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Original Article

Reduced predation and competition from herring may have contributed to the increase of three-spined stickleback in the Baltic Sea

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Abstract

In many areas of the Baltic Sea, three-spined stickleback (*Gasterosteus aculeatus*) has increased several fold since the early 2000s. Two major planktivores of the Baltic Sea, Atlantic herring (*Clupea harengus)* and European sprat (*Sprattus sprattus*), may interact with stickleback via competition for food and predation, but the potential implications at the population level are still unknown. Here, we explored interactions between stickleback, herring, and sprat using (i) herring diet analyses and (ii) fish biomass estimates from hydroacoustics for 2001–2019 covering the largest Baltic Sea basins—the Central Baltic and the Bothnian Sea. The diet analyses revealed that stickleback is an important prey for large herring along the Swedish Baltic Sea coast, comprising up to 64% of the diet of individuals >22 cm. We found a negative influence of large herring (>18 cm) on stickleback in the Central Baltic, and a negative relationship between sprat and small herring (<18 cm) (pooled) and stickleback in the Bothnian Sea. The decline in herring and sprat population after the mid-1990s could have contributed to the increase in stickleback population via reduced predation and competition. Overall, herring may be an underappreciated piscivore, and high fishing pressure on herring could generate cascading effects on lower trophic levels.

Keywords: three-spined stickleback; Atlantic herring; sprat; Baltic Sea; temporal trends; species interactions; predation; competition

Introduction

Decades of ecological research have shown the importance of top-down control for ecosystem structure, functioning, and resilience (Duffy 2002, Hunsicker et al. 2011, Eriksson et al. 2024). The effects of top-down control often become evident after perturbations, such as those caused by anthropogenic impacts (Baum and Worm 2009). For example, human overexploitation of predator populations can relax the top-down control over populations of mesopredators (Daskalov et al. 2007, Estes et al. 2011), which may generate trophic cascades and alter the ecosystem structure and functions in such a radical way that they produce so-called “regime shifts” (Scheffer et al. 2001, deYoung et al. 2008). Competitive interactions are also a key process structuring natural communities (Morin 1999), where release from interspecific competition can lead to fast population expansion (Bolnick et al. 2010, Wiens et al. 2021).

The Baltic Sea ecosystem is structured with strong species interactions and has undergone both changes in environmental conditions and in the biological communities (Österblom et al. 2007, Casini et al. 2008, 2012, Bergström et al. 2016). A recent change in the Baltic Sea is the increase of the opportunistic mesopredator three-spined stickleback (*Gasterosteus aculeatus*), which is found in both coastal and offshore areas, and in the last two decades has become approximately 5 and 13 times more abundant in the Bothnian Sea and in the Central Baltic, respectively (Bergström et al. 2015, Olin et al. 2022). Stickleback abundances started to increase in the 1980s, and population growth rates accelerated in the 2000s, so that stickleback have reached remarkably high numbers in the north-western Central Baltic Sea and in the Bothnian Sea (see Olin et al. 2022 and references therein). Simultaneously, declines of several large predatory fish species have been observed, especially in the areas where stickleback densities have increased. In particular, populations of northern pike (*Esox lucius*) and, in some areas, European perch (*Perca fluviatilis*) known to prey on stickleback (Olin et al. 2022), have decreased along the coasts of the Central Baltic (Olsson 2019, Bergström et al. 2022, Olsson et al. 2023). The reduction of these predator fish populations could be partly responsible for the increase in stickleback population size, due to reduced top-down control (Eklöf et al. 2020, Olin et al. 2022). On the other hand, stickleback predates on the eggs and larvae of these predatory fishes (Nilsson et al. 2004, Bergström et al. 2015, Byström et al. 2015, 2019, Eklöf et al. 2020). When mesopredator species feed on the early life stages of their predators, this may trigger cultivation-depensation mechanisms, whereby the ecosystem becomes dominated by the prey and the recovery of the predator species is hampered by hysteretic responses (Liermann and Hilborn 2001, Gårdmark et al. 2014, Stier et al. 2016, Eklöf et al. 2020). Coastal areas of the Baltic Sea tend to be dominated either by predatory fish or by stickleback, and the stickleback-dominated state is expanding, causing a spreading regime shift (Eklöf et al. 2020). Furthermore, stickleback dominance tends to trigger a trophic cascade that benefits filamentous nuisance algae (Donadi et al. 2017), which in turn negatively affect habitat-forming vegetation by competing for light and nutrients (Baden et al. 2010).

While the effects of the stickleback increase on coastal ecosystems are well described, much less is known about how stickleback affect offshore ecosystems, particularly its interaction with the pelagic fish community of the Baltic Sea. Juvenile stickleback migrate offshore at the end of their first summer and return to coastal areas to spawn at 2–3 years of age, after which many die (Bergström et al. 2015). As sticklebacks spend most of their lives in the open sea, they may interact with the two dominating pelagic fish species of the Baltic Sea: Atlantic herring (*Clupea harengus*) and European sprat (*Sprattus sprattus*). All three species are planktivorous in the open sea and can show substantial diet overlap (Peltonen et al. 2004, Jakubavičiūtė et al. 2016, Ojaveer et al. 2017), although this may vary with time and area considered (Lankov et al. 2010, Novotny et al. 2022). However, a few studies suggest that herring is to some extent also piscivorous (Köster and Möllmann 2000, Corten 2013, Gagnon et al. 2021), and one study from the Bothnian Sea shows that large herring (>18 cm) predate on both stickleback larvae and juveniles during summer and autumn (Parmanne et al. 2004). Herring and sprat are the most important species for the Baltic commercial fisheries, and their status is assessed annually by the International Council for the Exploration of the Sea (ICES). Fishing mortality of herring and sprat has increased in the Baltic Sea in the last decades, sometimes exceeding the precautionary reference limit (ICES 2023). The herring stock has more than halved in the Central Baltic and the Bothnian Sea since the 1980s-1990s (Olin et al. 2022), and so did the sprat stock, which after an increase from the early 1990s, decreased again, and more so in the northern areas (Casini et al. 2011, Lindmark et al. 2023). Together, these findings suggest that the decline of herring and sprat populations could have released stickleback from (i) competition for shared food resources with small herring (i.e. the planktivorous life stage) and sprat, and (ii) top-down control from large herring (i.e. the potentially piscivorous life stage). Furthermore, a feedback loop may occur, where the stickleback increase could in turn contribute to a further decline in sprat and herring populations, via competition for food and/or predation on eggs and larvae (Casini et al. 2011, Kotterba et al. 2014, Olsson et al. 2019, Olin et al. 2022). A better understanding of how these species interact is needed for an effective management of clupeid stocks and marine ecosystems.

This study investigates the interactions between stickleback, herring, and sprat in the two main basins of the Baltic Sea, i.e. the Central Baltic Sea and the Bothnian Sea (Fig. 1). First, we collected and analyzed data on the diet composition of herring obtained from a field survey along the western coast of these basins, to evaluate the role of herring as a stickleback predator. Second, we explored the long-term trends (2000–2019) in stickleback, herring, and sprat biomasses across the Central Baltic Sea and the Bothnian Sea using data from a large, annual hydroacoustic survey, to determine whether the increases in the stickleback populations occurred before or at the same time of declines in herring and sprat populations. Third, by analyzing the spatiotemporal patterns in the same dataset, we evaluate the hypotheses that negative relationships occur between the biomass of large herring (>18 cm) and stickleback via predation (H1), and between the biomass of stickleback and the planktivorous clupeids, i.e. sprat and small herring (<18 cm), presumably acting via competition for food (H2). As herring and sprat are key target species for the Baltic Sea pelagic fishery, this study could contribute knowledge to support an ecosystem-based approach to fisheries management, both to prevent declines of valuable clupeid populations and to find successful strategies to counteract the stickleback increase and its adverse effects on the ecosystem.

Materials and methods

Herring stomach content analyses

Herring were sampled in 2020 from 18 sites along the Swedish coast of the Central Baltic Sea (ICES Subdivisions [SDs] 25, 27–29) and 9 sites from the coast of the Gulf of Bothnia (SD 30–31) (Fig. 1). Sampling was carried out in August to December 1st, when the spatial overlap between herring and juvenile stickleback is at its highest. In a local study at the Bothnian Sea coast, a shift from planktivory to piscivory was observed at approximately 18 cm length (Parmanne et al. 2004). For this reason, we aimed to collect at least 20–30 individuals <18 cm length (hereafter "small herring") and 20–30 individuals ≥18 cm (hereafter "large herring") at each site, although in some cases fewer were caught. Gillnets with mesh sizes 17–25 mm were used to target herring of the size classes of interest. Sampling was done in shallow (<10 m depth) coastal waters at dusk for a maximum of 2 hours. A total of 1513 individuals were collected: 189 in August (13%), 465 in September (32%), 305 in October (21%), 457 in November (31%), and 40 in December (3%) (for 57 individuals, the month of sampling was missing). All individuals per basin, regardless of the sampling site, contributed equally to the calculations. In total, we collected 957 individuals from the Central Baltic Sea and 556 from the Gulf of Bothnia. The fish were frozen as soon as possible after capture and stored until analysis. After thawing the samples, fish total length was measured, and the fish were assigned to different length categories representing potential shifts in diet composition (based on Parmanne et al. 2004): 154–179 mm (794 individuals), 180–219 mm (533 individuals), and 220–315 mm (186 individuals). Freezing can produce a shrinkage in body length; however, the percentage change is small (between 0.7% and 6.6% for herring, Blass 2015), and would not affect our results. Stomach content was sorted to the lowest possible taxonomic level, but is aggregated into broader taxonomic groups in the presentation of the results. Stomach fullness was estimated on a 5-level linear scale, and the relative volume of each taxon of the total was estimated by eye (Jacobson et al. 2019). Proportions in the diet are based on the relative volumes weighted by the stomach fullness of each individual. Frequencies of occurrence of stickleback in herring stomachs were calculated per herring size classes and basin. A total of 382 (25%) stomachs were empty.

Species biomass estimates

The data on fish biomasses were collected by the Baltic International Acoustic Survey (BIAS), which is performed yearly in September–October under the coordination of the Interna-

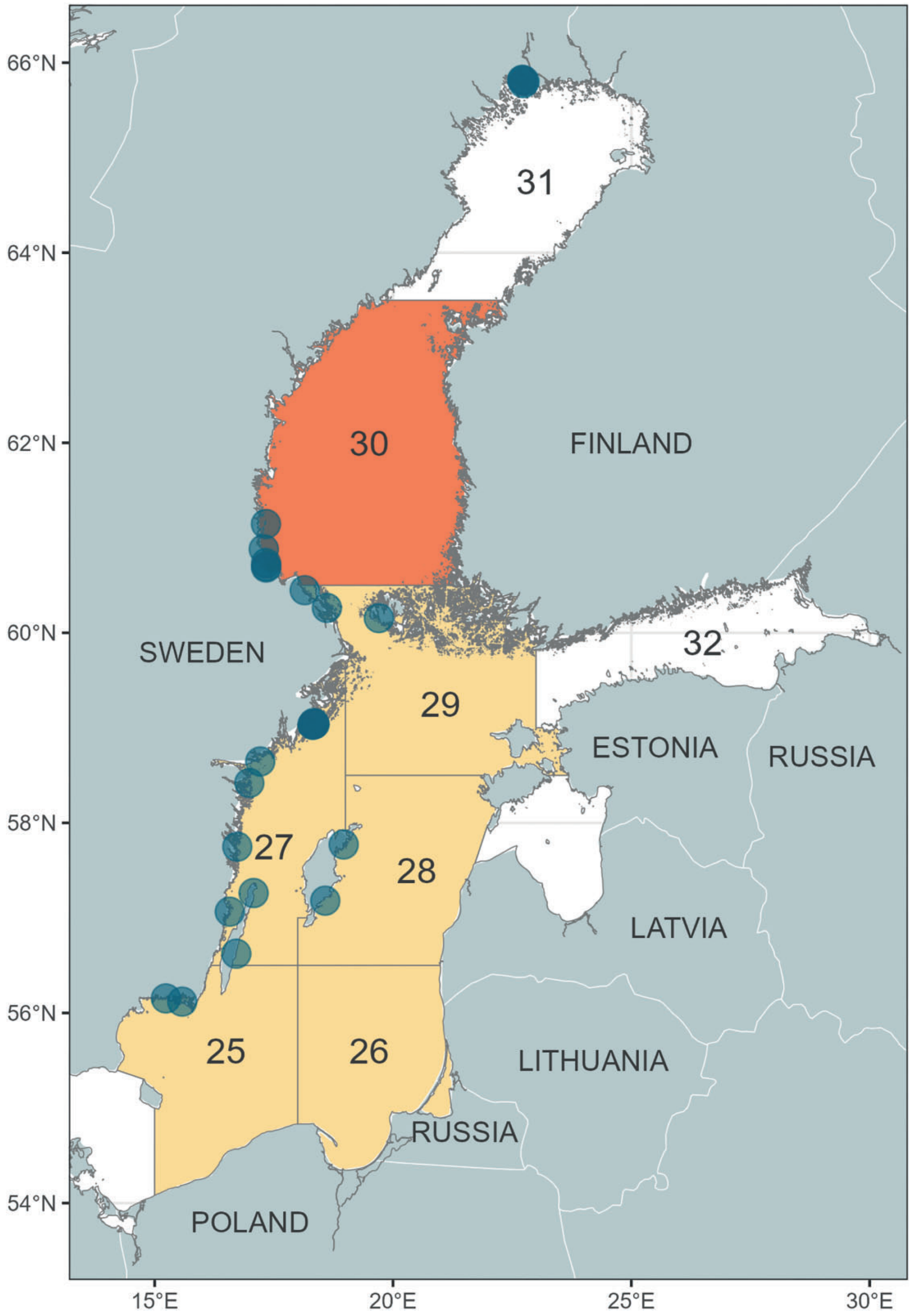

Figure 1. Map of the Baltic Sea. The numbers indicate ICES subdivisions (SD) included in the study. SD 30 corresponds to the Bothnian Sea, and SD 25–29 to the Central Baltic Sea. The dark circles indicate the approximate locations where herring were collected in 2020 for stomach content analyses (note that few sites were missing geographical coordinates).

tional Council for the Exploration of the Sea (ICES) (Table 1). Trawl hauls are performed by trained personnel on research vessels to reliably identify species and estimate size distributions. This information is then combined with hydroacoustic fish counts to estimate abundance and biomass of pelagic fish across the Baltic Sea. Biomass estimates of stickleback, herring, and sprat per year within spatial units of approximately 0.5 degrees in latitude × 1 degree in longitude (henceforth

Table 1. Time-series datasets included in the study.

Data	Basin	Time period	Owner/source
Herring biomass	Central Baltic	2001–2019	ICES
Herring biomass	Bothnian Sea	2007–2019	ICES
Sprat biomass	Central Baltic	2001–2019	ICES
Sprat biomass	Bothnian Sea	2007–2019	ICES
Stickleback biomass	Central Baltic	2001–2019	ICES
Stickleback biomass	Bothnian Sea	2007–2019	ICES
Landings herring	Both	2003–2015	STECF
Landings herring	Both	2016–2019	JRC
Landings sprat	Both	2003–2015	STECF
Landings sprat	Both	2016–2019	JRC
Temperature, salinity, nutrients	Both	2001–2019	Copernicus Marine Service Information

Data are given per year and ICES statistical rectangle.

known as "ICES statistical rectangle") were available from 2001 in the Central Baltic and from 2007 in the Bothnian Sea. Fish biomass calculations for the Bothnian Sea in 2007–2019 and for the Central Baltic in 2014–2019 were made using the StoX software (version 2.7) and the disaggregated BIAS data available in the ICES database for acoustic and trawl surveys (https://www.ices.dk/data/data-portals/Pages/acoustic.aspx), according to the method developed by the Working Group on Baltic International Fish Survey (WGBIFS) (ICES 2021). Few rectangles had acoustic data but lacked trawl samples and were therefore excluded from calculations (i.e. in the Bothnian Sea: one rectangle in 2007, two in 2008, and one in 2016; in the Central Baltic: seven rectangles in 2014, due to bad weather, one in 2015, three in 2016, five in 2017, nine in 2018, due to gear failure, and two in 2019). Due to a lack of disaggregated BIAS data for the Central Baltic in 2001–2013, sprat and herring biomass estimates were extracted from the ICES WGBIFS access database for aggregated BIAS data ("BIAS_DB.mdb") (ICES 2021), while stickleback biomass estimates were obtained from the BIAS data including only Swedish areas (Olsson et al. 2019). Total biomass of stickleback, herring, and sprat per year and ICES statistical rectangle were divided by the water area of the respective rectangle at 10 m depth to obtain yearly estimates of biomass per square nautical mile (nmi^2).

Abundance and biomass of herring were calculated separately for each herring length-class in each ICES rectangle. This was done by splitting total abundance of herring into length-classes based on the information on herring length distributions from the trawl hauls (all trawl hauls inside a specific rectangle were given equal weight in the calculation process). Biomass of each length-class was then obtained by multiplying abundances by the mean weight of the corresponding length-class. Abundance and biomass of herring belonging to length-classes below and above (or equal to) 18 cm were summed up to represent small and large herring, respectively. To be able to investigate temporal trends, we excluded ICES statistical rectangles that were only sporadically sampled, so that the final dataset contained rectangles that were sampled a minimum of 8 years (maximum: 19 years, median: 15 years). Also, we ensured that the data were collected within approximately the same time interval across ICES statistical rectangles, i.e. 2001–2019 in the Central Baltic, and 2007–2019 in the Bothnian Sea. The rectangles included were fairly constant over time (Figs S1–S4), and covered almost the whole spatial extent of the Bothnian Sea and the Swedish part of the Central Baltic (i.e. the western rectangles). The spatial replication of our data was 20 ICES statistical rectangles for the Bothnian Sea and 30 ICES statistical rectangles for the Central Baltic, which with repeated surveys across years made up a total number of 253 replicates for the Bothnian Sea, and 515 replicates for the Central Baltic (504 for large and small herring biomass due to missing data for this species).

Fisheries landings data

Commercial landings of herring and sprat expressed as tons per ICES statistical rectangle were provided by the Scientific, Technical, and Economic Committee for Fisheries (STECF, https://stecf.jrc.ec.europa.eu/dd/effort/graphs-quarter) for the years 2003–2015, and by the Joint Research Centre (JRC, https://jeodpp.jrc.ec.europa.eu/ftp/jrc-opendata/FAD/fdi2020/) for the years 2016–2019 (Table 1). Data for 2001–2002 were not publicly available and therefore not included in the analyses of fishing pressure effects (see section *Multiple regressions of biomass of stickleback and clupeids)*. Herring in the Baltic Sea form several genetically and behaviorally distinct populations, which can differ in migration and spawning patterns, or diet (Lamichhaney et al. 2012, Barrio et al. 2016). Hence, different herring populations are to a large extent spatially separated from each other, and we assumed that landings reported in each basin were representative of the local stocks, in accordance with the analytical stock assessments performed by ICES.

Hydrographic data

Data on water temperature, salinity, and nutrient concentrations for the period 2001–2019 for each ICES statistical rectangle were extracted from Copernicus Marine Service Information (Table 1). The nutrient concentration data were produced using the biogeochemical model ERGOM one-way online coupled with the ice-ocean model system NEMO (doi.org/10.48670/moi-00012). The salinity and temperature data were produced by DMI (Danmarks Meteorologiske Institut) using NEMO (doi.org/10.48670/moi-00013). All variables were averaged over two depth intervals, 0–20 m and 0–100 m depth, as stickleback are usually found in the surface waters while herring and sprat utilize a broader depth span (Peltonen et al. 2004). The average value of the whole water column was used in cases when water was less than 20 m depth or <100 m depth for the two depth intervals. Temperature and salinity can show large seasonal variations, and while summer is the main feeding and growth season of Baltic clupeids (Casini et al. 2006), the availability and abundance of zooplankton species during summer can be controlled by hydro-climatic factors during the preceding winter and spring (Dippner et al. 2000, Dippner 2001). Moreover, clupeids reproduce from late winter to summer in the Baltic Sea, and winter conditions can affect the gonad development, while summer conditions can affect the eggs and larvae survival. Hence, we estimated separate temperature and salinity averages for summer (April–September) and winter (October–March). Concentrations of nitrate, ammonium, and phosphate (nmol/m^3) were estimated for the period October–March, as nutrient concentrations during the winter season reflect available nutrients for primary production.

Time series analyses of biomasses

We analyzed temporal trends in biomasses of stickleback, sprat, small herring, and large herring using generalized additive models (GAMs), which allow fitting non-linear trends of response variables. We calculated the average biomasses for each year for the two basins (i.e. pooling the values from all ICES statistical rectangles in the same basin), and used them as response variables. For each species (and size class in the case of herring), we used the following model formulation:

$$\text{Biomass}_{Basin,\,Year} = \alpha + \text{f}_{Basin}\,(\text{Year}) + \varepsilon_{Basin,\,Year}$$

where α is an intercept, f_{Basin} is a smoothing function of year, and $\varepsilon_{Basin,\,Year}$ is the unexplained variation. Preliminary data exploration showed that the temporal trends of the species in general differed between the Central Baltic and the Bothnian Sea, and we therefore allowed the temporal trend to differ by basin (as indicated by the index *Basin*). To model the curve for the term year, we used cubic regression splines (a smoother that fits third-order polynomials on segments of data) and cross-validation to estimate the optimal level of smoothing (Wood 2017). Temporal autocorrelation was null or negligible, as revealed by the comparison of models with and without temporal residual autocorrelation structures ($\Delta\text{AIC} < 2$). This is expected with highly mobile species, suggesting that replicates can be considered to be statistically temporally independent. To accommodate for some degree of heteroscedasticity, a Tweedie error distribution with a log link function was used when modeling sprat biomass. Model diagnostics were performed by visual inspection of residuals versus fitted values and histograms of model residuals (Fig. S5).

Multiple regressions of biomass of stickleback and clupeids

To test our hypotheses regarding interactions between stickleback and clupeids, we used generalized least squares models, which extend linear regression by modeling residual autocorrelation with temporally or spatially dependent data. We constructed two models. Model 1 tested the first hypothesis, i.e. the occurrence of negative effects of large herring on stickleback, presumably acting via predation, and part of the second hypothesis, i.e. the occurrence of negative effects of planktivorous clupeids (sprat and small herring) on stickleback, presumably acting via competition for food. Model 2 tested the complementary hypothesis that stickleback could have negative effects on planktivorous clupeids, also because of competition for food. This set-up allowed us to account for species-specific drivers (abiotic factors and landings) affecting stickleback (Model 1) or planktivorous clupeid biomass (Model 2). Analyses were carried out separately for the Central Baltic and the Bothnian Sea, as the two basins differ substantially in environmental conditions, and as the herring stocks are managed separately. Model 1 was run using the full dataset ($N = 253$ and 515 for the Bothnian Sea and Central Baltic, respectively). However, due to missing commercial catch data and biomass of large and small herring, the number of replicates for Model 2 was smaller ($N = 207$ and 448, respectively).

In Model 1, the response variable was total stickleback biomass and the explanatory variables were the biomass of large herring and the pooled biomass of sprat and small herring. Stickleback abundance has been suggested to be favored by higher temperatures (Lefébure et al. 2014, Lajus et al. 2020, 2021), and a higher nutrient load (Oksanen et al. 1981, Eriksson et al. 2021), and we therefore included temperature (one of summer or winter) and nitrate, ammonium, and phosphate concentrations, all estimated at 0–20 m, as covariates in the models.

In Model 2, the response variable was the pooled biomass of sprat and small herring, and the explanatory variable was the biomass of stickleback. We included the commercial catch data of herring and sprat (pooled) as a covariate, as well as all alternative combinations of temperature (one of summer or winter), salinity (one of summer or winter), as well as nitrate, ammonium, and phosphate concentrations, all estimated at 0–100 m.

We initially constructed several alternative models with all combinations of the described abiotic variables (again, for salinity and temperature, only including either summer or winter values in the model), and determined our best models based on the following criteria (Tables S1–S3):

(i) exclusion of collinear abiotic variables, based on the variance inflation factor (VIF) of each predictor (using a threshold value of 4)
(ii) parsimony, assessed by comparing AICc scores
(iii) ecological criterion (the direction of the effect is supported by previous ecological knowledge).

To verify the robustness of our findings regarding species interactions and acknowledge that we do not have a perfect understanding of the functioning of the ecosystem, we also examined the results of the best models after ignoring the ecological criterion (see sectio "Results").

A Gaussian spatial correlation gave the largest improvement in model fit compared to alternative types of residual spatial and temporal autocorrelation structures, and was therefore included in the final models. Biomasses were 4th root transformed to improve distributional properties, minimize heterogeneity of variance, and meet model assumptions, as confirmed by plots of residuals versus fitted values, and histograms of residuals (Figs S6 and S7). The significance of predictors was determined through a stepwise backward elimination method, where nested models were compared via a likelihood ratio test (LRT), which approximately follows a chi-square distribution (Zuur et al. 2009). All analyses were conducted in R Statistical Software version 4.2.0 (R Development Core Team 2020). We used the *mgcv* package (version 1.8–40) for specifying, fitting, and visualizing the GAMs (Wood 2011), and the *nlme* package (version 3.1–162) for fitting generalized least square models (Pinhero et al. 2016).

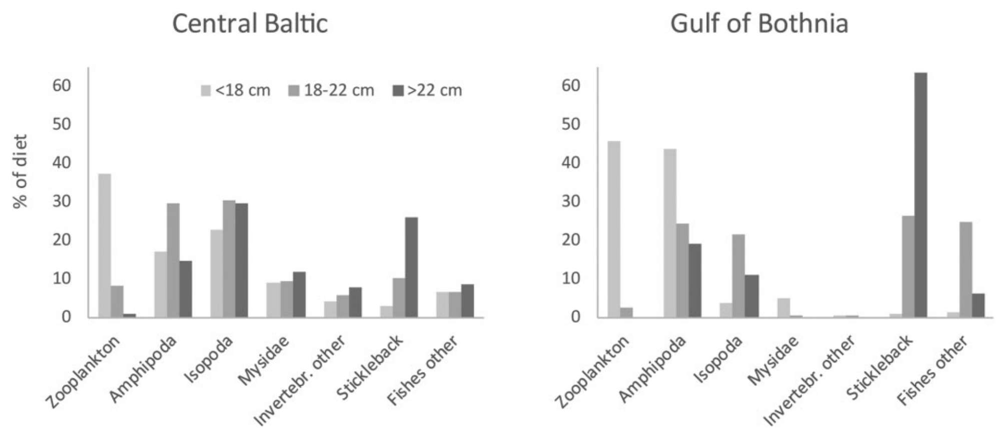

Figure 2. Diet of herring in the coastal zone of the Central Baltic Sea ($N = 957$) and the Gulf of Bothnia ($N = 556$), based on stomach content data collected August–November 2020. The relative volume of each taxon of the total stomach volume is shown for each of the three size groups.

Results

Stomach content results

We found a large difference in the diet of herring from the different size classes (Fig. 2). For individuals <18 cm, the diet was dominated by zooplankton, followed by amphipods and isopods. In contrast, herring ≥18 cm relied almost fully on large benthic crustaceans and fish, with the proportion of fish increasing with herring size. The proportion of fish in the diet was notably higher in the Bothnian Sea than in the Central Baltic. Stickleback was the main species of fish prey, constituting on average 10% and 27% of the diet of 18–22 cm herring in the Central Baltic and the Gulf of Bothnia, respectively, and 26% and 64% of the diet of herring >22 cm. A similar pattern was found when looking at the frequencies of occurrence of stickleback in herring stomachs (i.e. the proportion of herring that had eaten stickleback): 7% (32 individuals) and 27% (19 individuals) of 18–22 cm herring in the Central Baltic and the Gulf of Bothnia, respectively, and 18% (29 individuals) and 48% (13 individuals) of herring >22 cm. Most of the stickleback in the stomachs were young-of-the-year (24 ± 5.9 mm; mean ± SD), with around 1% of the stickleback prey being older/larger individuals.

Spatial patterns of species biomass

The biomass of small herring was generally higher in the Bothnian Sea than in the Central Baltic, often reaching values ≥ 30 tons/nmi^2 (Fig. S1). Sprat biomass was instead higher in the Central Baltic, especially in the northeastern part (SD 28–29, Fig. S2). Sprat was largely absent from the Bothnian Sea, which can be explained by the salinities being too low for successful spawning (HELCOM 2021)). The spatiotemporal distribution of large herring biomass was variable, with peak values in the southern part of the Central Baltic between 2011 and 2015, and relatively high biomasses in the northern and western Bothnian Sea across the time series (Fig. S3). Stickleback biomass increased several fold (see next section) across the study period in both the Central Baltic and the Bothnian Sea, showing the highest values, among those recorded in our dataset, in the northern part of the Central Baltic (SD 27–28) and in the Bothnian Sea (Fig. S4).

Temporal trends in species biomass

Stickleback biomass has increased substantially over time both in the Bothnian Sea ($p = 0.008$) and in the Central Baltic ($P < 0.001$) (Fig. 3a, explained deviance = 50.2%). Model estimates of average values went from 1.3 tons/nmi^2 in 2007 (SE = 0.90) to 5.6 tons/nmi^2 in 2019 (SE = 0.92) in the Bothnian Sea, showing a 4.3-fold increase over 13 years. In the Central Baltic, stickleback biomass increased from a model-estimated average value of 0.5 tons/nmi^2 in 2001 (SE = 0.78) to 6.5 tons/nmi^2 in 2019 (SE = 0.78); a 13-fold increase.

The temporal trend of large herring biomass followed a hump-shaped pattern in the Central Baltic ($P < 0.001$), with an estimated peak value of 18.3 tons/nmi^2 in 2013 (SE = 1.51), followed by a sharp 81% decline to 3.4 tons/nmi^2 in 2019 (SE = 2.29) (Fig. 3b, explained deviance = 73.8%). There was, however, no statistically significant temporal trend in the Bothnian Sea ($P = 0.213$).

Small herring biomass decreased by 26% between 2007 and 2019 in the Bothnian Sea ($P = 0.006$), from an estimated average of 29.8 tons/nmi^2 in 2007 (SE = 3.02) to 22.1 tons/nmi^2 in 2019 (SE = 3.12) (Fig. 3c, explained deviance = 43.6%). In the Central Baltic, however, we found no evidence of a temporal change ($P = 0.136$).

Finally, the biomass of sprat also decreased in the Bothnian Sea ($P < 0.001$), from an estimated average of 5.7 tons/nmi^2 in 2007 (SE = 1.32) to values close to zero in 2019 (Fig. 3d, explained deviance = 92.6%). In the Central Baltic, the temporal trend of sprat biomass showed two peaks followed by declines ($P < 0.001$). The first and higher peak occurred in 2003, when sprat biomass reached an estimated average value of 31.1 tons/nmi^2 (SE = 1.15). Then sprat biomass declined sharply to 14.1 tons/nmi^2 in 2010 (SE = 1.16), increased again reaching a second peak of 20.6 tons/nmi^2 in 2015 (SE = 1.16), and then declined to 16 tons/nmi^2 in 2019 (SE = 1.28).

Relationships between stickleback, herring, and sprat

We found evidence of a negative effect of large herring biomass on stickleback biomass in the Central Baltic (Fig. 4a), but not in the Bothnian Sea, and a negative relationship between the biomass of sprat and small herring and the biomass of stickleback in the Bothnian Sea (Figs 4c and 5a), but not in the Central Baltic (Table 2).

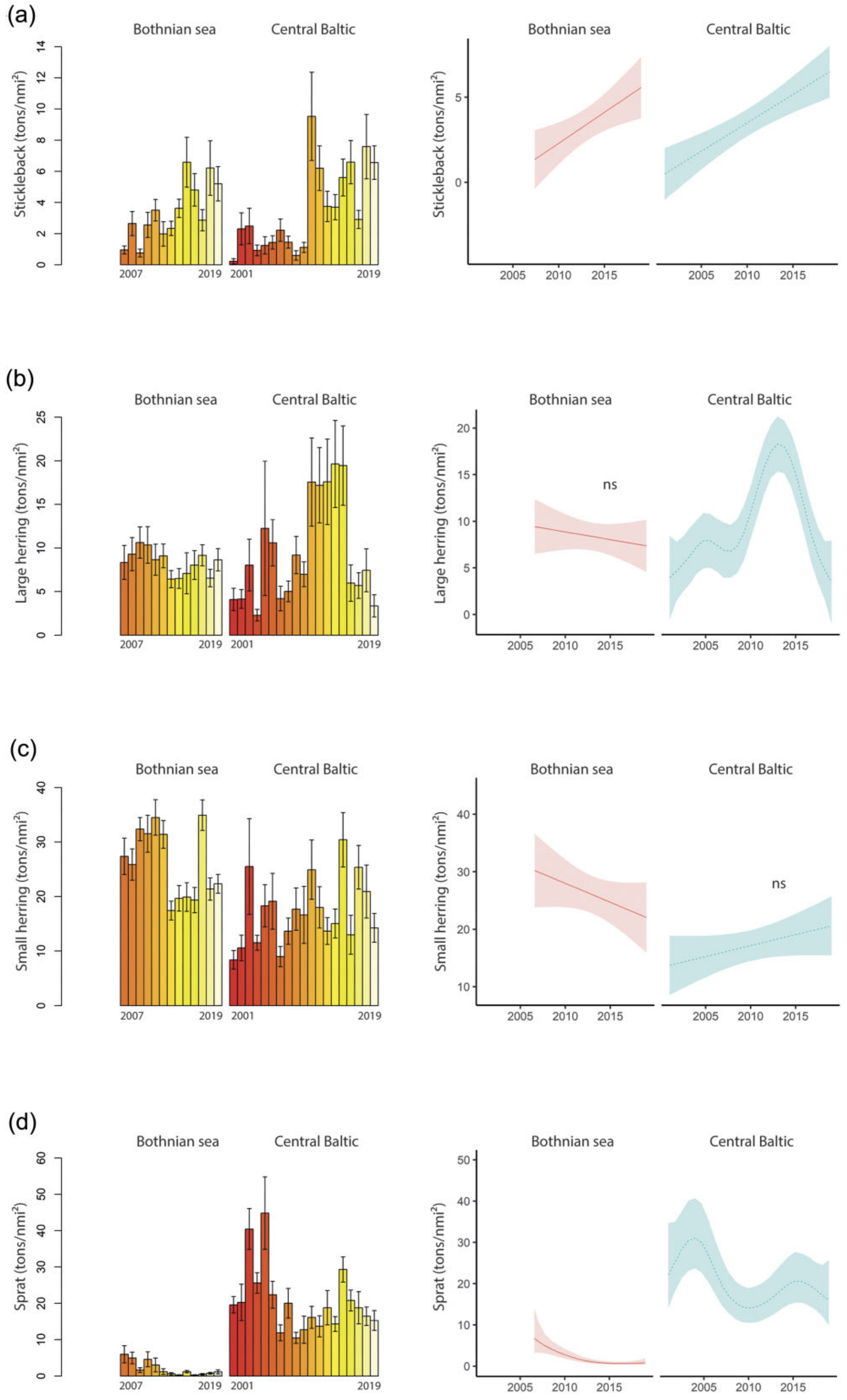

Figure 3. Barcharts of average biomasses per year (left column), and temporal trends as predicted by the generalized additive models (right column) for (a) stickleback, (b) small herring (<18 cm), (c) large herring (>18 cm), and (d) sprat for the period 2001–2019. Standard errors around the mean values are shown in the barcharts. Shaded regions around the smoothers represent 95% confidence bands.

Model 1 estimated that a 1 ton/nmi^2 decrease in large herring biomass could produce an increase in stickleback biomass of 0.16 ton/nmi^2 in the Central Baltic (model predictions performed while holding all the other significant variables at their medians). The model also suggested that a 1 ton/nmi^2 decrease in sprat and small herring biomass (pooled together) could produce a 0.29 ton/nmi^2 increase in stickleback biomass in the Bothnian Sea. The final models explaining stickleback

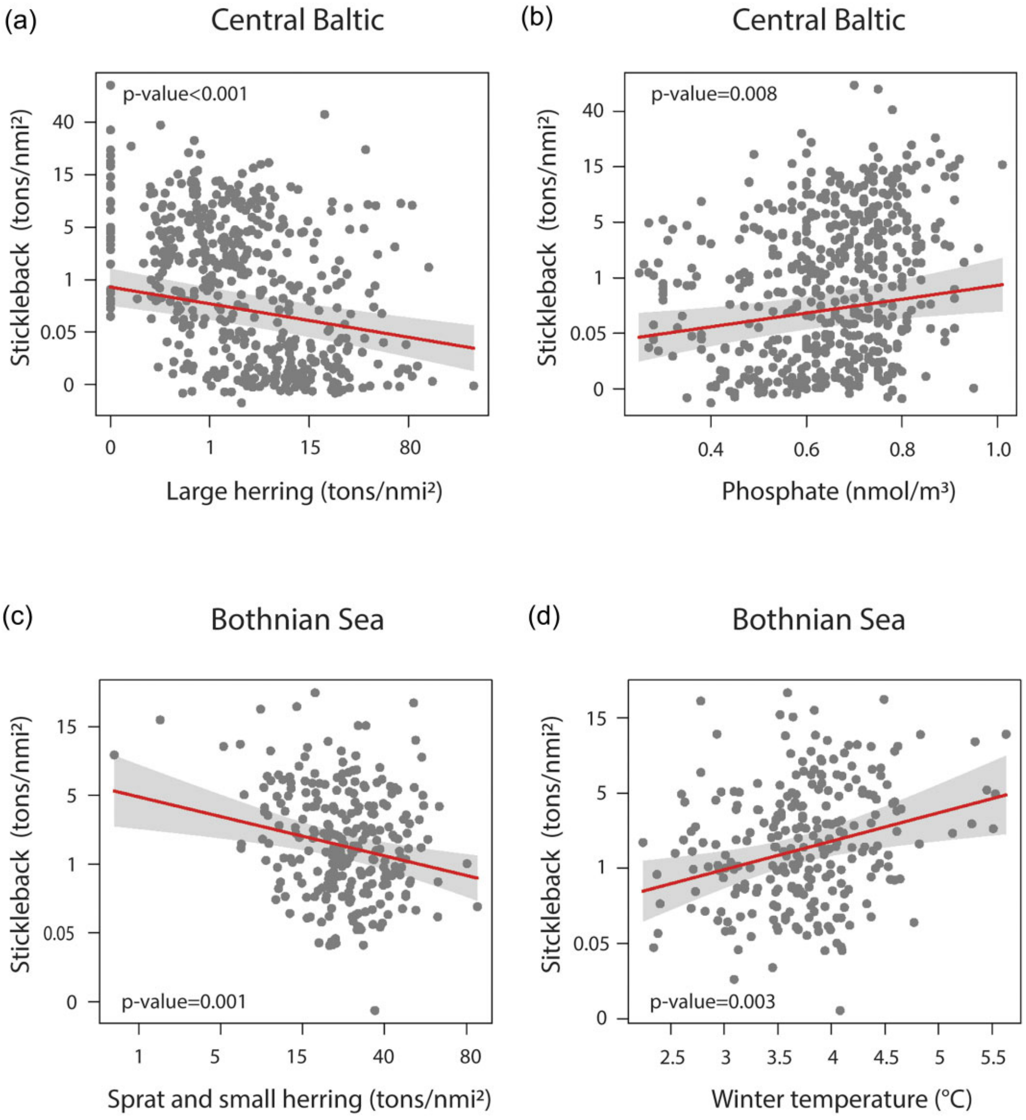

Figure 4. Effects on stickleback biomass of (a) large herring biomass (*P*-value < 0.001) and (b) phosphate (*p*-value $= 0.008$) in the Central Baltic, and (c) sprat and small herring biomass (*P*-value $= 0.001$), and (d) winter temperature (*P*-value $= 0.003$) in the Bothnian Sea, as predicted from Model 1. Gray dots are partial residuals and red lines are partial regression lines, with shaded areas representing 95% confidence intervals. Model predictions were performed while holding all the other significant variables in the model constant at values corresponding to their medians. Note the power scale on the y axes for stickleback biomass (a–d), and on the x axes for large herring (a), and sprat and small herring biomasses (c).

biomass (Model 1) in the Central Baltic and in the Bothnian Sea had R^2-values of 0.57 and 0.31, respectively, and also included significant positive effects of phosphate in the Central Baltic (Table 2, Table S1, Fig. 4b) and winter temperature (which always had higher explanatory power than summer temperature) in the Bothnian Sea (Table 2, Table S1, Fig. 4d).

Model 2, which tested the effect of increased competition from stickleback on sprat and small herring, suggested that a 1 ton/nmi^2 increase in stickleback biomass in the Bothnian Sea could produce a 0.15 ton/nmi^2 decrease in sprat and small herring biomass. The final models explaining sprat and small herring biomass (Model 2) in the Central Baltic and in the Bothnian Sea had R^2-values of 0.22 and 0.29, respectively, and included a positive effect of summer temperature (which outperformed winter temperature) in the Bothnian Sea (Table 2, Table S2, Fig. 5b), but no effects of abiotic covariates in the Central Baltic (Table 2, Table S3). Commercial fishery landings of herring and sprat did not have statistically significant effects on sprat and small herring biomass in either basin.

When identifying the best models, we excluded a large part (between 75% and 93%) of the alternative models where no collinearity was detected because they did not meet the ecological criterion, i.e. they included abiotic effects that did not agree with previous knowledge (Tables S1–S4). Counterintuitive relationships included negative effects of nitrate and ammonium on stickleback biomass, negative effects of winter temperature on stickleback biomass in the Central Baltic, a negative effect of phosphate on the biomass of sprat and small herring in the Bothnian Sea, and a negative effect of winter salinity on the biomass of sprat and small herring in the Central Baltic (Table S4). However, the negative relationships between species identified by the best models discussed above were consistently supported even when we did not apply the ecological criterion (Tables S1–S4). Negative reciprocal effects

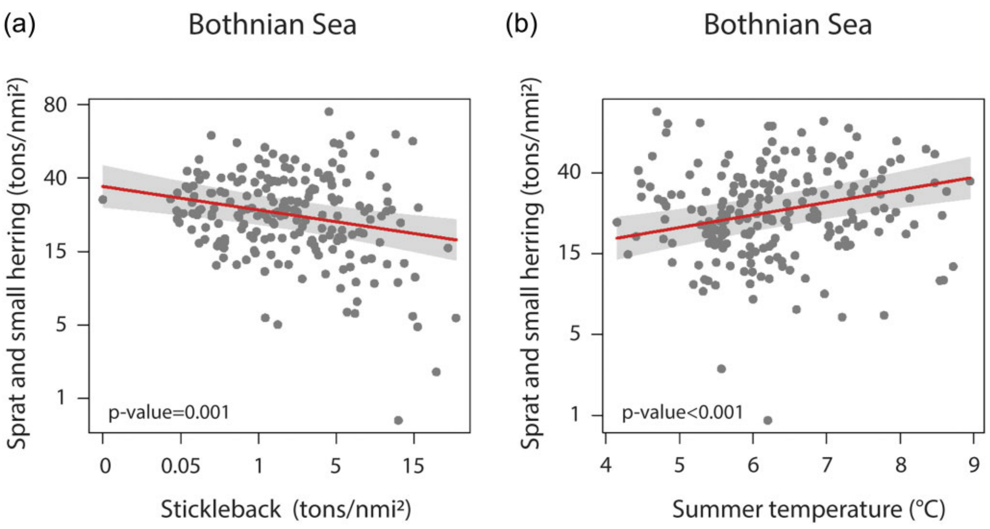

Figure 5. Effects on sprat and small herring biomass of (a) stickleback biomass (*P*-value = 0.001) and (b) summer temperature (*P*-value < 0.001) in the Bothnian Sea, as predicted from Model 2. Gray dots are partial residuals and red lines are partial regression lines, with shaded areas representing 95% confidence intervals. Model predictions were performed while holding all the other significant variables in the model constant at values corresponding to their medians. Note the power scale on the y axes for sprat and small herring biomass (a–b), and on the x axes for stickleback biomass (a).

Table 2. Coefficients and standard errors of the significant factors included in the final models.

Model 1: stickleback biomass ∼ large herring biomass + sprat and small herring biomass + temperature + nutrients

	LRT	*P*-value	Estimate	SE
Bothnian Sea				
Intercept			1.07	0.330
Sprat + small herring biomass	10.74	0.001	− 0.29	0.087
Winter temperature (0–20 m)	8.70	0.003	0.19	0.064
Central Baltic				
Intercept			0.51	0.167
Large herring biomass	19.99	<0.001	− 0.16	0.034
Phosphate (0–20 m)	7.01	0.008	0.62	0.234

Model 2: sprat and small herring biomass ∼ stickleback biomass + landings herring and sprat + temperature + nutrients + salinity

	LRT	*P*-value	Estimate	SE
Bothnian Sea				
Intercept			1.96	0.144
Stickleback biomass	13.13	0.001	− 0.16	0.045
Summer temperature (0–100 m)	15.47	<0.001	0.08	0.018
Central Baltic				
Intercept			2.32	0.057

LRT and *P*-values are given. "0–20m" and "0–100m" between brackets indicate depth intervals.

between stickleback and planktivorous clupeids were still evident in the Bothnian Sea (Table S4). Furthermore, the negative effect of large herring on stickleback biomass was significant not only in the Central Baltic, but also in the Bothnian Sea (Table S4).

Discussion

Our results support the idea that important interactions may occur between three-spined stickleback and clupeids, potentially affecting the dynamics of their populations in the Baltic Sea. Different lines of evidence, i.e. stomach content data, time series analyses, and multiple regression modeling, together point to the role of herring as an underappreciated piscivore, and a potential important predator on stickleback. We found evidence of a negative association between the biomass of large herring and the biomass of stickleback in the Central Baltic, and possibly also in the Bothnian Sea. In the Bothnian Sea, we also found negative relationships between the biomass of stickleback and the biomass of sprat and small herring, which could be the result of competition for food. As such, there was some support for both our hypotheses, that predation by large herring could affect stickleback populations (H1), and that there is competition between stickleback and sprat and small herring (H2). The estimated effect sizes of these interactions were however moderate, suggesting that other factors, such as direct and indirect effects of abiotic conditions, and/or changes in the coastal food web (see below) are important for the dynamics of both clupeids and stickleback populations.

The diet analyses showed that large herring includes a substantial proportion of fish in their diet along the Swedish Baltic

Sea coast. The main fish prey species was three-spined stickleback, and especially the largest herring, those over 22 cm in length, included a large proportion of stickleback in their diet (Fig. 2). The proportion of fish prey was higher in the Gulf of Bothnia than in the Central Baltic, likely reflecting different availability of coastal benthic crustaceans (amphipods, isopods, and mysids) in the environment (Nohrén et al. 2009)). A previous study of herring diet in the coastal zone of the Bothnian Sea (Parmanne et al. 2004) also showed that fish constituted the main prey for herring over 18 cm length. In that study (conducted in 1987–1992), young-of-the-year herring was by far the dominating prey, but stickleback was also eaten. In another study conducted in a shallow lagoon in the Baltic Sea in the falls of 2010–2012, the authors also found fish, although mainly demersal species, in the stomachs of herring (Kotterba et al. 2024). These studies thus also suggest that herring may be an important piscivore in the Baltic Sea. While Parmanne et al. (2004) only found high densities in one location at one time point, our results show that stickleback is currently the most common prey fish of larger herring along the Swedish Baltic Sea coast in autumn. This suggests that a shift in fish prey composition of large herring may have taken place with the increase in the Baltic Sea stickleback population, although data from more years and locations are needed to confirm the generality of our findings.

So far there is no evidence that stickleback is included in the diet of herring in the offshore Baltic Sea (Casini et al. 2004, Peltonen et al. 2004, Lankov et al. 2010, Jakubavičiūtė et al. 2016, Ojaveer et al. 2017, Novotny et al. 2022). This could potentially be a consequence of vertical separation, i.e. stickleback reside in surface waters while larger herring mostly stay in deeper waters in the open sea (Jurvelius et al. 1996, Olsson et al. 2019). However, we found that in the BIAS surveys generating the data of this study, herring and stickleback were often caught together (i.e. all acoustic targets were classified as mixed in the echogram, and the allocation of biomass to different species was done according to species relative abundances estimated from the trawl hauls). As such, it seems as if herring in the open sea prefer to feed on zooplankton even though they co-occur with stickleback, and that the predation on stickleback instead takes place mainly in the coastal zone during autumn, when densities of young-of-the-year stickleback that are migrating towards the open sea are high. This likely means that the offshore biomass data that we used to investigate the potential negative effects of large herring on stickleback are not ideal for capturing a predation effect (and may contribute to the modest effect size; see above). That we still identified a negative association between stickleback and large herring may indicate that the biomasses measured in ICES statistical rectangles in the open sea are still to some extent representative of interactions taking place at the nearby coast (i.e. the large herring and stickleback co-occurring in a given rectangle would also co-occur at the coast). Further studies are thus still needed to quantify the effect of herring predation on stickleback recruitment in relation to other drivers.

Densities of large herring in the Bothnian Sea remained stable over the study period, while densities in the Central Baltic peaked in 2013 to then drop by ca. 80% in 2019 (Fig. 3b). These patterns are in line with those reported by the stock assessment (ICES 2022, 2023), even though our dataset sporadically missed a few ICES statistical rectangles and did not cover the whole Swedish Central Baltic. Meanwhile, stickleback populations continued to increase both in the Bothnian Sea and the Central Baltic (Fig. 3a). Importantly, our dataset was collected *after* large declines in the herring stock from peak densities in the 1990s (Bothnian Sea) and the 1980s (Central Baltic), which preceded the stickleback increase (Olin et al. 2022). The observed, opposite trends in large herring and stickleback densities, combined with the results from the diet analyses and the multiple regression modeling, suggest that reduced predation from large herring could be contributing to (but that it is not the sole driver of) the ongoing stickleback increase. Further, in recent years (2021–2022), there has been a more pronounced drop in the densities of large herring (ICES 2022, 2023), which is not captured by our dataset (where the most recent year is 2019) that could have benefited the stickleback further.

Our results also provide some evidence that small herring, together with sprat, compete with stickleback in the open sea. The negative relationships between the biomass of stickleback and the biomass of sprat and small herring in the Bothnian Sea could be explained by two mechanisms. It could represent an effect of competition for food manifested as poor growth and/or increased mortality, and/or it could represent an avoidance effect manifested as spatial separation. Several studies indicate a high degree of diet overlap between these three species, supporting the hypothesis that competition for food may occur (Peltonen et al. 2004, Jakubavičiūtė et al. 2016, Ojaveer et al. 2017; but see Lankov et al. 2010;, Novotny et al. 2022). Furthermore, we observed from survey echograms that at night time most fish biomass was close to the sea surface (between 10 and 30 m depth), where the three species mixed, as showed by the trawl hauls. This is in line with knowledge from literature, showing that, especially during the season of intensive feeding, herring and sprat perform extensive diurnal vertical migrations, and at nighttime they may co-occur with stickleback at the same depth (Jurvelius et al. 1996, Cardinale et al. 2003, Nilsson 2003). In light of this evidence, we suggest that direct competition for food resources could be the driver explaining the observed negative association between the biomass of stickleback and the biomass of sprat and small herring.

We also found support for fairly strong relationships with abiotic drivers (see section "Methods" for motivations), including a positive effect of winter temperatures on stickleback biomass in the Bothnian Sea, a positive effect of phosphate concentrations on stickleback biomass in the Central Baltic, and a positive effect of summer temperatures on the biomass of sprat and small herring in the Bothnian Sea. Only in the case of the positive effect of phosphate concentrations was the effect size larger than that of the interacting species. When not applying the ecological criterion and including abiotic drivers, whatever the direction of the effect, the results pointed to some counterintuitive relationships, such as negative effects of nutrients on clupeids and stickleback biomass, of salinity on clupeids biomass, and of temperature on stickleback biomass (Table S4). While these may represent spurious correlations, they could also point to interesting dynamics worth examining further. At extreme levels, nutrient load can result in deteriorated habitat conditions and increased fish mortality (Rodgers 2021); however, this is unlikely the case for the Baltic Sea. Instead, nutrient load is suggested to increase fish biomass (Eero et al. 2016, Bossier et al. 2021). Moderate eutrophication is also thought to benefit stickleback, by promoting vegetation growth, increasing turbidity, and hence decreasing predation risk from visual predators and intraspecific aggressive interactions rate, and increasing food availability (see Olin et al. 2022 and references therein). Salinity has been previously found to correlate positively with sprat condition (Casini et al. 2006). Yet periods of low salinity may also coincide with large volumes of warm, well-oxygenated water that favor sprat (Ojaveer and Kalejs 2010)), which aligns with the possible negative effect of winter salinity observed in our models. Finally, while warmer temperatures are expected to favor stickleback populations by increasing growth, reproductive rates, and food availability (e.g. zooplankton) (see Olin et al. 2022 and references therein), negative direct effects on reproductive success may occur (Hopkins et al. 2011, Hani et al. 2019), as well as negative indirect effects mediated by temperature-induced increases in predator densities (Svensson et al. 2017). Given the multitude of pathways through which temperature can affect stickleback, the net effect is still unclear. Importantly, regardless of whether the ecological criterion was applied or not, the identified effects of the interacting species were generally consistent (cf. Table 2; Table S4). The only difference was that, while negative effects of large herring on stickleback in the Central Baltic were always present, models ignoring the ecological criterion also pointed to a similar effect in the Bothnian Sea.

There was no relationship between fisheries landings and biomass of sprat and small herring in our data. This is perhaps not unexpected, as landings represent a source of mortality (i.e. a possible negative relationship between landings and biomass), but also reflect the set management quotas, which will increase as the stock increases (i.e. a possible positive association). Fishing mortality has been close to, or above, the precautionary reference limit for decades for the Central Baltic herring stock, and since the mid-1990s for the Baltic Sea sprat stock (ICES 2023). In the Bothnian Sea, herring quotas have been increased since the early 1990s, with the aim of reducing stock size down to a level that aligns with the management objective of Maximum Sustainable Yield (ICES 2022). Landings of herring and sprat are thus adjusted so that the stocks do not decrease below the management reference points, and our results should not be interpreted as fishing having no effect on these species. To assess the role of fishing, we would ideally have included fishing mortality as a predictor of species biomass instead of landings, but this is estimated at the scale of the stock rather than the rectangle and could therefore not be included in the analysis.

Our study focused on the interactions of two clupeid species, herring and sprat, with three-spined stickleback. These are the only major competitors with stickleback in the open sea ecosystem in the Baltic Sea. When it comes to predators, cod (*Gadus morhua*) and Atlantic salmon (*Salmo salar*) have also been shown to feed on stickleback (Hansson et al. 2001, Almqvist et al. 2010). However, cod currently only occurs in large numbers in the southernmost part of the study area (Orio et al. 2019), and salmon biomass in the Baltic Sea is overall relatively low. One potential limitation of our study is that we did not consider coastal predators and competitors in our analyses, such as northern pike and European perch (Ljunggren et al. 2010, Bergström et al. 2015, Olin et al. 2022). These species may have contributed to, but are not the sole drivers of, the stickleback increase (Bergström et al. 2015). Perch and pike have been shown to locally control stickleback numbers at the coast under specific conditions, i.e. strong habitat connectivity with nearby predator spawning areas, and low densities of fish-eating top predators, such as the gray seal (*Halichoerus grypus*) and the great cormorant (*Phalacrocorax carbo sinensis*) (Olin et al. 2024). The gray seal and the great cormorant also consume herring (Hansson et al. 2018), and have been hypothesized to feed more on pike and perch as a consequence of herring populations decline. Given these multiple interrelated factors, including potential interactions with changes in hydrographic factors driven by a warmer climate (Olin et al. 2022), and that stickleback is a migrating species, we do not yet know what are the main drivers that triggered the stickleback increase, the factors that are fueling it, or the time and place when key interactions have occurred and occur. Following a precautionary approach and in light of our findings, we suggest that herring and sprat should be included in future studies where the relative importance of open sea versus coastal predators and competitors of stickleback is explored, as well as the role of top predators, climate drivers, and anthropogenic stressors.

We need to acknowledge some additional limitations of our study besides those already addressed above. For example, the herring and sprat biomass dataset is likely more accurate than the stickleback biomass dataset, as the methods used in the monitoring are not designed for targeting stickleback. However, these were the only data available for stickleback at the spatial scale of the study. The collection method was the same for the entire area and period, and for the three species, and even though stickleback biomass may be underestimated, our main aim was not to assess total stickleback biomass but rather to investigate patterns of association between the species. Also, our study is correlative and to infer causation manipulations of fish stocks would be helpful. The ongoing initiation of a trial along part of the Swedish coastline where the trawl limit will be extended to 12 nautical miles from the baseline (i.e. including all Swedish territorial waters) in SD 27, 29, and 30, from the current 4 nautical miles (Wennerström et al. 2023), could provide a natural experiment of how fishing pressure influences the herring stock locally and whether a possible increase in herring will contribute to stabilizing or even reducing stickleback biomass. However, an overall reduction, rather than only a displacement, of fishing pressure is likely necessary to maintain the herring stocks within safe limits. In fact, the European Commission proposed that the catch of herring in both the Gulf of Bothnia and the Central Baltic should be limited to unavoidable bycatch for 2024, after the stock assessments pointed to a > 5% risk that the stocks would fall below a critical biomass limit (https://ec.europa.eu/commission/presscorner/detail/en/ip_23_4287). However, the final quotas, as decided by the Council of the European Union, still allowed fishing on the herring stock (https://oceans-and-fisheries.ec.europa.eu/news/baltic-sea-agreement-reached-2024-fishing-opportunities-2023-10-24_en). The fishing industry has also shown an interest in exploiting the increasing stickleback population (Olin et al. 2022), although the risk for bycatch and unintended ecological consequences warrants a precautionary approach (Pearson et al. 2022). In fact, a severe reduction of stickleback abundances could have negative effects on the many species of fish, birds, and marine mammals that prey on it (Olin et al. 2022). The interactions identified here point to the importance of an ecosystem-based approach in fisheries management, as changes in one stock will also affect other species in the food web. Importantly, as stickleback can feed on the eggs of herring (Kotterba et al. 2014) and may compete with herring for food (Peltonen et al. 2004, Jakubavičiūtė et al. 2016, Ojaveer et al. 2017), there is a risk that the stickleback increase results in a predator-prey reversal, in which the sticklebacks suppress their own predators and competitors, further boosting their own population growth. These dynamics have been recently documented in the interactions between stickleback and coastal stickleback predators, and have resulted in a regime shift with consequences for the whole coastal food web (Eklöf et al. 2020, Olin et al. 2024). Following the precautionary principle, we suggest that fishing mortality of herring should decrease to avoid the risk for adverse ecosystem effects from a loss of herring, which is a true keystone species of the Baltic Sea.

Small pelagic fish such as herring and sprat have high global economic and ecological importance. They support large fisheries worldwide, sustaining food security in many countries, and they constitute important prey for many species (including fish, marine mammals, and seabirds), and are thus critical for transferring energy to higher trophic levels (Pikitch et al. 2014, Peck et al. 2024). However, our study place emphasis on their role not as fishing targets and prey, but as competitors and predators. Our results are in line with other work pointing to the importance of competition for governing the dynamics of herring and sprat in the Baltic Sea (Casini et al. 2004, 2006), which do show high overlap in diet with both each other and with stickleback (e.g. Möllmann et al. 2004, Peltonen et al. 2004, Jakubavičiūtė et al. 2016, Ojaveer et al. 2017). There are many studies documenting overlapping diet in other co-occurring planktivores too (Möllmann et al. 2004, Raab et al. 2012, Óskarsson et al. 2016), but while overlap in prey choices is a prerequisite of competition for food, low densities of competitors or high food availability may mean that high diet overlap does not translate into actual competition for food. Here we have demonstrated an approach using biomass estimates to compare trends and explore inter-specific relationships in order to determine whether diet overlap also manifests as negative effects at the population level, and thus whether competition constitutes an important driver of population dynamics. A similar approach could be applied in other ecosystems where dietary overlap between potentially competing planktivores has been demonstrated, such as the North Sea (Raab et al. 2012), around the waters of Iceland (Óskarsson et al. 2016), and the Bay of Biscay (Bachiller and Irigoien 2015).

While our results thus suggest that small herring may play an important role as a competitor for plankton resources in the Baltic Sea, they also suggest that large herring may instead be an important piscivore in the coastal ecosystem. Herring piscivory has been documented in the Atlantic Ocean (Randall et al. 2022), the North Sea (Segers et al. 2007), the Baltic Sea (Köster and Möllmann 2000), and the Barent Sea (Gjøsæter and Bogstad 1998). Yet, it is largely unknown how predation by herring could affect population dynamics of fish prey species, e.g. cod (Köster and Möllmann 2000) and capelin (*Mallotus villosus*) (Shikon et al. 2019), and what the consequences are at the ecosystem level. Given the ubiquity and abundance of herring, future studies on their role as predators and the potential impacts on large-scale trophodynamics could provide useful information for an effective management of marine ecosystems. Our approach of combining diet studies with analyses of trends and inter-specific relationships between biomasses of herring and their potential prey could be a useful way of further elucidating the role of herring as a piscivorous predator in marine ecosystems.

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Author contributions

Serena Donadi: conceptualization, formal analysis, visualization, and writing - original draft; **Agnes Olin**: visualization, writing - review & editing; **Michele Casini**: conceptualization, writing - review & editing; **Johan Eklöf**: writing - review & editing; **Mårten Erlandsson**: data curation; **Ronny Fredriksson**: visualization, data curation; **Olavi Kaljuste**: investigation, formal analysis, writing - review & editing; **Niklas Larson**: investigation, formal analysis, writing - review & editing; **Jonas Nilsson**: investigation, formal analysis, writing - review & editing; **Ulf Bergström**: conceptualization, funding acquisition, writing - review & editing

Supplementary data

Supplementary material is available at the *ICES Journal of Marine Science* online version of the manuscript.

Conflict of interest: The authors have no conflicts of interest to declare.

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Data availability

The data underlying this article are available from the Swedish National Data Service Repository: https://doi.org/10.5878/ka8r-8e34

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