Quantifying competition between two demersal fish species from spatiotemporal stomach content data

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Running head: Inferring food-competition from diet

Abstract

Competition is challenging to quantify in natural systems and inference is often made on indirect patterns of potential competition, such as trends in population trajectories and overlap in spatiotemporal distribution and resource use. However, these indicators are not direct measures of fitness, nor do they say if the contested resource is limited in supply, which are key features of competition. Here we combine stomach content and biomass density data from scientific bottom trawl surveys to evaluate if competition is occurring between two dominant demersal fish species in the southern Baltic Sea: Atlantic cod (*Gadus morhua*) and flounder (*Platichthys spp*). We use multivariate generalized linear latent variable models (GLLVMs) to quantify diet similarities across the domain, diet overlap indices on relatively small spatial scales to test if predator density drives diet overlap, and spatiotemporal GLMMs fit to prey weights in individual predators to evaluate the effects of local biotic and abiotic covariates. We find clear dietary clusters by species and size. The latter is especially pronounced in cod, which shift from benthic to pelagic prey at around 30 cm. Overall, the dietary overlap is low and unaffected by predator density. However, signs of resource partitioning to reduce interspecific competition is evident in the most local scale analysis. As flounder densities increase, small and large cod tend to feed less on the isopod *Saduria entomon* — an important prey species. However, the benthic prey weight in small cod, and benthic and total prey weight in large cod, are not affected by flounder densities. We do not find evidence of intraspecific competition. Our results suggest that interspecific competition is not limiting cod feeding rates but affects their diet composition. These findings illustrate the importance of local scale processes when inferring competition from stomach content data. Quantifying ecological interactions is important for increasing our understanding of changes in the productivity of populations, and for developing ecosystem-based management.

Keywords: Diet, Stomach content, Competition, Spatiotemporal models, Multivariate, Trophic interactions

Introduction

Competition occurs when individuals — whether of the same or different species — interact for access to the same limited resource that improves their fitness; the concept has been a long-standing central tenant of ecological theory (Volterra 1926, Smith 1935, Elton 1949, Macarthur and Levins 1967, Schoener 1983, Holomuzki *et al.* 2010). Competition affects population dynamics via individual-level processes such as growth, dispersal and survival (Andersen 2020). On a community level, competition regulates species composition via competitive exclusion and partitioning of resources in space or time (Chesson 2000), and on an evolutionary level it drives trait diversity (Grant and Grant 2006). Competition has mostly been studied using mathematical models (Macarthur and Levins 1967, Lotka 1978, Tilman 1982) or by experimentally manipulating the abundance of a potential competitor in either a laboratory or field setting (Paine 1966, Werner and Hall 1977, Larson 1980, Goldberg and Barton 1992, Schoener 1983, Link and Auster 2013).

In natural systems, much of the empirical work on competition has been done on relatively small spatiotemporal scales, such as intertidal zones, freshwater lakes, or forest patches and on more or less sessile organisms using manipulative approaches (Paine 1966, Werner and Hall 1977, Lubchenco 1978, Link and Auster 2013). However, numerous organisms, including many marine fishes, are widely distributed and undergo seasonal migrations, as well as ontogenetic habitat and diet shifts (Heincke 1913, Stevenson *et al.* 2022, Ciannelli *et al.* 2022), such that the relevant spatiotemporal scales are much larger than what is covered by much of the seminal experimental work on competition. In such cases, competition is often inferred using statistical models fitted to observational spatial or temporal data of abundance or biomass (Jennings and Kaiser 1998, Link 2002, Ovaskainen *et al.* 2017, Godefroid *et al.* 2019). Despite the limitations of such correlative approaches, numerous studies have identified strong effects of interspecific interactions in marine food webs, where the majority of food web links are often weak compared to terrestrial ecosystems (see reviews in Jennings and Kaiser 1998, Minto and Worm 2012). Studies have often leveraged the fact that commercial fishing alters species composition and relative abundance within marine fish communities, thus constituting a form of semi-controlled manipulation experiment (Jennings and Kaiser 1998, Szuwalski *et al.* 2017) either via removal of predators, which can increase competition among prey, or by removal of potential competitions, by targeting specific species. However, it is difficult to attribute patterns in population abundance to competition (Schoener 1983, Goldberg

and Barton 1992, Jennings and Kaiser 1998, Dormann *et al.* 2018), since population dynamics of marine fishes are heavily influenced by stationary and non-stationary environmental drivers acting on different time scales, which may also affect biotic interactions (Jennings and Kaiser 1998, Ohlberger *et al.* 2022).

A more direct test of competition is by relating some measure of fitness, such as feeding rates, growth, or body condition to densities of potential competitors. An early example of this is the strong decline in growth in adult North Sea plaice following the Second World War when the stock biomass increased as a result of the reduced fishing mortality (Margetts and Holt 1948, Rijnsdorp and van Leeuwen 1992). As for interspecific competition, Casini *et al.* (2006) found that the body condition of sprat and herring were largely driven by the biomass of the sprat stock in the Baltic Sea. In contrast, Lindmark *et al.* (2023), in a study of Atlantic cod (*Gadus morhua*) in the eastern Baltic Sea, did not find effects of cod or flounder (*Platichthys flesus* and *Platichthys solemdali*) density on cod condition. However, despite no indication of competition affecting the body condition of eastern Baltic Sea cod, the system still constitutes an interesting case study that warrants further investigation. This is because investigating competitive interactions in non-manipulative systems requires a diversity of approaches, using multiple indicators at different spatiotemporal scales (Pianka 1976, Link and Auster 2013).

In the Baltic Sea, studies have identified potential competition between cod and flounder; opposite population trajectories, high spatiotemporal overlap, high dietary overlap, and some indication of resource limitation. Specifically, in recent decades, there has been a spatial contraction of the distribution of cod and an increase in the spatiotemporal overlap with flounder. It has also been suggested that the growth of medium-sized Baltic cod is limited by benthic prey availability (Orio *et al.* 2019, 2020, Neuenfeldt *et al.* 2020). There is also some dietary overlap between cod and flounder (Haase *et al.* 2020), and on a decadal time scale, some evidence of opposing population trajectories (Orio *et al.* 2017). Moreover, the productivity of eastern Baltic cod is at the moment historically low due to a reduced body growth (Mion *et al.* 2021), body condition (Casini *et al.* 2016b, Lindmark *et al.* 2023) and increased natural mortality (Casini *et al.* 2016a), to the degree that the population is expected to remain below limit reference points even in the absence of fishing (ICES 2023). Alongside deteriorating environmental conditions, such as increased hypoxia (Casini *et al.* 2021, Brander 2020, ICES 2023), these changes have partly been also attributed to inter- and in-

traspecific competition (Svedäng and Hornborg 2014, Casini *et al.* 2016b, Neuenfeldt *et al.* 2020). Specifically, changes in the abundance and distribution of flounder, and the size-structure of cod, may have led to increased intra- and interspecific competition for benthic prey such as *Saduria entomon* (henceforth *Saduria*).

In this study, our aim is to advance our understanding of intra- and interspecific competitive interactions by contrasting large-scale dietary patterns, small-scale dietary overlap indices and local stomach content data (weight of prey in stomachs), in relation to the density of competitors and abiotic covariates. We use the cod and flounder system in the southern Baltic Sea as a case study. To explicitly test for food competition, we fit spatiotemporal generalized linear mixed models (GLMMs) to stomach content data (weights of key prey groups relative to the individual predator weights) collected from bottom trawl surveys for the two species between 2015–2022. Stomach contents reflect ecological interactions on a much shorter time scale (days to weeks depending on prey), and are hence more straightforward to relate to local environmental and biotic variables. Specifically, we seek to answer the following questions: (1) To what extent do diets of cod and flounder overlap? (2) Does fish biomass density affect the diet overlap? (3) How does the local density of inter- and intraspecific competitors affect relative prey weights in their diets? (4) How does dissolved oxygen affect relative prey weights in their diets?

Methods

Data

We use an extended version of the recent dataset used in Haase *et al.* (2020). Cod and flounder stomachs were collected by the Swedish University of Agricultural Sciences, Department of Aquatic Resources, Sweden, during the bi-annual Baltic International Trawl Survey (BITS) conducted in the first and forth quarter of the year following the BITS protocol (ICES 2017). We used data from the southwestern Baltic Proper (Fig. 1) between 2015 and 2022 (data from quarter one in 2019 were not available), because during this period both cod and flounder stomachs were collected. The stomach sampling was designed to collect flounder and cod stomachs from the same trawl hauls. Whenever possible, one flounder and one cod stomach were collected for each 1 cm of fish length and trawl haul. Stomachs were extracted and frozen as quickly as possible by staff on-

board. Frozen stomachs were sent to the National Marine Fisheries Research Institute in Gdynia, Poland, for taxonomic identification of prey organisms to the lowest level possible and for calculation of total prey weights. The number, size and weight of individual prey were also measured when possible. Regurgitated stomachs were removed during data processing. After data processing, 5103 cod stomachs (2906 in the first quarter and 2197 in the fourth quarter), and 3851 flounder stomachs (2081 in the first quarter and 1770 in the fourth quarter) were available for analysis.

Diet similarity using model-based ordination

To quantify the main patterns and similarities in the diets of cod and flounder, we used a model-based unconstrained ordination approach (Warton *et al.* 2012, Hui *et al.* 2015). Model-based ordination explicitly models the mean-variance relationship, which is typical in count data and if not accounted for, can lead to misleading distance-based ordination plots (Hui *et al.* 2015). We used a generalized linear latent variable model (GLLVM), which fits multivariate data using a factor analytic approach with a set of latent variables that can be interpreted as unconstrained ordination axes. The multivariate data is in this case the relative prey weight (prey-to-predator weight ratio) of the 15 prey groups depicted in Fig. 2A, following Haase *et al.* (2020). The stomachs were averaged by 2 cm size bins for cod and flounder separately for fish sizes larger or equal to 10 cm and 50 cm or smaller. The averaging by 2 cm size group was because the model could not capture the left skew of the residuals (see Fig. S1 for the final QQ-plot). This resulted in a 39×15 matrix of stomachs, where the 39 rows correspond to average relative prey weights for a 2 cm class of cod or flounder. We then fit a GLLVM with two latent variables and no covariates, and a Tweedie distribution with a log link function because of the continuous positive response variable and presence of zeroes. The model can be written as:

$$\log(E(y_{ij})) = \boldsymbol{u}_i' \boldsymbol{\theta}_j, \tag{1}$$

where E is the expected value, y_{ij} is the observed relative prey weight j in the size-and predator species averaged stomach i, $\boldsymbol{\theta}_j$ are coefficients related to the latent variables $\boldsymbol{u}_i$ that provide coordinates for average stomach contents in the ordination plot, which provides a graphical representation of stomachs that are similar in terms of their prey composition. We visualized the

ordination by species and size. Specifically, small cod were defined as being $\geq$ 10 and $\lneq$ 25 cm, and large cod were defined as being > 25 and $\lneq$ 50 cm. These groups are also used in subsequent analysis. We fit this model in R version 4.3.2 (R Core Team 2020) with the R package gllvm (Niku *et al.* 2019, 2023) (version 1.4.3), which maximizes the log-likelihood of a TMB (Template Model Builder) (Kristensen *et al.* 2016) model with random effects integrated over using the Laplace approximation. We evaluated the model fit using QQ-plots based on randomized quantile residuals (Fig. S1).

Schoener's diet overlap index

Next we tested if diet similarity varies with biomass density of competitors. The hypothesis here is that if potentially competing species occur in high densities at the same place at the same time, there would be a higher diet separation (resource partitioning) to reduce competition (Macarthur and Levins 1967). To this end, we calculated the Schoener´s overlap index (Schoener 1968, see also e.g. Barnes *et al.* (2018)). Schoener's overlap is a symmetric measure of niche equivalency and varies between 0 and 1 (values above 0.6 are typically viewed as important). It is calculated as:

$$D_{ijk} = 1 - \frac{1}{2} \sum_{t}^{Q} |W_{g1,tijk} - W_{g2,tijk}|, \tag{2}$$

where D_{ij} is the overlap index $W_{g1,tij}$ and $W_{g2,tij}$ are the proportions of prey taxa t by weight in the stomachs of predator group 1 and 2 (where predator group is flounder, small cod and large cod), aggregated by year i, quarter j and ICES rectangle k (and ICES rectangle is 1 degree of longitude by 0.5 degrees of latitude). The variable Q is the total number of prey taxa observed. We used the same prey taxa groups as in the GLLVM model, and used only ICES rectangle-year combinations that had at least 3 predator stomachs of any predator group. This yielded $n = 244$ overlap values across ICES rectangle, year and predator-combinations or overlap groups.

To evaluate how the overlap differs between combinations of groups, and how the overlap varies with the average densities of cod and flounder, we fit a zero-inflated beta model since our overlap data are ≥ 0 but < 1. The zero-inflated model is a mixture model defined by the mean and precision of a beta distribution, which takes values between 0 and 1, and an additional zero-inflation parameter. We used overlap group (predator combination) as a predictor for all model

components. To evaluate if the overall biomass density of cod and flounder affects the diet overlap index, we included the natural logarithm of average biomass density of small cod, large cod, and flounder (scaled by subtracting the mean and dividing by the standard deviation) for the same subset of ICES rectangles and years for which we had overlap data. We note however that these biomass densities are not absolute values, and that catchability of the sampling gear might vary among species. We conducted sensitivity analysis by scaling predator-group densities by the maximum within species to acquire a more relative density index, and found nearly identical results (not shown). We included average predator biomass density as a predictor for the mean of the beta distribution and let it interact with overlap group to allow biomass density to have different effects on each predator overlap combination. The model can be written as:

$$Y_i \sim \mathrm{ZIBeta}(\mu_i, \phi_i, \alpha_i), \tag{3}$$

$$\mathrm{logit}(\mu_i) = \beta_1 g_{flc} + \beta_2 g_{fsc} + \beta_3 g_{sclc} + \beta_4 d + \beta_5 (d \times g_{fsc}) + \beta_6 (d \times g_{sclc}), \tag{4}$$

$$\log(\phi_i) = \beta_1 g_{flc} + \beta_2 g_{fsc} + \beta_3 g_{sclc}, \tag{5}$$

$$\mathrm{logit}(\alpha_i) = \beta_1 g_{flc} + \beta_2 g_{fsc} + \beta_3 g_{sclc}, \tag{6}$$

where Y_i is the overlap index, μ_i and ϕ_i represent the mean and the precision of the beta distribution, respectively, and α_i represents the probability that an observation is 0. The symbol g is an indicator variable that denotes overlap group, such that β_{1-3} are the mean overlap indices for groups flounder and large cod (subscript $_{flc}$), flounder and small cod (subscript $_{fsc}$), and small cod and large cod (subscript $_{sclc}$), respectively. The parameter β_4 is the slope of biomass density (d) for overlap group flounder and large cod, β_5 is the difference in biomass density slope relative to β_4 for the group flounder and small cod, and β_6 is the difference biomass density slope relative to β_4 for the group small cod and large cod. We fit the model fit in a Bayesian framework using Stan (Carpenter *et al.* 2017, Stan Development Team 2024) via the R package brms (Bürkner 2017, 2018) (version 2.20.4). Because the overall intercept is omitted, we assigned default improper flat priors for all coefficients, as is default in brms.

We sampled from the models with 4000 iterations on each of 4 chains and discarded the first half of each chain as warmup. We assessed model convergence by ensuring potential scale reduction

factors were smaller than 1.01, suggesting all four chains converged to a common distribution (Gelman *et al.* 2003). Model fit was assessed by visually inspecting posterior predictive checks (Fig. S2). We made conditional predictions and manipulated posterior draws with the R package tidybayes (Kay 2019).

Spatiotemporal food competition models

Lastly, we tested if the relative prey weight in the diet of predators on local scales was affected by biomass of potential competitors. Both the ordination and the Schoener's overlap index require some spatial aggregation, and hence do not address local scale variability and effects. However, one can imagine a scenario where the overall food consumed (or the consumption of particular prey) rather than the prey composition varies with predator density, and that overall biomass of prey (or the biomass of certain important prey) in predator stomachs is more closely related to competition and fitness than prey composition. Lastly, competitive interactions may also vary on more local scales than the rather arbitrary ICES rectangle (Schoener's overlap analysis) or the entire domain (GLLVM ordination). To evaluate if there is evidence for intra- and/or interspecific food competition in cod and flounder, we fit spatiotemporal GLMMs to relative prey weights of individual predators. As in Grüss *et al.* (2023), we chose to use individual predators as the sampling unit rather than haul-averaged diets even though stomachs within a haul may not be independent because diet vary considerably with predator size. We fit models to flounder, small cod, and large cod separately. The separation between small and large cod was based on the proportion of pelagic food in the diet (Fig. 2A).

Response variables

We used three different response variables: relative weight of (1) *Saduria*, (2) all benthic prey, and (3) total prey. Benthic prey is here defined as the sum of all prey except pelagic fish (sprat, herring and Clupeidae, see Fig. 2A). The latter was only fit to the large cod group since nearly all prey are benthic for the other predator groups. The rationale for this model setup was as follows: we looked specifically at *Saduria* because it is a prey that is less common in cod stomachs in the 2000s compared to the 1960s–70s (Kulatska *et al.* 2019, Haase *et al.* 2020, Neuenfeldt *et al.* 2020), and this reduction has been linked to the decreased growth of cod (Neuenfeldt *et al.* 2020). Moreover,

it is one of the few prey cod and flounder have in common in relatively large numbers (> 10% weight-proportion for a 20 cm cod and 10–40% of flounder diets depending on its size, see Fig. 2A). Hence, the *Saduria* models were to test if there is competition for a limited *Saduria* resource. With the benthic prey weight models, we aimed to evaluate if there was evidence for competition for benthic prey more broadly. Competition for *Saduria* in particular and benthos in general has been hypothesised to occur due to the combined effect of the range contraction of cod (Orio *et al.* 2019, 2020) and the expansion of hypoxic areas (Casini *et al.* 2016b, Haase *et al.* 2020). We fit the total prey model for large cod to understand if large cod are able to compensate with pelagic food to keep total food contents constant, should there be competition for benthic food.

Covariates

We matched monthly predicted values of dissolved oxygen at the sea floor with individual-level stomach data. These stem from the biogeochemical model ERGOM (Ecological Regional Ocean Model, https://ergom.net/), using the version in Neumann *et al.* (2015), downloaded from the Copernicus Marine Service Information (CMEMS 2023)). As a sensitivity analysis, we also fitted the models to oxygen data acquired from CTD samples taken at or near the location of the trawl hauls where stomachs were collected. Using measured data as a covariate would have been the first choice. However, since these measured data come with other limitations, such as variability in data quality and quantity, as well as uncertainty with respect to the distance from the sea bottom, we opted for the modelled oxygen data as the main choice, followed by a sensitivity analysis where we compared the oxygen estimates of modelled and measured oxygen (Fig. S9). We also used depth as a covariate, since it greatly influences benthic communities in the Baltic Sea (Karlson *et al.* 2002). Depth was matched to the stomach data using raster files from the EMODnet Bathymetry project (https://emodnet.ec.europa.eu/en/bathymetry) funded by the European Commission Directorate General for Maritime Affairs and Fisheries. We followed the approach in Lindmark *et al.* (2023), and acquired predicted values of *Saduria* biomass density from the habitat distribution model in Gogina *et al.* (2020), applied with modelled hydrographical data from the regional coupled ocean biogeochemical model ERGOM (Neumann *et al.* 2015, 2021). The *Saduria* model was trained to the time period 1981–2019 and predicted for the time period 1993–2019. Therefore, this variable represents long-term spatial, but not temporal variation in *Saduria* biomass density

(Fig. S7). Lastly, we used the natural logarithm of haul-level densities (kg/km^2) of cod and flounder from the same BITS survey that collected stomach data as covariates to evaluate the effects of inter- and intraspecific competition. Zeroes in the covariate were substituted with half the minimum observed value for that predator prior to taking the natural logarithm of it. We included interactions between biomass density of flounder and *Saduria*, and small cod and *Saduria* for the *Saduria* weight models. For the benthic and total prey weight models, we included interactions between flounder and oxygen and small cod and oxygen. This served to explore the hypothesis that the effect of inter and intraspecific competition is stronger when prey are scarce. Since we do not have spatially resolved estimates of total benthic prey, we used oxygen as a proxy, as it affects benthic prey biomass and in particular its depth distribution (Karlson *et al.* 2002, Ojaveer *et al.* 2010, Gogina *et al.* 2016). Hence, the oxygen variable relates both to the direct effect of dissolved oxygen on food consumption (via metabolic rate) and as a proxy for benthic prey abundance. All variables were scaled by subtracting the mean and dividing by the standard deviation. None of the covariates included in a single model had absolute correlation coefficients > 0.4.

Model description

The spatiotemporal GLMMs were assumed to follow a Tweedie distribution because of the presence of zeroes and the positive continuous values of relative prey weights. Despite the response always being < 1 (prey weight less than predator weight), we chose a Tweedie observation model over a beta hurdle model (a Bernoulli distribution for zero vs. non-zero and a beta distribution for positive ratio) after inspecting residuals. The spatiotemporal models can be written as:

$$Y_{\boldsymbol{s},t} \sim \text{Tweedie}(\mu_{\boldsymbol{s},t}, p, \phi), 1 < p < 2, \tag{7}$$

$$\mu_{s,t} = \exp(\boldsymbol{X}_{\boldsymbol{s},t}\boldsymbol{\beta} + \omega_{\boldsymbol{s}} + \epsilon_{\boldsymbol{s},t}), \tag{8}$$

$$\boldsymbol{\omega} \sim \text{MVNormal}\left(\mathbf{0}, \Sigma_{\omega}\right), \tag{9}$$

$$\boldsymbol{\epsilon}_t \sim \text{MVNormal}\left(\mathbf{0}, \Sigma_{\epsilon}\right), \tag{10}$$

where $Y_{s,t}$ represents the relative prey weight (*Saduria*, benthic or all prey) of an individual predator in space $\boldsymbol{s}$ and time t, μ represents the mean relative prey weight, p represents the Tweedie power parameter, and ϕ represents the Tweedie dispersion parameter. The symbol $\boldsymbol{X}$ represents

the design matrix and $\boldsymbol{\beta}$ represents a vector of fixed effect coefficients. The covariates include year and quarter (as categorical variables), depth, oxygen, and biomass density of small cod, large cod, flounder and *Saduria*. See section *Covariates*.

The spatial and spatiotemporal random effects $\omega_{\boldsymbol{s}}$ and $\epsilon_{\boldsymbol{s},t}$ capture spatially correlated latent effects that are constant through time and that vary through time, respectively. For example, here spatially constant latent effects might include sediment type, which is largely constant through time, and spatiotemporal latent effects might include plankton productivity, which changes through time. These random effects are assumed drawn from Gaussian Markov random fields (GMRFs) with covariance matrices Σ_ω and Σ_ϵ constrained by Matérn covariance functions (Rue *et al.* 2009, Lindgren *et al.* 2011). The Stochastic Partial Differential Equation (SPDE) approach (Lindgren *et al.* 2011), which links Gaussian random fields with GMRFs, requires piece-wise linear basis functions defined by a triangulation, commonly referred to as a "mesh". We formed this mesh using triangles with a minimum distance between vertices of 5 km — i.e., a "cutoff" of 5 km and all other arguments in fm_rcdt_2d_inla() (Lindgren 2023) at their defaults (Figs. S3–S5). We ensured the estimated range at which spatial correlation is present was, as a minimum, approximately twice the minimum distance between vertices (Fig. S8). For each model, we fit four different random effect structures: no random effects, spatial random effects, spatiotemporal random effects, and spatial and spatiotemporal random effects. We compared these structures using the Akaike Information Criterion (AIC) (Akaike 1974), and selected the random effect structure that had the lowest AIC (Table 1).

Model fitting

We fit the spatiotemporal models with the R package sdmTMB (Anderson *et al.* 2024), version 0.4.2.9000. 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 GMRFs from the R package fmesher (Lindgren 2023). Estimation is done via maximum marginal likelihood. We confirmed that the non-linear 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 model with the data by calculating randomized quantile residuals (Dunn and Smyth 1996) with fixed effects

held at their maximum likelihood estimates and random effects sampled via Markov chain Monte Carlo (MCMC) (Thygesen *et al.* 2017) using Stan (Carpenter *et al.* 2017, Stan Development Team 2024) via tmbstan (Monnahan and Kristensen 2018) (Fig. S6) .

Results

The diet of cod changes with size (Fig. 2A). In terms of prey weight, the smallest cod (5–10 cm) feed predominantly on polychaetes. As the cod grow in size, crustaceans, of which Mysidae is the largest group, start to dominate the diet. *Saduria* and sprat become a part of the cod diet at around 15–20 cm, and at 30 cm, sprat and herring together constitute more than half of the prey biomass. The proportion of fish in the diet of cod continues to increase with size. Cod and flounder emerge in the cod diet at around 45–50 cm.

The ontogenetic diet shift in flounder is more subtle. Small flounder (5–10 cm) feed mainly on mysids, while flounder between 15–40 cm have fairly similar diets, dominated by bivalves, *Saduria*, and other crustaceans (Fig. 2A). The ordination plots constructed from the first two latent variables revealed a clear clustering by species and for cod also by size (Fig. 2B).

Schoener's dietary overlap metrics varied across ICES rectangle and year combinations between 0 and 0.97 (Fig. 3A). The average overlap across all years and ICES rectangles was low; 0.07 [95% credible interval: 0.05, 0.08] for flounder and large cod, 0.16 [0.13, 0.2] for flounder and small cod, and 0.3 [0.24, 0.35] for small cod and large cod (Fig. 3A). This can be compared to 0.6, which is often considered to be ecologically significant (Zaret and Rand 1971). We find varying effects of biomass density on the mean of the beta distribution (Fig. 3B–C). For the overlap between small and large cod, the estimate is negative, and for the overlap between flounder and small cod, the effect of biomass is positive (Fig. 3B). The overlap between flounder and large cod is not associated with biomass density (Fig. 3B).

Across all predator and prey groups, the AIC model comparison either favoured models with (1) both spatial and spatiotemporal random fields (all *Saduria* models and the benthic prey models for flounder) or (2) spatiotemporal random fields (benthic prey in small and large cod, and total prey in large cod) (Table 1). The spatial and spatiotemporal random effects were larger in magnitude and the spatial clustering was more pronounced due to the high degree of latent variable spatial

correlation within the *Saduria* models compared to the benthic and total prey models (Fig. S12–S14).

The relative weight of *Saduria* was negatively associated with flounder biomass density in all predator groups, but the 95% confidence intervals overlapped 0 for flounder predators (Fig. 4A). The conditional predictions shows that with increasing flounder density the weight of *Saduria* in stomachs declines for all three species (Fig. 5). The biomass density of *Saduria* was associated with higher relative weights of *Saduria* across all predators, but the 95% overlap 0 for flounder and large cod (Fig. 4A). The interactions between flounder and *Saduria* were close to 0 for all predators (Fig. 4A), meaning the density of *Saduria* in the environment does not matter for the effect of flounder on *Saduria* weight in stomachs, as can also be seen in the conditional predictions of flounder density for two densities of *Saduria*(Fig. 5). Relative *Saduria* weights in stomachs were positively associated with the density of small cod density in flounder predators. Relative weights of benthic prey were not associated with flounder density in any predator (Fig. 4B).

Depth was negatively related to relative prey weights of all prey groups and all predators, except total prey weight in larger cod (Fig. 4), and in the *Saduria* model with flounder predators, the 95% confidence interval overlapped 0. In the model with *Saduria* weights as the response variable, the effect of oxygen was nearly 0 for flounder and large cod, and negative for small cod predators, although the 95% confidence interval overlapped 0 (Fig. 4A). With benthic prey as the response variable, oxygen had a clear positive effect for small and large cod, but not for flounder (Fig. 4B). While the absolute oxygen estimates varied depending on whether oxygen measurements came from CTD or modelled oxygen, the sensitivity analysis resulted in sign-agreement in the oxygen estimates for all models except for benthic prey in flounder predators and *Saduria* in large cod (but both oxygen sources result in oxygen coefficients with confidence intervals overlapping 0); see the oxygen estimates in Fig. S9A. The absolute value of the oxygen coefficient was smaller when using CTD data for all models except benthic prey in flounder predators. The positive effect of oxygen on benthic prey changed from clearly positive to overlapping with 0 when using observed rather than modelled oxygen in large cod (Fig. S9B). The relative weights of total prey in adult cod were positively associated with the density of large cod (Fig. 4C).

There was interannual variation in the relative weights of benthic prey and total prey for all predators, but the uncertainty of the prediction made it difficult to detect any trends. The effect

of quarter was more similar within prey groups than across predators (Fig. S11). For benthic prey, the relative weights tended to be higher in the fourth than the first quarter, and for *Saduria* it was reversed, for all predators (Fig. S11).

Discussion

In this study we analysed competition using statistical modelling of stomach content data at different spatial scales, using Atlantic cod and flounder in the Baltic Sea as a case study. Overall, we found low dietary overlap between these two predators in the studied domain (southwestern Baltic Sea). Moreover, on a smaller scale (ICES rectangle, 1×0.5 degrees longitude and latitude grid cells), we did not find support for increased diet differentiation as predator densities increased, as is often expected under resource partitioning to reduce competition and facilitate coexistence (Macarthur and Levins 1967). However, at the local scale (individual stomachs at the trawl haul level), we find that the relative weights of the isopod prey *Saduria entomon* in the diets of small and large cod decline with increasing flounder densities. The total prey weight on the other hand is not affected — large cod do not have less benthic prey or total prey weights when flounder are abundant. Similarly, small cod have less *Saduria* in their stomachs when flounder are abundant, but there is no effect of flounder on their total prey weight (which is benthic prey). Hence it seems the food competition from flounder does not mean less total food in cod stomachs. Rather, they feed less on *Saduria*, but compensate this loss with other prey.

Are the inconsistent signs of food competition among predator groups, and the ability to switch prey, a general pattern in marine fish communities in coastal and continental shelf ecosystems? It has been hypothesised that the high productivity and often generalist behaviour of many fish species result in low food competition (Sherman 1991, Link 2002). There are numerous examples in the literature supporting and rejecting this, but three well-studied cases illustrate there might be signals of food competition in large aquatic systems. First, the crash of the Peruvian anchovy, one of the most heavily exploited fish in the world, led to an increase in its competitor Peruvian Pacific sardine, but only partially, as the upwelling system is largely driven by environmental fluctuations (De Vries and Pearcy 1982). Second, the collapse of the Californian sardine in the late 1940s was followed by an increase in Northern anchovy, but not until a decade later. There were no signs of

density-dependent body growth, and analysis of sediment cores suggests there have been periods with high abundance of both species (MacCall 1986, Baumgartner *et al.* 1992, Jennings and Kaiser 1998). Last, the exceptionally strong year classes of gadoid species (codfishes) in the North Sea in the late 1960s — referred to as the "gadoid outburst" — could not convincingly be linked to the decline in Atlantic mackerel and North Sea herring stocks (Cushing 1984, Hislop 1996), as would otherwise be natural to assume given they compete with juvenile gadoids for zooplankton. Furthermore, Ursin (1982) noted that despite the 5-fold increase in biomass of haddock, whiting, and Norway pout in 1968–69 relative to previous years, which likely at least doubled the stock of demersal fish for years, no negative effect on growth in demersal life stages of gadoid fish was found (Ursin 1982, Jones 1983). Despite the extreme contrasts in biomass in these examples, the inconclusive results seem emblematic in temperate marine fish communities, possibly due to large influences of environmental drivers and an overall ability to find prey (Ursin 1982).

We find low diet overlap between cod and flounder, but in itself this does not inform our understanding of competition (Pianka 1976, Schoener 1983). A high overlap could indicate a tendency to compete, should the resource be limiting, such that intake of the shared resource declines with competitor biomass. A low resource overlap could be a result of dietary resource partitioning shaped over evolutionary time scales to avoid competition, but it could also arise as a behavioral response over short time scales as a form of prey switching by a generalist predator. We estimate negative effects, no effects, and positive effects of biomass density on the overlap for our three predator groups. Hence, we do not find conclusive evidence for overall negative effects of predator density on the diet overlap between these predator groups when aggregated on the ICES rectangle scale.

On a local scale (haul-level), we find signs of resource partitioning and interspecific competition for *Saduria*, but not declines in total prey weights. The latter could indicate competition if the predator switches to a worse prey in terms of nutrients or energy and fitness is negatively affected by it. It could be that *Saduria* is an especially important prey for cod relative to its weight contribution in the diet. Lindmark *et al.* (2023) found that *Saduria* biomass was weakly positively related to body condition, and while the energy density is lower compared to pelagic prey (Pedersen and Hislop 2001, Neuenfeldt *et al.* 2020), crustaceans, such as *Saduria*, have been considered important dietary components due to their high levels of astaxanthin (Røjbek *et al.* 2012). In the southern

Baltic Sea, we know that *Saduria* declined in the cod diet over time (Haase *et al.* 2020), as has the body condition and growth since the early 1990's (Lindmark *et al.* 2023, Mion *et al.* 2021). Haase *et al.* (2020) showed that in the 1960s, the relative weight proportions of *Saduria* ranged between 15–25% for cod above 21 cm, which can be compared to the ≈10% in our study for cod between 20–30 cm. However, whether or not this is a causal link can also be questioned given that *Saduria* weights in stomachs and condition and growth do not match temporally over longer time scales. Between 1963–1974, when *Saduria* proportions in cod stomachs were highest (Haase *et al.* 2020), somatic growth of cod was the lowest recorded (including present times) for cod of 25 cm (Mion *et al.* 2021).

While we do find many signs of what could be interpreted as interspecific competition for the isopod *Saduria*, the signs are not conclusive. In line with competition, the relative prey weight of *Saduria* in small and large cod stomachs are negatively associated with flounder density. Moreover, we find positive effects of *Saduria* biomass density in the environment and the weight of *Saduria* in predator stomachs, which suggests saduria is to some degree a limited resource. However, as *Saduria* densities decline, the effect of flounder ought to be more negative. We do not find such interactive effects between *Saduria* and flounder; instead, relative weights of *Saduria* decline with flounder densities at similar rates irrespective of *Saduria* densities (Fig. S11).

From a metabolic perspective, feeding activity and food assimilation require oxygen, and the latter becomes more costly as food rations increase. Therefore, a behavioral response to lower oxygen availability is a reduced appetite (Jobling 1997). In line with this theoretical prediction and experimental and in-situ studies supporting it (Chabot and Dutil 1999, Moriarty *et al.* 2020), Brander (2020) suggested that the decline in feeding levels of cod over time could be linked to the negative trends in dissolved oxygen, causing a state of mild hypoxia (Brander 2020). In this study, we for the first time explicitly test if feeding is related to oxygen in Baltic cod by including local dissolved oxygen as a covariate for prey weights in individual-level cod stomachs. We find statistically clear and positive effects of oxygen in small and large cod feeding on benthic prey, but no positive effects for any other combination of predator and prey. However, there is still some uncertainty as to the positive effect of oxygen for benthic prey because the significance is sensitive to which oxygen data are used. For modelled oxygen data, in small and large cod feeding on benthic prey, the positive effect seems fairly large. The relative weight of benthic prey in the diet increases

from 0.0025 to 0.004 when oxygen increases from 4.8 to 7.6 ml/L. This range of oxygen values is similar to the lower and upper end of the interquartile range of oxygen conditions cod experienced between 1993–2019 (Lindmark *et al.* 2023). We cannot completely disentangle the direct effects of oxygen affecting fish appetite and the effect of oxygen on prey availability. However, given that oxygen is only statistically related to benthic prey, and not total prey in large cod nor *Saduria* for any predator, and that oxygen strongly affects benthic communities (Karlson *et al.* 2002), it seems likely that the main effect of oxygen is via food availability rather than a direct effect on the appetite.

Our findings that cod feed less on *Saduria* when there is flounder, are in line with previous studies on fish documenting behavioural resource partitioning in that it is the more specialist species (in our case, flounder) that successfully interferes the generalist (cod) (Colwell and Fuentes 1975, Larson 1980). Although other mechanisms can also lead to resource partitioning, (Ross 1986), the observation that *Saduria* has declined in cod stomachs since the 1960's (Haase *et al.* 2020, Neuenfeldt *et al.* 2020), while flounder biomass has generally increased (Tomczak *et al.* 2022), is consistent with our pattern.

The reason this resource partitioning is not detected in the dietary overlap analysis could be that the spatiotemporal scale used to aggregate the individual diets was too large. When calculating overlap indices, it is important to ensure a large enough sample size per spatial and temporal aggregation unit to characterize a representative diet, given the large individual variation in diets (Barnes *et al.* 2018). However, increasing the scale over which to aggregate individual stomachs comes at the cost of accurately representing the local biotic and abiotic conditions at the time and location of the stomach sample. While our spatiotemporal GLMMs rely on univariate analysis of specific prey or prey groups rather than the whole prey community, a strength is that it avoids this aggregation over arbitrary spatial units. This is a potential reason why we can detect signs of resource partitioning, if part of the variation within aggregation units can be attributed to variation in environmental conditions within units that drive changes in stomach contents.

In conclusion, our approach to quantifying competitive interactions leveraging local-scale diet and biomass data illustrates the importance of scale and type of indicators when assessing competition. For instance, food competition is expected to occur if predators with similar diets co-occur in space, and the diet similarity is expected to decline as predator densities increase (resource

partitioning). In our system, we find low dietary overlap, and no overall negative effect of predator density on the overlap at an aggregated scale. However, when modelling local-scale stomach contents of specific shared prey, rather than spatially aggregated diet similarities, we find negative effects of flounder densities on the weights of *Saduria* in cod stomachs, but the total prey weights in cod are not affected by flounder. This indicates that cod, a generalist predator, is able to adapt its foraging in response to prey and predator densities, although the energetic effects of this switch are still unknown. We believe that using individual-level data with local scale covariates in spatiotemporal models, as done, here can improve our understanding of competitive interactions across scales, which is important for developing ecosystem-based management of wild populations.

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Author contributions

All authors contributed to the manuscript. M.C. coordinated the study, M.L. prepared the raw data, M.G. provided *S. entomon* data, M.L. led the design and conducted the statistical analyses with contributions from S.C.A and F.M., and input from M.C. M.L. wrote the first draft. All authors contributed to revisions and gave final approval for publication.

Data Availability Statement

Code and data to reproduce the results are available on GitHub (https://github.com/maxlindmark/cod-interactions) and will be deposited on Zenodo.

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Tables

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

		Δ AIC			
Response variable	**Group**	**Non-spatial**	**Spatial**	**Spatiotemporal**	**Spatial & Spatiotemporal**
Saduria	Flounder	911	206	39.7	0
Saduria	Small cod	181	9.59	26.3	0
Saduria	Large cod	338	41.8	16.4	0
Benthic prey	Flounder	416	97.6	24.5	0
Benthic prey	Small cod	194	130	0	2
Benthic prey	Large cod	261	166	0	1.92
Total prey	Large cod	73.2	51.9	0	1.97

Figures

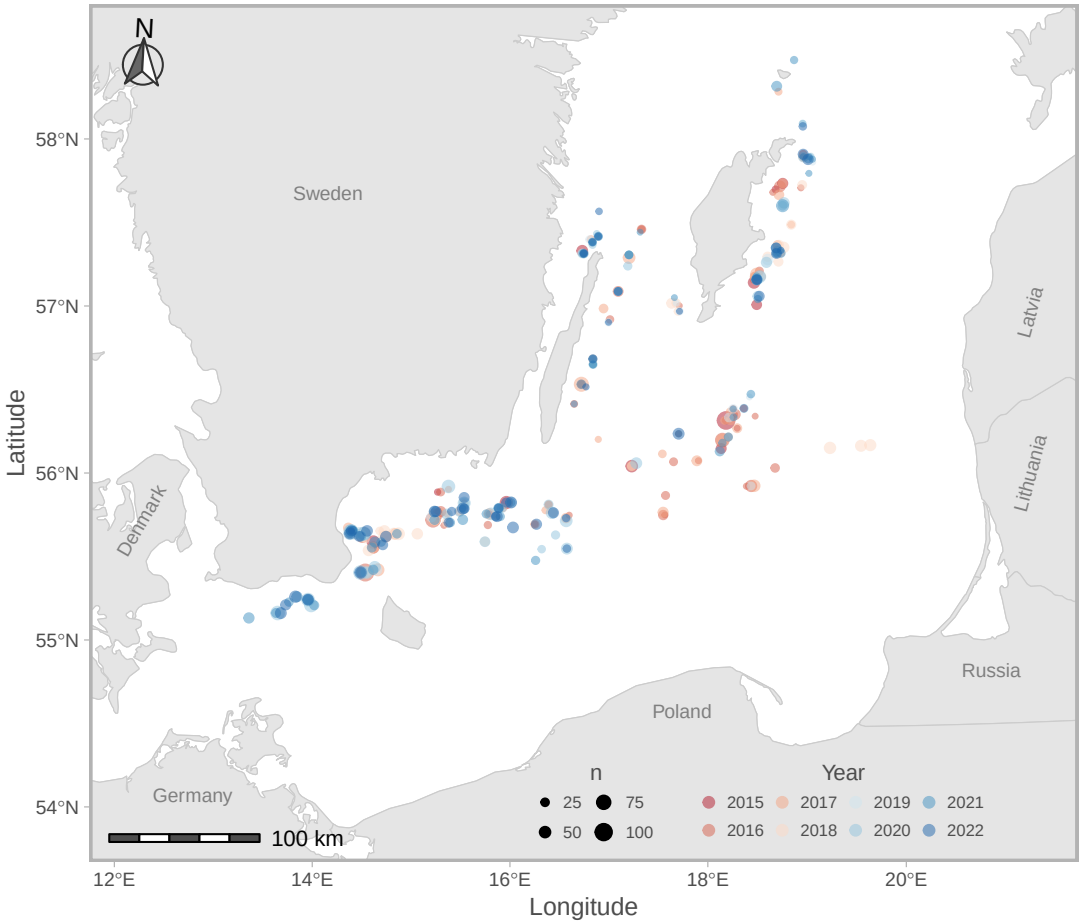

Figure 1: Location of stomach samples in the southern Baltic Sea. Colors correspond to years and the size (radius) of the point corresponds to sample size by year at that location.

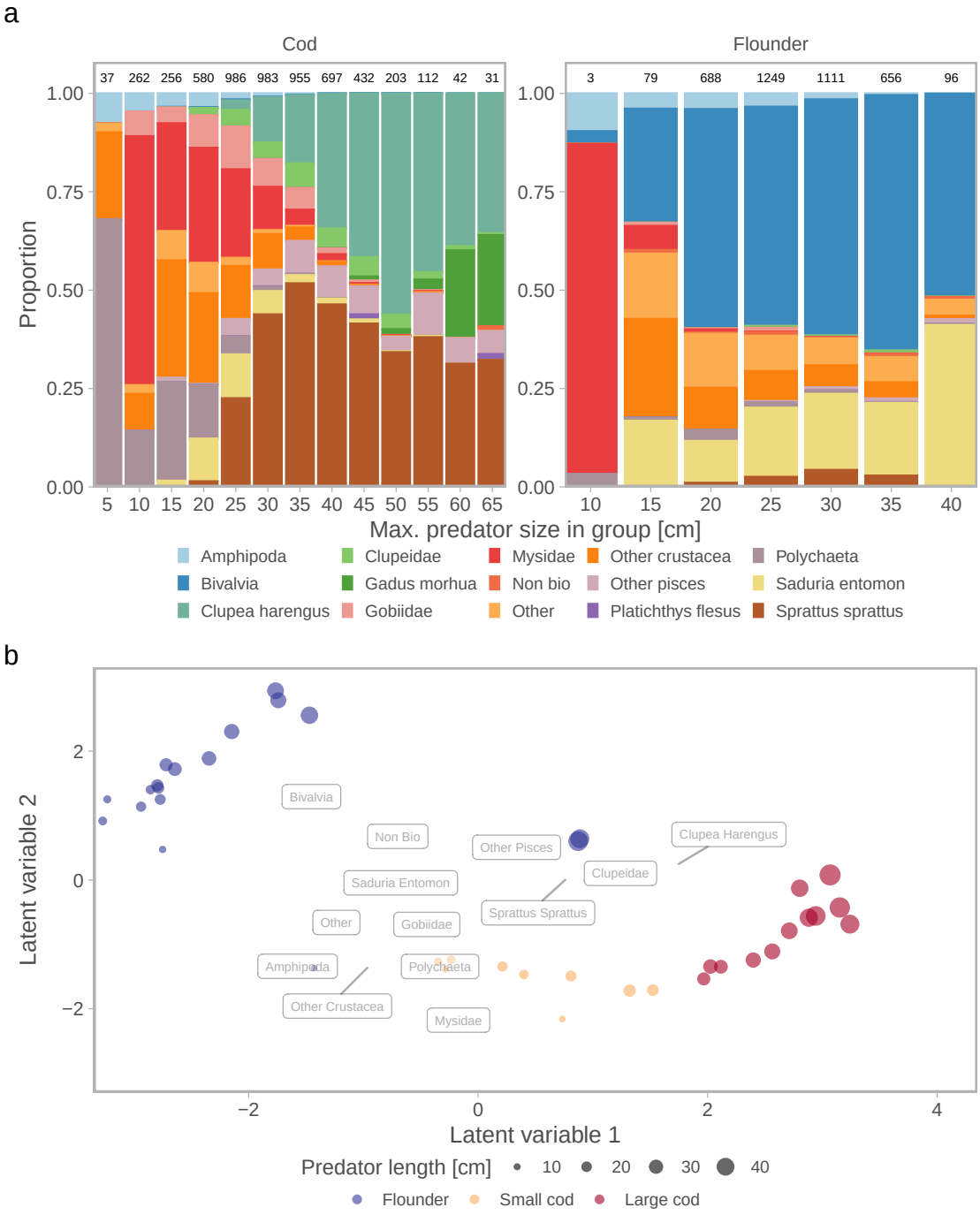

Figure 2: Diet over ontogeny and diet overlap between cod and flounder. Panel A depicts the average diet by 5 cm size groups of the predator and prey groups as weight proportions (the size is the maximum in that group). The number above each bar corresponds to the sample size. Panel B depicts the unconstrained ordination constructed from the two latent variables in the multivariate generalized linear latent variable models (GLLVM), where colors indicate predator groups (flounder in blue, small cod in yellow and large cod in red), and point size (radius) corresponds to the predator length in 2 cm groups.

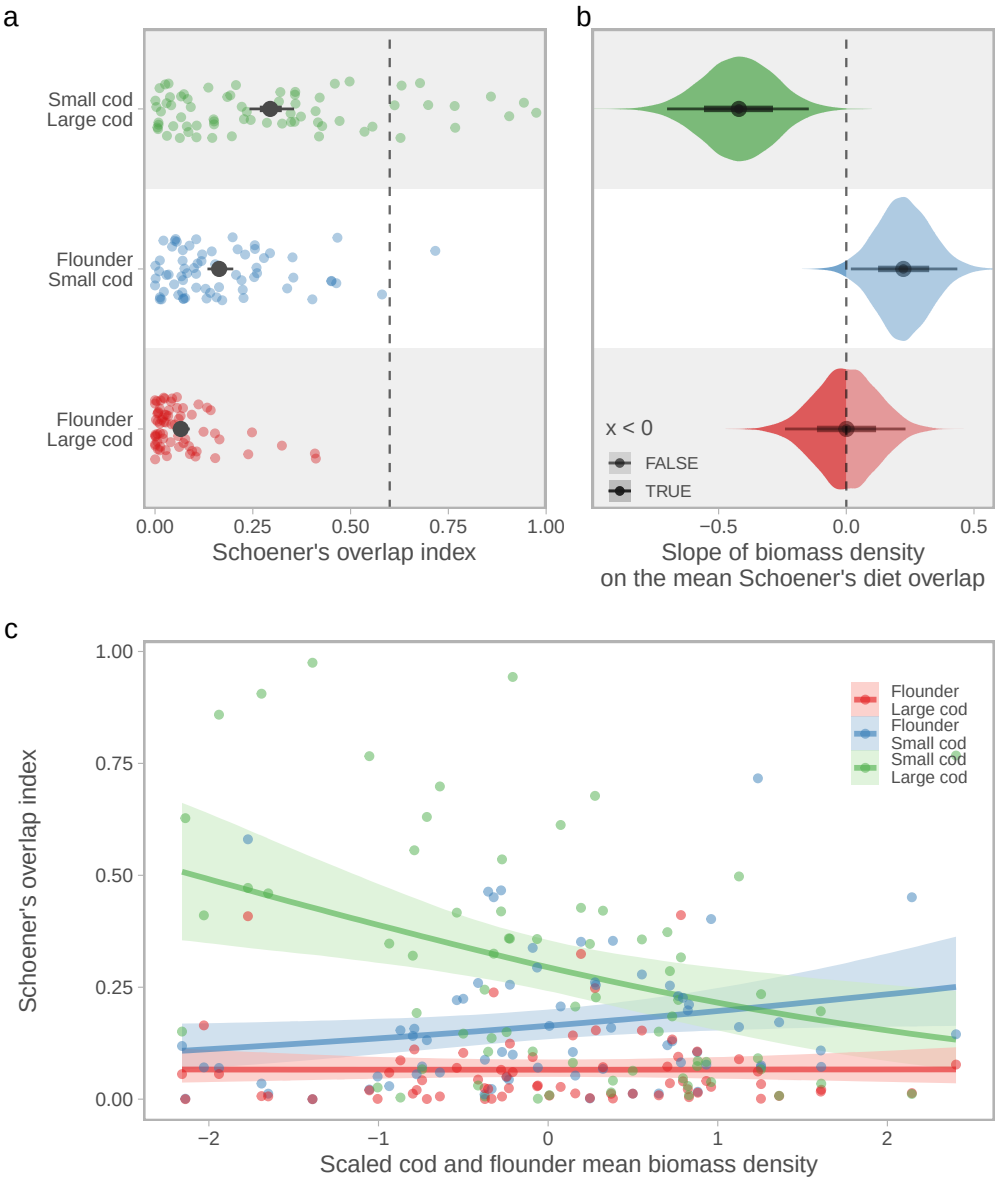

Figure 3: Schoener's diet overlap index and the effects of biomass density. Panel A depicts the overlap values across all combinations of predator groups (x-axis), where each gray point represents an overlap value for stomachs aggregated for a combination of ICES rectangle and year. The black points correspond to the average predicted overlap index keeping biomass density at the average; specifically, the dots and lines illustrate the median, 66% and 95% credible intervals based on draws from the expectation of the posterior predictive distribution. The vertical line is 0.6, which is often considered ecologically relevant. Panel B depicts violin and interval plots of the posterior distribution for the slope of biomass density on the mean of the beta distribution (points and horizontal lines depict the median and the 66% and 95% credible intervals). The area of the posterior that is positive (indicating the diet overlap increases with predator density) is filled with more transparent colors. Panel C depicts conditional predictions based on draws from the expectation of the posterior predictive distribution, the ribbon corresponds to the 95% credible interval, and color indicates predator overlap groups.

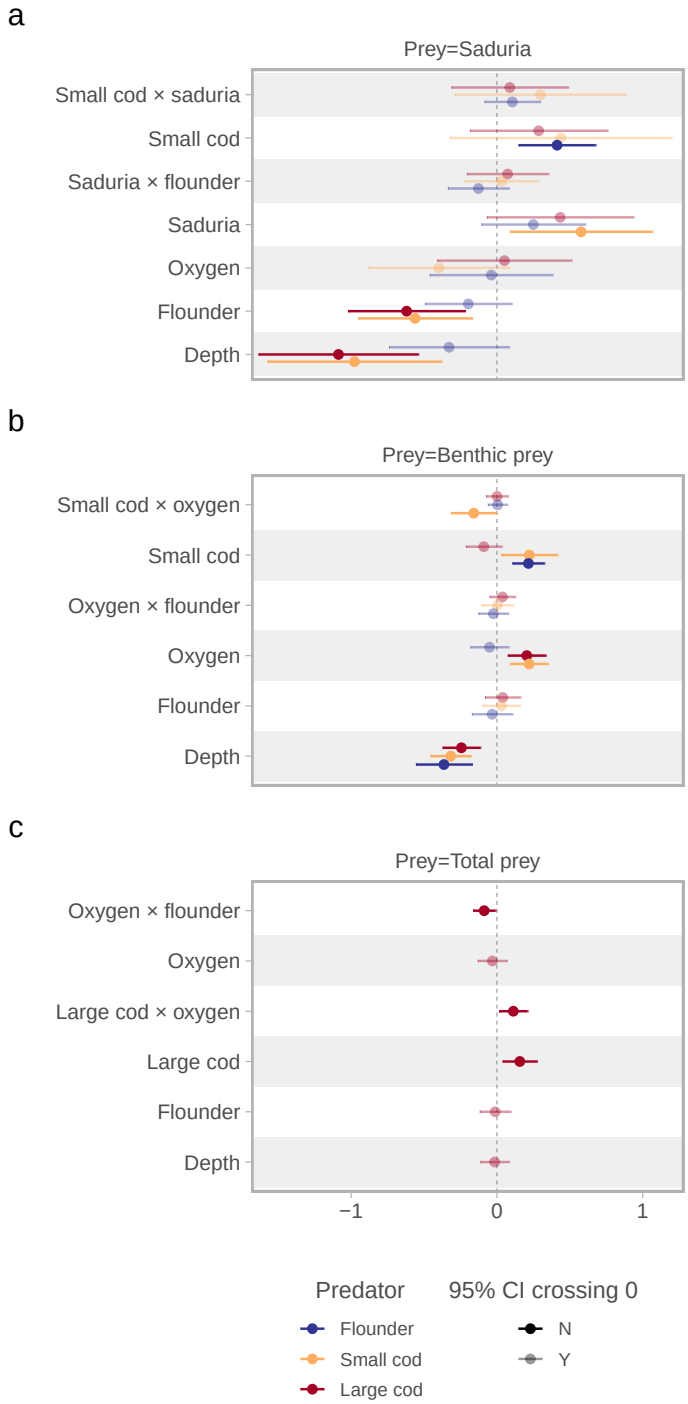

Figure 4: Standardized coefficients from the spatiotemporal generalized linear mixed model fitted to relative prey weights. Each panel represents a prey species (response variable), where saduria prey are shown in A, benthic prey in B and total prey in C, and the y-axis shows the predictor variable. Colors indicate group (predator species + life stage), and the transparency corresponds to the support (yes/no = Y/N) for the effect, such that semi-transparent points show estimates with 95% confidence intervals overlapping 0.

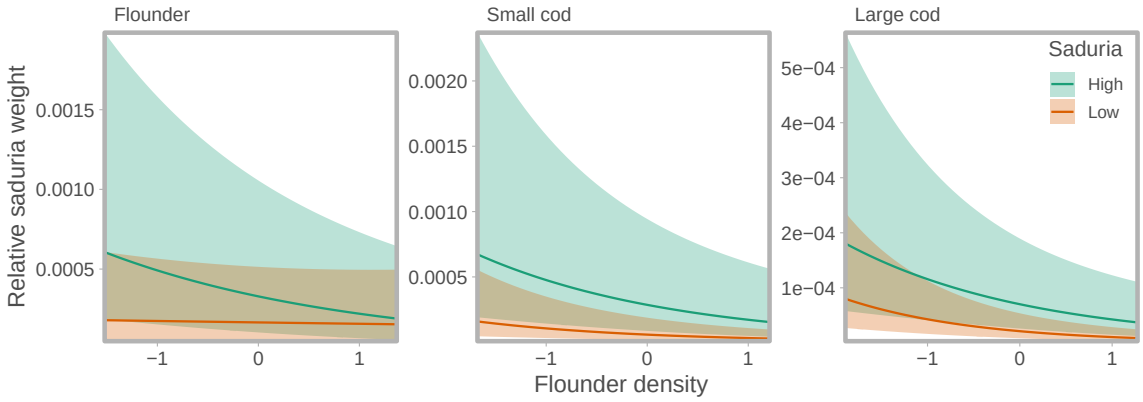

Figure 5: Conditional effect on the response scale of flounder density on the relative weight of *Saduria* in stomachs of flounder (left), large cod (middle) and small cod (right), for two levels of *Saduria*: high in green (95th percentile) and low in orange (5th percentile). All other covariates are held at their mean, quarter is set 1 and year is 2020, and random fields are set to 0. The ribbon corresponds to the 75% confidence interval, to illustrate differences between high and low *Saduria* conditions while still illustrating the uncertainty of the prediction. Note the different y-axes.