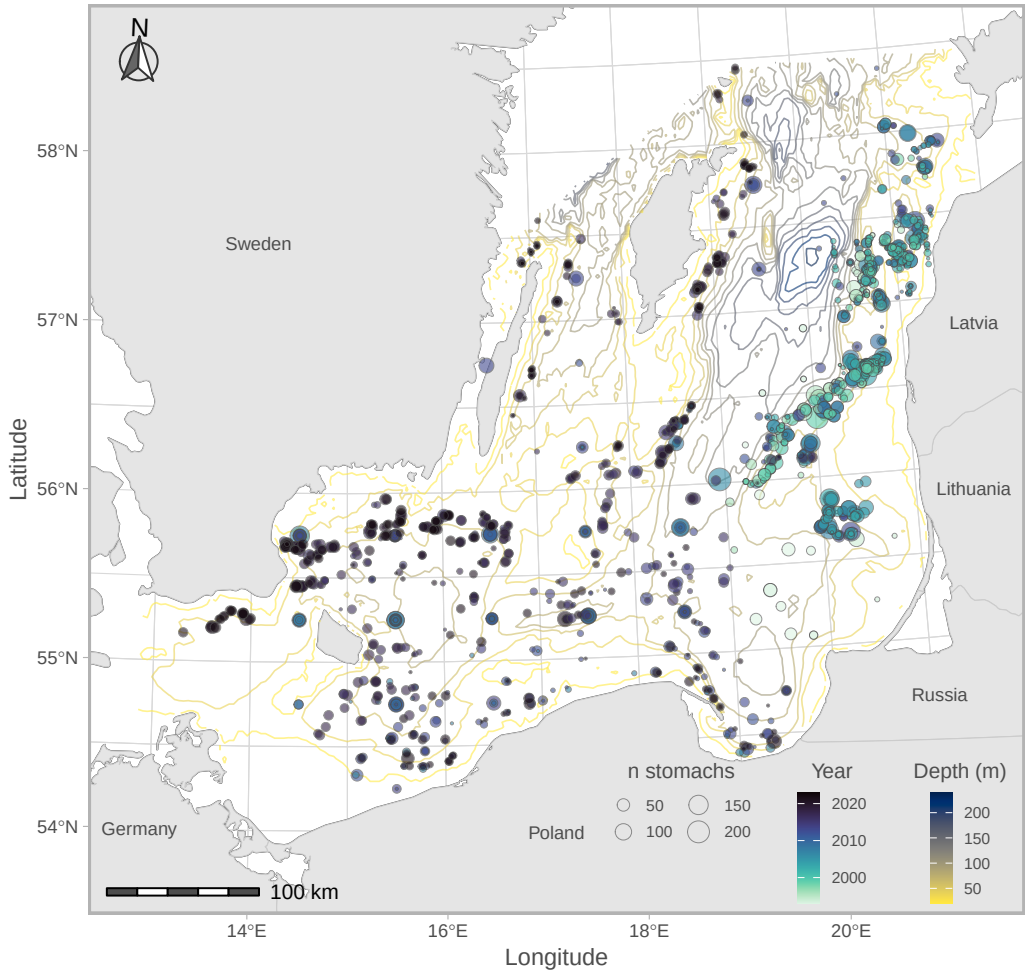

Figure 1: Location of stomach samples in the southern Baltic Sea. Colored contours correspond to depth, the fill color of the points correspond to year, and the size (area) of the points corresponds to sample size by year at that location. Rectangles correspond to ICES rectangles.

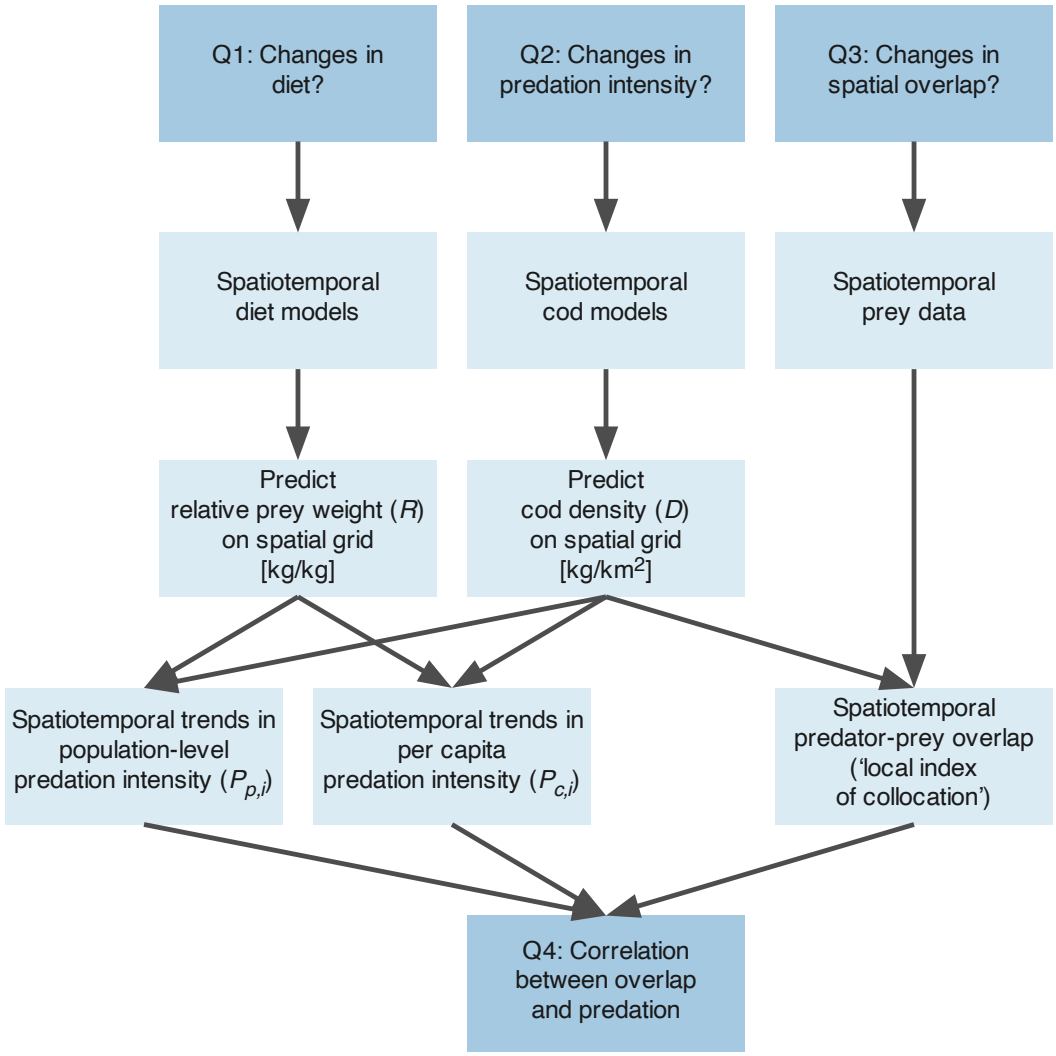

Figure 2: Chart describing the data and modeling process to acquire predation indices (population-level and per-capita) as well as predator-prey overlap. For the definition of $P_{p,i}$ and $P_{c,i}$, see equations 10–11. Research questions are indicated in darker blue boxes.

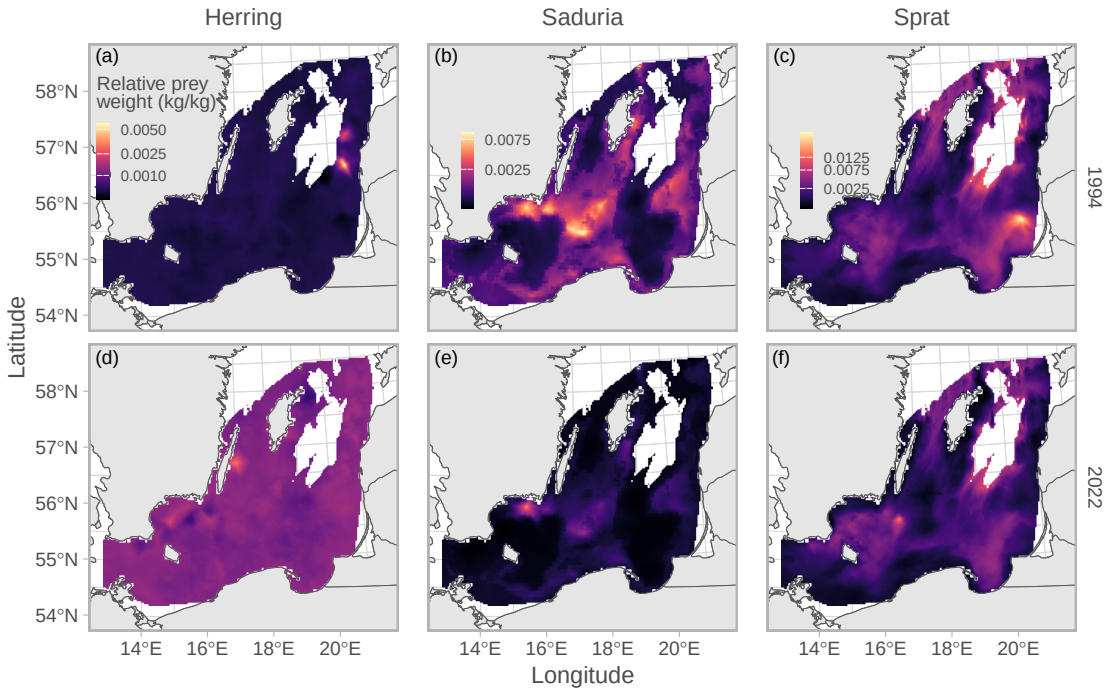

Figure 3: Relative prey weight for a cod of 33 cm. Colors indicate the median value across 500 simulated spatial predictions for herring (a, d), *Saduria* (b, e), and sprat (c, f), for years 1994 (top row, a–c) and 2022 (bottom row, d–f), as examples. The color scale is square-root transformed to better visualize the spatial patterns. Note that scales are shared within species, across years. Only grid cells with depth <130 m are included in the plot.

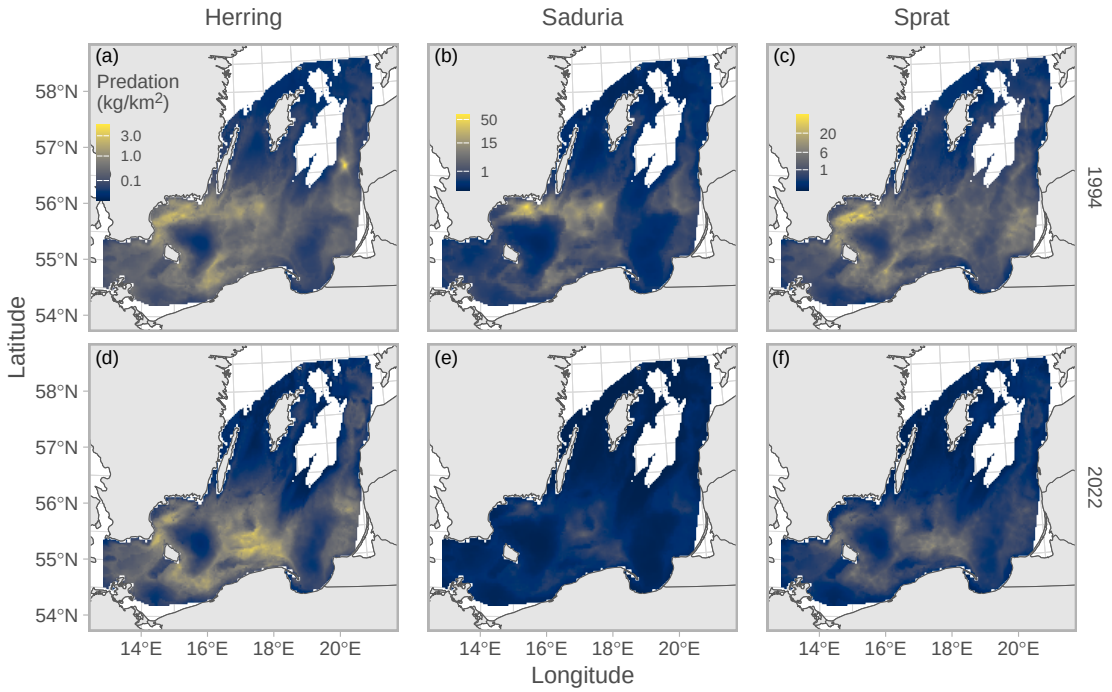

Figure 4: Cod density × relative prey weight (i.e., predation) plotted in space. Colors indicate the mean across 500 simulated spatial predictions of both relative prey weight and cod density for herring (a, d), *Saduria* (b, e), and sprat (c, f), for years 1994 (top row, a–c) and 2022 (bottom row, d–f), as examples. The sum of this metric (expanded by grid cell area) across space is the relative population-level predation intensity depicted in Fig. 6. Note that the color scale is 3rd-root transformed, and that scales are shared within species, across years. Only grid cells with depth <130 m are included in the plot.

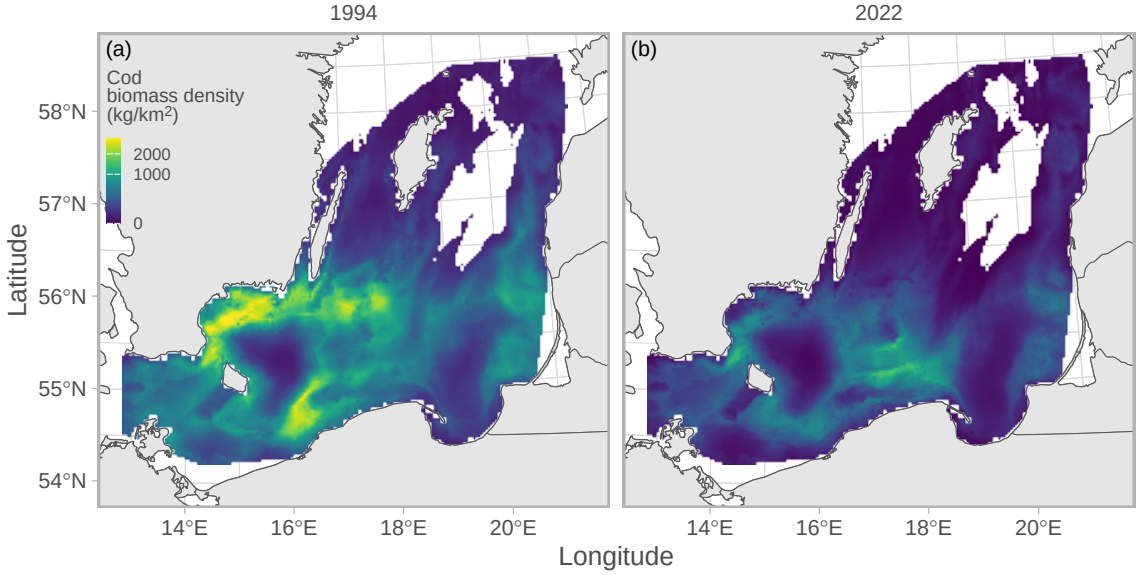

Figure 5: Cod biomass density in space. Colors indicate the mean across 500 simulated spatial predictions for years 1994 (a) and 2022 (b), as examples. Note that the color scale is square-root transformed and truncated at the 99.9th percentile to better visualize the spatial patterns (maximum cod biomass density is 3608 kg/m^2). Only grid cells with depth <130 m are included in the plot.

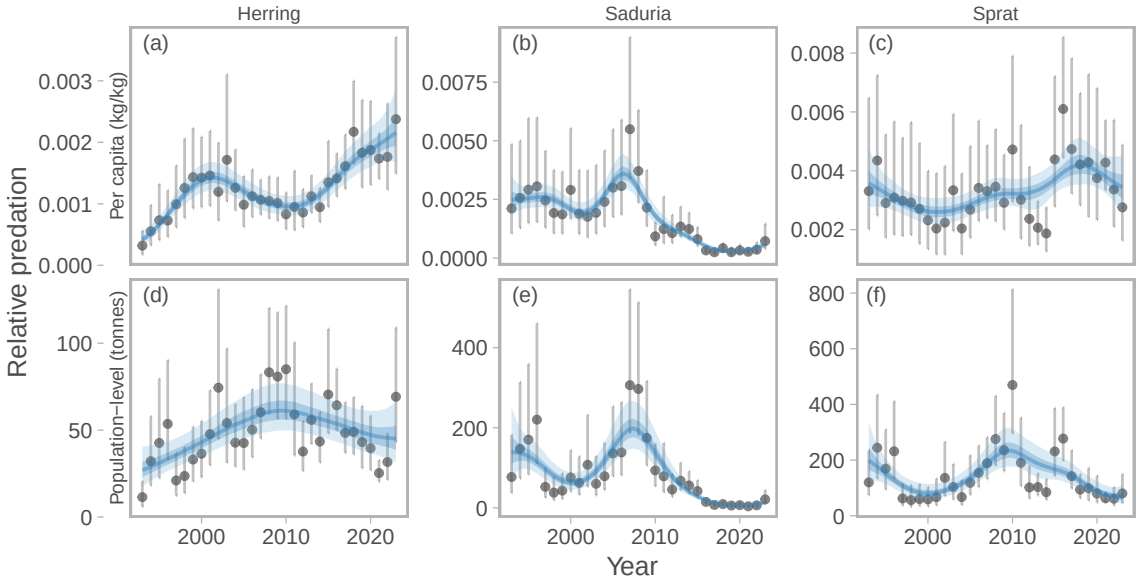

Figure 6: Relative per-capita (top row, a–c) and population-level predation (bottom row, d–f) by cod on herring (a, d), *Saduria* (b, e), and sprat (c, f) over time. Points depict the median predation, and vertical lines depict the range between the 10th and 90th percentile of predation, calculated from 500 simulated spatial predictions of both relative prey weight and cod density. Blue lines depict fits from a generalized additive model with year modelled as a penalized spline, and ribbons correspond to the 50% and 90% credible interval of the prediction.

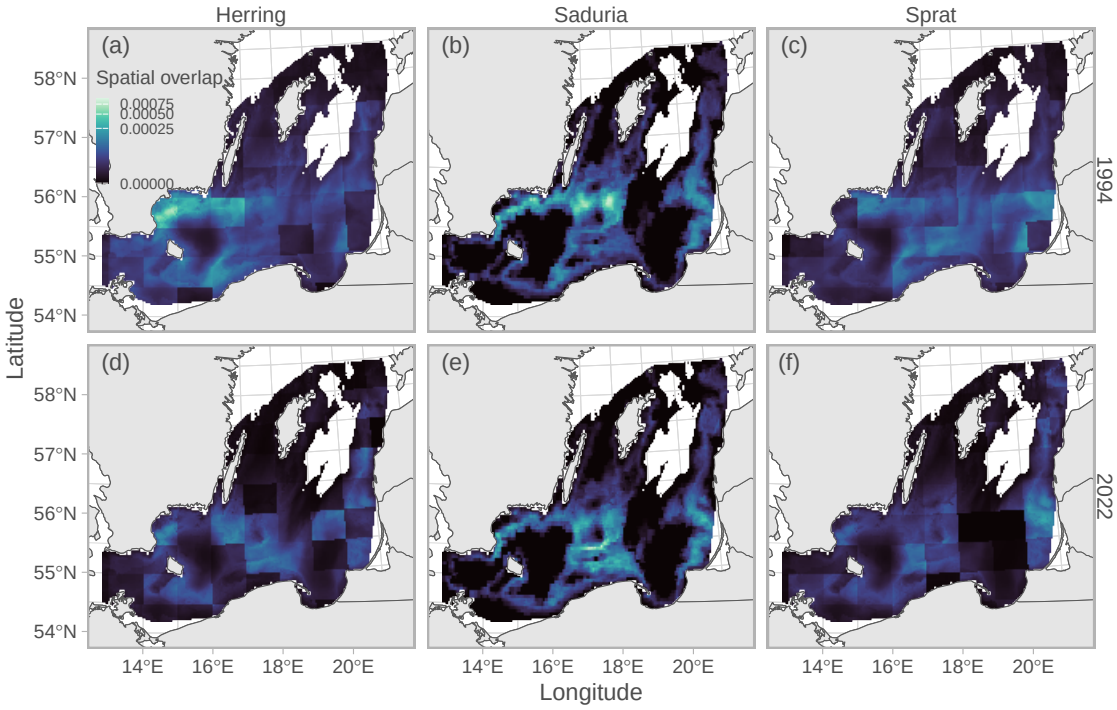

Figure 7: Spatial overlap between cod and its prey herring (a), *Saduria* (b), and sprat (c). Colors indicate the mean across 500 simulated spatial predictions of cod density in years 1994 (top row, a–c) and 2022 (bottom row, d–f), as examples. The color scale is 3rd root transformed to better visualize the spatial patterns. Only grid cells with depth <130 m are included in the plot.

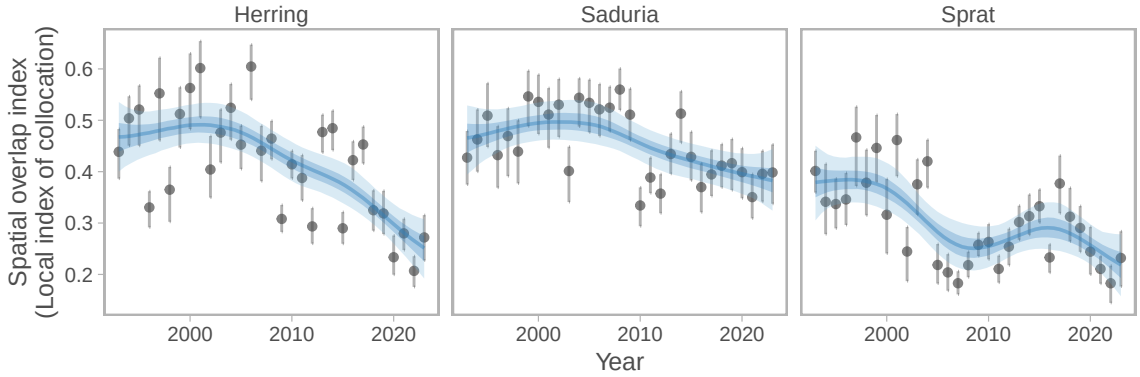

Figure 8: Spatial overlap between cod and its prey herring (a), *Saduria* (b), and sprat (c). Points depict the median overlap, and vertical lines depict the range between the 10th and 90th percentile of overlap, calculated from 500 simulated spatial predictions of cod density. Blue lines depict fits from a generalized additive model with year modelled as a penalized spline, and ribbons correspond to the 50% and 90% credible interval of the prediction.

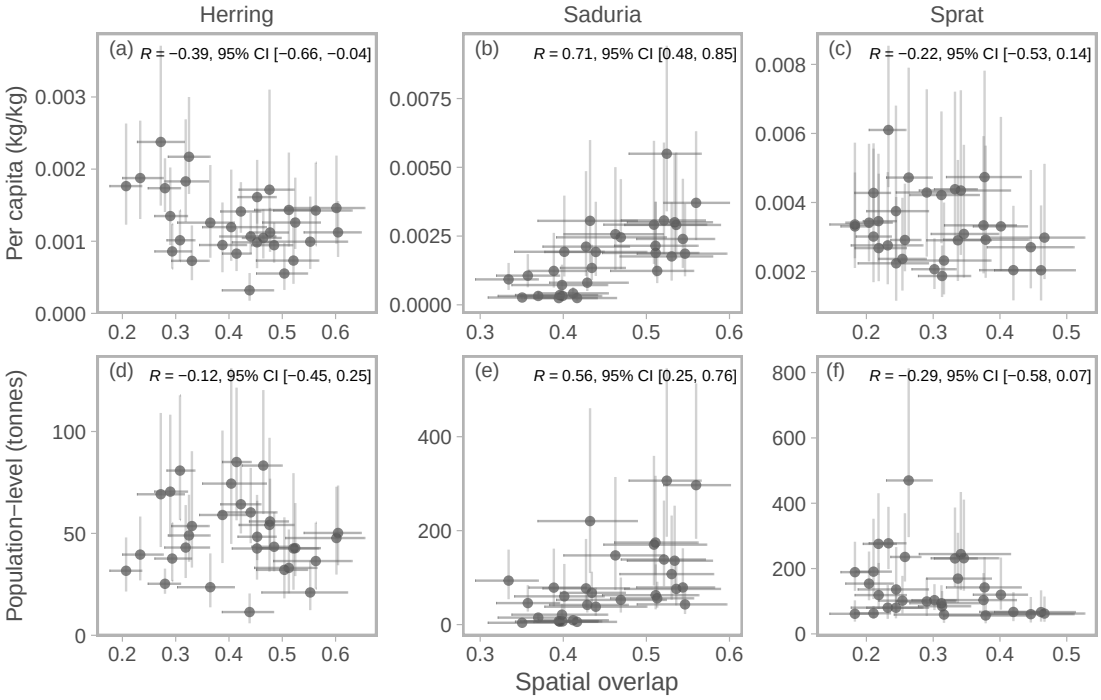

Figure 9: Correlation between relative per-capita predation and spatial overlap (top row, a–c), and relative population-level predation and spatial overlap (bottom row, d–f). Points depict the median, and vertical and horizontal lines depict the range between the 10th and 90th percentile of predation and spatial overlap, respectively, calculated from 500 simulated spatial predictions of predation and cod density. The Pearson correlation coefficient and its 95% confidence interval is printed in the top right corner of each panel for herring (a,d), *Saduria* (b, e), and sprat (c,f).