ICES Journal of
Marine Science

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2021), 78(5), 1900–1908. https://doi.org/10.1093/icesjms/fsab094

Original Article

Size-selective competition between cod and pelagic fisheries for prey

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Kulatska, N., Woods, P. J., Elvarsson, B. Þ., and Bartolino, V. Size-selective competition between cod and pelagic fisheries for prey. – ICES Journal of Marine Science, 78: 1900–1908.

Received 6 August 2020; revised 15 April 2021; accepted 16 April 2021; advance access publication 1 June 2021.

Predators often predate on a limited size range of prey, which may or may not overlap with size ranges of same prey targeted by fisheries. When they do overlap, the effect of competition over that prey is immediate, as the predator removes prey, which are at the same time suitable for the fishery. However, if the predator consumes the same prey species as the fishery, but targets smaller prey sizes, this predation on smaller sizes may result in a potential loss of future, rather than current, fishing opportunities. Comparative analyses of predator size preference and fisheries selectivity are scarce, despite their relevance in the context of integrated management of fish populations. We evaluated how size-selective cod predation influences the dynamics of sprat and herring in the Baltic Sea, as well as the competition with pelagic fisheries through immediate and delayed effects. We found a large overlap (30–60%) between prey lengths targeted by cod and fisheries, which was largest in the 1970s–1980s, when cod had higher abundance and was larger in size. Cod generally consumes herring and sprat, which are smaller than those caught by the fisheries, causing both immediate and delayed effects on prey biomass available for the fisheries.

Keywords: Baltic Sea, competition with fisheries, mortality, multi-species model, size-selective predation

Introduction

Targeting the same prey makes competition between humans and predators unavoidable. Competition between fisheries and marine mammals (reviewed in Plagányi and Butterworth, 2009) and sea birds (reviewed in Sydeman *et al.*, 2017) has been widely described. A few studies of competition with predatory fish have also been reported (Hjermann *et al.*, 2004). However, these have focused mainly on comparing biomasses of fish consumed by predators vs. that harvested by fisheries (Punt and Butterworth, 1995; Trites *et al.*, 1997; Croll and Tershy, 1998; Hjermann *et al.*, 2004; Kaschner and Pauly, 2005; Plagányi and Butterworth, 2009; Chasco *et al.*, 2017; Sydeman *et al.*, 2017). Nevertheless, this direct comparison is only valid if size ranges of fish comprising these biomasses are similar. Predators often predate on a limited size range of prey, which may or may not overlap with size ranges targeted by fisheries. When they do overlap, the effect of competition on that prey is immediate, as consumption by the predator affects the availability of fish to a fishery that is conducted simultaneously. This effect has been most often described in previous comparisons (Hjermann *et al.*, 2004; Plagányi and Butterworth, 2009; Sydeman *et al.*, 2017). However, if the predator consumes the same prey species as the fishery, but targets smaller prey sizes, this predation on smaller sizes may result in a potential loss of future, rather than current, fishing opportunities. That is, the effect of competition will be delayed, as predator consumption would affect the availability of fish to a fishery later in time compared to when the predation occurred. Conversely, when the fishery targets smaller individuals than the predator, there could be a delayed effect of competition for the predator. Another example of a delayed effect of competition is when one of two competitors targets larger prey individuals that are likely to be more fecund (Blueweiss *et al.*, 1978), thus decreasing the number of recruits and prey available in future years.

The comparison between lengths of prey targeted by predators and fisheries is generally lacking in previous studies, with few exceptions (Andersen *et al.*, 2007; Östman *et al.*, 2013; Hilborn *et al.*, 2017). This implies a knowledge gap regarding the impact of the predator and fisheries on the dynamics of size-structured prey population, and what implications a delayed effect of predation could have on fisheries. Additionally, prey size selection depends on the size structure of predator population, which further complicates the evaluation of potential competition between predators and fisheries. Ignoring length preferences of a predator and fisheries when evaluating the competition between them may result in misleading conclusions. Analysing the effects of size-dependent predator–prey interactions and fisheries on population dynamics is especially important when fishery management faces choices that involve making decisions on trade-offs between species or when the aim is to rebuild the predator population or to implement integrated management of fish resources.

Herring and sprat are among the most important commercial species in the Baltic Sea, together comprising ca. 93% of the catches in 2017 (ICES, 2019a). At the same time, herring and sprat are important prey species for cod in the Baltic Sea (Uzars, 1975; Bagge *et al.*, 1994; Sparholt, 1994; Kulatska *et al.*, 2019), together comprising up to 80% of the diet of cod above 35 cm (Kulatska *et al.*, 2019).

The abundances of Baltic cod, herring, and sprat have gone through dramatic changes during the last 40 years. The Baltic Sea was cod-dominated prior to the late 1980s; however, after the drastic decline in the cod abundance due to a combination of overexploitation and unfavourable environmental conditions (Casini, 2013), the sprat population experienced an outburst. It is thought that the release from cod predation, combined with favourable environmental conditions, turned the Baltic system into sprat-dominated (Alheit *et al.*, 2005; Österblom *et al.*, 2007; Casini, 2013). Herring abundance was steadily declining from the beginning of the time series; however, it started to increase from the early 2000s. From the mid-2000s, cod abundance started to increase; however, the cod population concentrated in the southern Baltic (ICES Subdivisions 25–26, Eero *et al.*, 2015). In addition, the cod size distribution shifted towards smaller individuals (Svedäng and Hornborg, 2014), likely due to a combination of fishery selectivity (Svedäng and Hornborg, 2014), density-dependent growth (Eero *et al.*, 2012; Svedäng and Hornborg, 2014; Casini *et al.*, 2016) and decreased feeding level (Neuenfeldt *et al.*, 2019).

These changes over time in predator and prey stock sizes and cod body size are likely to have caused changes in cod predation, and therefore natural mortality of sprat and herring, over time.

The need to account for the predation mortality in the stock assessment has been recognized since the 1970s (Andersen and Ursin, 1977; May *et al.*, 1979). Predation mortalities are often higher than those traditionally assumed in the stock assessment (Tyrrell *et al.*, 2011); they depend on predator species and size and are usually variable in time (Gislason and Helgason, 1985). However, most stock assessment models are single species and do not account for predation directly; out of ∼1 250 managed stocks, only few single-species assessments account for predation mortality (Skern-Mauritzen *et al.*, 2016). Understanding predation dynamics may not only improve the stock assessment process, but also inform the selection of harvest strategies by analysing interacting effects of predation by multiple predators (including humans) or the consumption of multiple prey.

In this study, we aimed to evaluate how size-selective cod predation influences the dynamics of sprat and herring (by which we mean changes in abundance) as well as competition with pelagic fisheries through immediate and delayed effects during three contrasting historical periods differing in the ecosystem state: a cod-dominated state (1974–1988), a sprat-dominated state (1989–2006), and the more recent period of high cod density with decreased cod size (2007–2013). The prey dynamics analysed in this study are restricted to those caused by direct size-selective predation and fishing, rather than a greater range of ecological effects [e.g. changes of density-dependent growth and "overcompensation" (de Roos and Persson, 2002; Gårdmark *et al.*, 2015)] because of the lack of data from which these predation effects can be directly estimated within a multispecies population dynamics model. Therefore, results can be interpreted as only one of various ecological scenarios, but with realistic predation effects that are scaled according to predation levels observed in diet data.

We first analysed the overlap of prey lengths targeted by cod and pelagic fisheries, which will give an indication of the extent of competition for specific length groups of prey. Next, we analysed how the mortality of the entire prey stock and of different prey length groups caused by cod predation differs from the mortality caused by fisheries exploitation. Finally, the extent of immediate and delayed effects of competition between cod and pelagic fisheries was quantified by comparing suitable prey biomass consumed by cod and harvested by fisheries with total available suitable prey biomass.

Methods

Study system

The Baltic Sea is a large semi-enclosed brackish water body with strong salinity and temperature gradients (Elmgren, 1984; Leppäkoski *et al.*, 2002), which limits the number of species that are able to live there. As a result, cod, herring, and sprat are both the bulk of commercial catches (together comprising ∼95% of them; ICES, 2013) and the key species of the ecosystem in the central Baltic Sea (Rudstam *et al.*, 1994; Sparholt, 1994). Three contrasting periods can be characterized by changes in the key species' abundances in the Baltic Sea system (Figure 1) within the time-frame of our study: (1) 1974–1988 with high cod and low sprat abundance (Möllmann *et al.*, 2004; Alheit *et al.*, 2005; Casini, 2013); (2) 1989–2006 with declined cod and herring abundances and increased sprat abundance; and (3) 2007–2013, with increased cod abundance, concentrated in the southern Baltic Sea (Eero *et al.*, 2015; Bartolino *et al.*, 2017) and a decrease in cod body size.

Modelling framework

We reconstructed the population dynamics of cod, herring, and sprat; cod predation on herring and sprat; and the effect of fisheries, in a length- and age-structured model built using Gadget (Globally applicable Area Disaggregated General Ecosystem Toolbox, Begley 2017). Gadget models represent biological processes like growth, maturation, reproduction, and consumption in the form of functions, which are often length- or length- and age-based. Various components of the ecosystem can be integrated (interactions between species, the impact of environmental variables) together with the impact of fisheries (Begley, 2017).

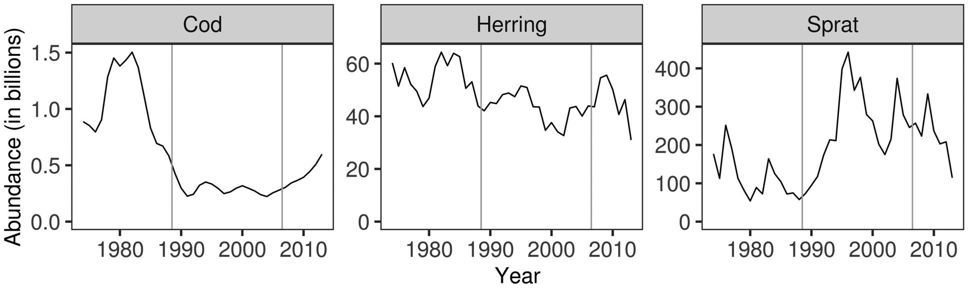

Figure 1. Stock abundances estimated in single-species stock assessments (ICES, 2013) characterizing shifts in cod (ages 2–8+), sprat (ages 1–8+, except for 2013, for which ages are 2–8+), and herring (ages 1–8+, except for 2013, for which ages are 2–8+) stocks. Vertical lines correspond to three contrasting periods: 1974–1988 (high cod and low sprat abundances), 1989–2006 (high sprat and low cod abundances), and 2007–2013 (increased cod abundance with decreased cod body size).

The Gadget model in this study was based on the model of Kulatska *et al.*, (2019) and ran using the Rgadget package (Elvarsson, 2015) for R (R Core Team, 2017), and a dedicated database, which was built and queried via the MFDB package (Lentin, 2014). To further improve the original model, the following changes were made:

- The average cod consumption at length was time-variable. It was separated into 5-year time-blocks, to reflect changes in the feeding level of the cod population (Neuenfeldt *et al.*, 2019).
- Minor improvements: (i) stratified likelihood function for an age–length key, and (ii) reference weight at length in the initial year of the model estimated using values of the length–weight relationship from the corresponding period.

The model (see Supplementary material for full description) covers 1974–2013 and represents the Baltic Sea as a single area. In the model, cod predates on herring and sprat, which are dynamically represented, as well as on a number of static prey: saduria, mysids, and generic food ("otherfood"). Fisheries are represented by those using pelagic trawl, targeting sprat and herring and modelled as distinct fleets, and those targeting cod and using active gear (mainly bottom trawl; "cod active") and passive gear (mainly gillnets, "cod passive"). The model is fitted to a multitude of data sources (e.g. biological information from commercial catches or obtained during surveys, cod stomach content, landings) to reconstruct the abundance, length, and age structure of fish populations and prey species and length composition of cod diet (see Supplementary material for more details).

Stomach content data are a key data source in the model. The average daily consumption by cod is estimated as a function of length directly from the stomach data using the evacuation rate model proposed by Jones (1978), and parameters of prey species preference and length selection by cod are estimated in the present model by fitting the stomach data [see Supplementary material and Kulatska *et al.*, (2019) for more details]. Stomach content data were obtained from the most complete up-to-date Baltic cod stomach database, covering 1964–2014 (Huwer *et al.*, 2014; ICES, 2014).

Overlap of prey lengths targeted by cod and pelagic fisheries

To compare prey length preferences between cod and pelagic fisheries, we estimated the overlap of prey lengths targeted by them. Since the prey length preferences by fisheries and cod differ, the fraction of this overlap in the respective prey length preference will also differ. As a result, the competition between cod and fisheries will have a different effect on cod compared to fisheries; thus, in further analysis, we evaluated them separately for cod (from here on "cod perspective") and fisheries (from here on "fisheries perspective").

In the Gadget model, the prey length preference of fisheries is represented by a logistic function and is assumed to be constant through time:

$$S_l = \frac{1}{1 + \exp\left[-\alpha(l - l_{50})\right]}, \tag{1}$$

where l is the fish length, l_{50} is the length at which the fish has a 50% probability of being caught, and α is the parameter influencing the steepness of the function.

In contrast, the prey length preference of cod is modelled as dome-shaped. It depends on the ratio between prey (l) and cod (L) lengths (Andersen and Ursin, 1977 equation converted from weight into length) and on the species preference d:

$$S_{lL} = d \times \exp\left[-\frac{\left(\ln (L/l) - p_1\right)^2}{p_2}\right]. \tag{2}$$

Parameters p_1 and p_2 were set to estimates of Kulatska *et al.* (2019; $p_1 = 1.27$ and $p_2 = 0.28$ for herring; $p_1 = 1.67$ and $p_2 = 0.28$ for sprat), while d was estimated using the Gadget model separately for each half of the year to represent seasonality (Quarters 1–2 and Quarters 3–4).

As the size structure of the cod population changes over time, the resulting prey length preference of the entire cod stock will also change: cod length groups with the highest abundance will have a larger contribution to the prey length preference of the entire cod stock. Also, since the average consumption (Q) of a predator increases with its body size, groups of larger cod consume more and thus have a higher impact on prey than other groups. To account for these aspects, we weighted the prey length preference of each cod length group by its abundance and the average consumption:

$$a_{Lt} = \frac{N_{Lt} \times Q_{Lt}}{\max\left(N_t \times Q_t\right)}, \tag{3}$$

where a is a weighting multiplier of the prey length preference of cod with length L, abundance N and the average consumption Q (kg year^{-1}) at year t. Abundances of different cod length groups were estimated using the Gadget model, while the average consumption was estimated from stomach data using the evacuation model developed by Jones (1978, for details see Supplamentary material).

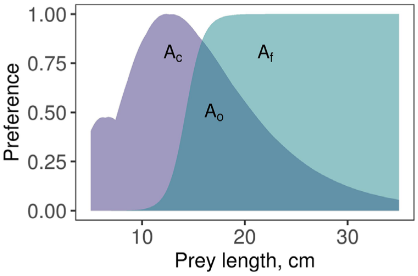

Figure 2. An example of herring size preference by cod (A_c) and fisheries (A_f) and the overlap between them (A_o) in 1974.

Two indices of overlap between the prey length preferences of cod and fisheries were estimated using the raster (Hijmans, 2019) package for R (R Core Team, 2017). Overlap index from fisheries perspective (OI_f) was the proportion of area underneath the function of fisheries preference (A_f in Figure 2) that was also underneath the function of cod preference (A_o):

$$OI_f = A_o / A_f. \tag{4}$$

Overlap from the cod perspective (OI_c) was the proportion of area underneath the function of cod preference (A_c) that was also underneath the function of fisheries preference (A_o):

$$OI_c = A_o / A_c. \tag{5}$$

Impact of cod predation compared to fisheries exploitation on different length groups of prey and its development through time

To evaluate the difference between the impact of cod predation and that of fisheries exploitation on prey stocks, we compared the mortalities caused on three length groups of prey: at l_{50}, at length 30% lower than l_{50}, and at length 30% above l_{50}. We also compared mortalities caused for the whole herring and sprat stocks. Mortalities were approximated from predation and harvest rates using the Gadget model:

$$M_{2l,t} = -\ln\left(1 - N_{pl,t}/N_{l,t}\right)/\Delta t, \tag{6}$$

$$F_{l,t} = -\ln\left(1 - N_{cl,t}/N_{l,t}\right)/\Delta t, \tag{7}$$

where M_2 and F are, respectively, the predation and fishing mortalities of fish of age/length l, $N_{l,t}$ is number of fish of age/length l at the beginning of time-step (t), and $N_{pl,t}$ and $N_{cl,t}$ are the number of fish of age/length l consumed by the predator and that harvested by fishery during the time-step, respectively. Δt is a proportion of a time-step in a year.

Extent of potential competition between cod and pelagic fisheries

To evaluate the extent of potential competition between cod and pelagic fisheries from the fisheries perspective, we quantified both the immediate and delayed effects of cod predation. For that, prey consumed by cod were divided into two groups: $\geq l_{50}$ (to represent the immediate effect of competition) and $< l_{50}$ (to be included in the evaluation of the delayed effect of competition). To evaluate the delayed effect of cod predation, we compared the biomass harvested by fisheries, as estimated using the Gadget model, to a harvest equivalent (Östman *et al.*, 2013). The harvest equivalent corresponds to the biomass that herring and sprat of sizes $< l_{50}$ would have reached at l_{50} if they would have survived without cod predation and that would have been added to the biomass of clupeids suitable for the fisheries:

$$H_{t+t_{\Delta l}} = \sum_{l}^{l_{50}} w \times N_{l,t} \times \exp\left[-M_1 \times t_{\Delta l}\right], \tag{8}$$

where H is the harvest equivalent, w is the average weight of the prey at l_{50}, N_l is the number of prey at length l consumed by cod, as estimated using Gadget, and subjected to background natural mortality rates (M_1 from sources other than cod predation) over the period $t_{\Delta l}$ that corresponds to the time that would take for the prey to grow from size l to l_{50}. The number of prey consumed at time t is, therefore, a harvest equivalent of that at time $t + t_{\Delta l}$, when prey would have reached l_{50}.

The specific prey length, to express sizes that are harvestable by fisheries, is required in the estimation H in order to account for the time it would take for smaller fish to grow into that size. Östman *et al.* (2013) originally used a minimum harvestable size; we, instead, decided to use l_{50} (as described in the beginning of this section), since we assumed that a 50% probability of fish being caught by fisheries (as at l_{50}) is more representative of immediate competition.

Results

Baltic cod targets a wide length range of herring and sprat, while pelagic fisheries select larger individuals (Figure 3). The overlap between the prey length preference of cod and prey length preference of fisheries from both the fisheries and cod perspectives was largest in the earliest, cod-dominated, period (1974–1988) and gradually decreased after that. The overlap of clupeid length ranges from the fisheries perspective decreased at a higher rate (0.15–0.2 between periods) than did the overlap from the cod perspective (0.06–0.09 between periods). The overlap betweenthe herring length preference of cod and herring length preference of fisheries was larger from the cod perspective (in a range of 0.5–0.59), while the overlap between sprat length preference of cod and fisheries was larger from the fisheries perspective (in a range of 0.46–0.65).

Cod predation caused higher mortality than fisheries for all herring and sprat length groups until mid-1980s (Figure 4). Co-occurring with a decrease in cod abundance from the 1990s, fisheries became the major source of mortality for the larger size groups of herring and sprat. From 2007, cod caused higher mortality than fisheries for herring at l_{50}, but not for sprat (Figure 4). For herring and sprat smaller than l_{50}, cod caused higher mortality than fisheries during the entire time series.

Herring and sprat showed similar trends in the entire stock mortality, which mirrored those for l_{50} (Figure 4). Cod was a major source of mortality during the 1980s until the beginning of the 1990s for herring and mid-1990s for sprat, after which fisheries became the major source until 2007 for herring and 2013 for sprat. During the last time period, the predation mortality of both clupeids increased and even surpassed the fishing mortality for herring. The impact of fisheries on the entire sprat stock was substantially lower than on l_{50} sprat from 1990 onwards.

Both immediate and delayed effects of competition between cod and fisheries for herring (Figure 5, upper panel) and sprat (Figure 5, lower panel) from the fisheries perspective were larger in the pe-

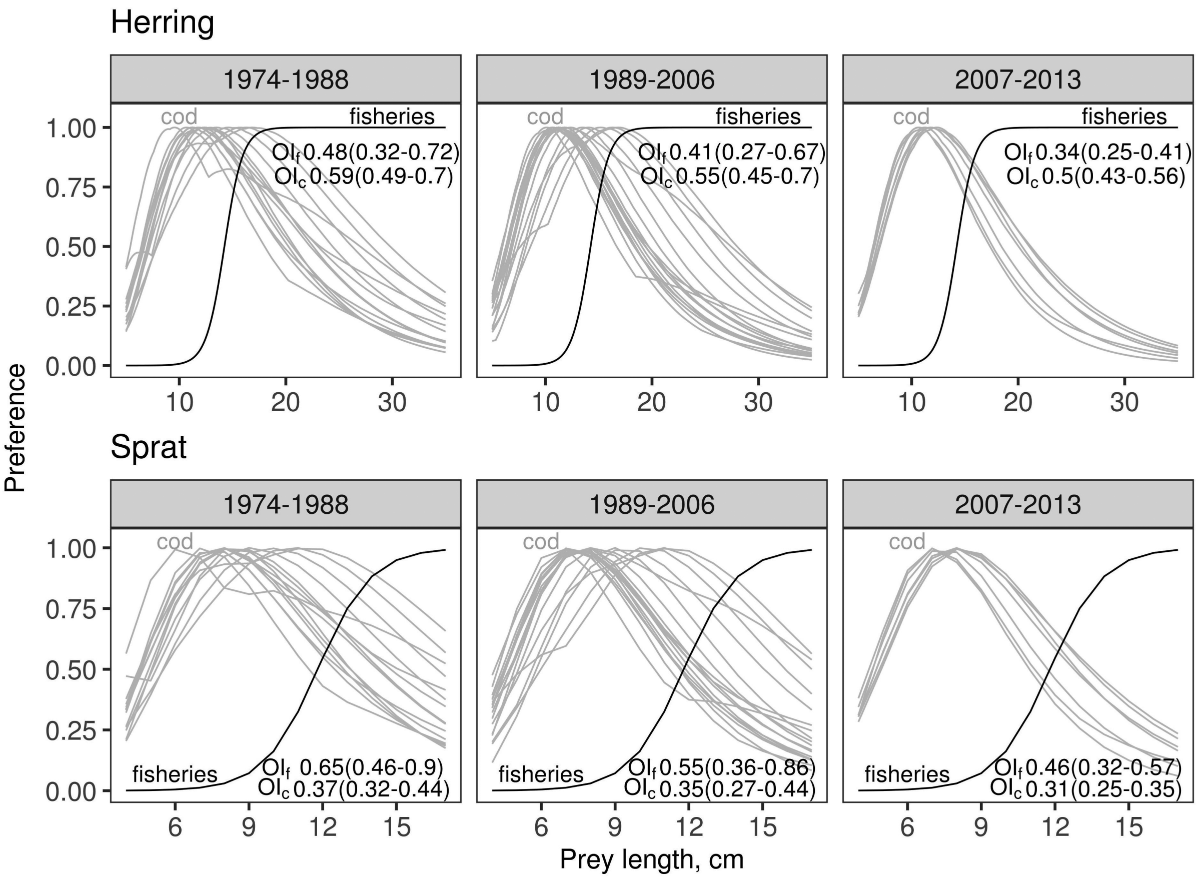

Figure 3. Comparison of prey length preferences by cod (grey, with individual lines representing years) and fisheries (black) in different periods. OI_f indicates the average overlap index between cod and fisheries length preferences from the fisheries perspective, while OI_c indicates the average overlap index between cod and fisheries length preferences from the cod perspective. Numbers in brackets correspond to the range of overlap values.

riod of high cod abundance, 1974–1988. In the case of sprat fisheries, these effects continued to be large even into the second period, up to 1997, when the biomass of harvestable sprat lost due to cod predation was equal to or exceeded the biomass harvested by fisheries. Harvestable herring biomass that survived until the end of the year was usually larger than biomass removals due to fishing and predation, except for 1980–1990 and 2000, when it was equal or lower. The opposite was found for sprat: harvestable sprat biomass that survived until the end of the year was usually lower than biomass removals due to fishing and predation. This indicates that the total effect of competition with cod is larger for sprat than for herring fisheries as the available biomass of harvestable herring may be sufficient to compensate for fisheries losses due to cod predation.

The analysis of competition from the cod perspective (Figure 6) showed that fisheries harvested higher biomass of herring than predated by cod from 1989 (until 2008–2013, when cod predation exceeded harvest) and higher biomass of sprat from 1996 (except for 2003–2004, when cod predation exceeded harvest). The available biomasses of clupeids suitable for cod were, however, usually larger than the biomass lost due to both fishing and predation, indicating that the prey pool for cod may be sufficient to compensate for competition with fisheries.

Discussion

We found a large overlap (30–60%) between prey lengths targeted by cod and fisheries. The overlap from both the fisheries and cod perspectives was largest in the period 1974–1988, when cod had higher abundance and was larger in size, and gradually decreased with time.

Cod had a higher impact than fisheries on all length groups of both herring and sprat in the period 1974–1988, when cod abundance was high. After cod abundance decreased, predation mortality caused by cod also decreased, with some increase after 2007, and was more pronounced for herring and sprat $\leq l_{50}$ (length at which fish have a 50% probability of being caught by the fishery).

The mortality caused by cod on prey $<l_{50}$ was higher than the mortality caused by the fishery during the whole time series. This caused a delayed effect on prey biomass available for the fisheries, since smaller individuals that could have grown into harvestable sizes were consumed by cod. Estimated prey biomass unavailable for fisheries due to a delayed effect of cod consumption, a novel contribution of our study, was often similar to the biomass unavailable due to an immediate effect, essentially doubling the total potential effect of cod consumption.

Biomasses of herring and sprat harvested by the fishery were comparable to the biomass consumed by cod. Nevertheless, they

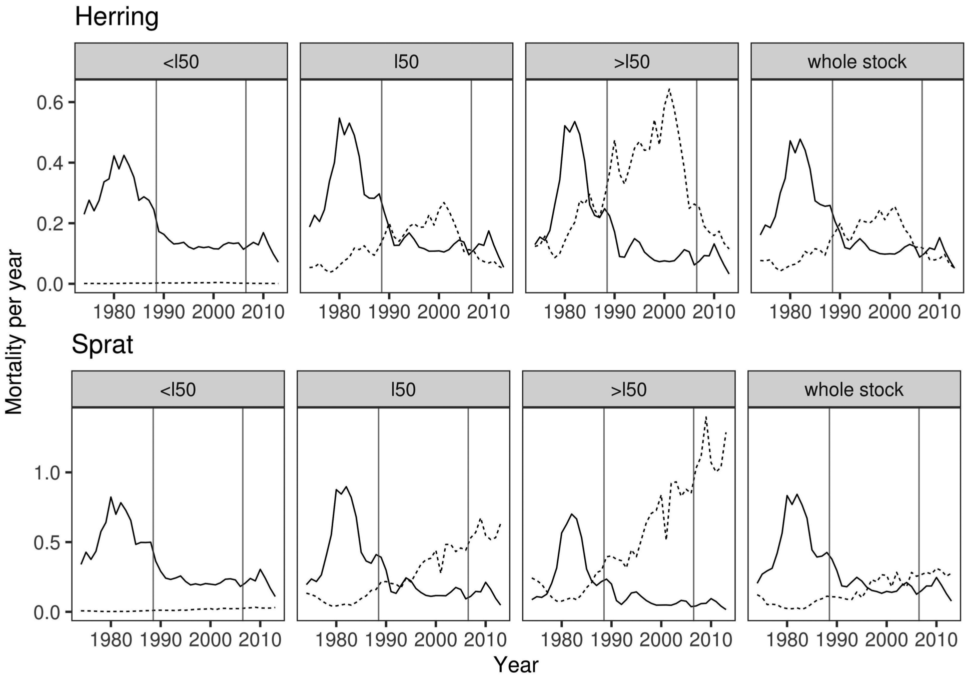

Figure 4. Temporal variability in herring and sprat annual mortality caused by cod predation (solid line) and fisheries exploitation (dashed line). Subpanels represent the mortality of different length groups of herring and sprat: at 30% below or 30% above l_{50} (length with 50% probability of being caught by fisheries), and for the whole stock. Vertical lines correspond to three contrasting periods: 1974–1988 (high cod and low sprat abundances), 1989–2006 (high sprat and low cod abundances), and 2007–2013 (increased cod abundances with decreased cod size).

were lower than the total suitable prey biomass available for cod, indicating that the prey pool for cod may be sufficient to compensate for the competition with fisheries. However, our study does not account for the spatial distribution of cod, sprat, herring and fisheries effort. Cod is concentrating progressively towards the southwestern part of the central Baltic Sea, while sprat and herring increase their densities towards the northeastern part (Casini et al., 2011; Eero *et al.*, 2012). Thus, if the biomass of suitable prey available for cod is smaller due to the spatial mismatch between predator and prey, the effect of competition with fisheries may be higher for cod than suggested by this study.

There is also a possibility of delayed effects of fisheries on prey available for cod, since fisheries target larger prey individuals that are likely to be more fecund (Blueweiss *et al.*, 1978), thus decreasing the number of recruits and prey available in future years. This analysis is, however, beyond scope of this study since recruits in the model are estimated using cohort analysis and not as a result of stock–recruitment relationship.

Natural mortality [M, including predation mortality (M_2) and background natural mortality (M_1)] estimated in the model presented here is comparable to values derived from an age-based multispecies model (SMS, ICES, 2019d) and used in the single-species stock assessment (ICES, 2020) for sprat and herring. The main differences are the values of M for older herring (from age 3) and older sprat (from age 2) that in the stock assessment are consistently lower during the period of high cod abundance (1980–1990) than the values estimated using Gadget. A possible explanation may be that the abundances of older cod reconstructed using our model in 1979–1985 were higher than those reconstructed using the Stock synthesis model (ICES, 2019e), output of which was used to represent cod stock in SMS. Since older (larger) cod shows higher preference towards larger prey, the high abundance of large cod would have caused higher mortality on older sprat and herring.

The results of the analysis can be interpreted as only one of various ecological scenarios, since prey dynamics were restricted to those caused by direct size-selective predation and fishing, rather than a greater range of ecological effects. Both intra- and interspecific competition between herring and sprat negatively affect their growth and condition (Casini *et al.*, 2006; Casini *et al.*, 2011). It has been suggested that by removing smaller prey individuals, the predator decreases competition between prey and the remaining prey individuals are able to grow to a larger size (the phenomenon called overcompensation; de Roos and Persson, 2002; Gårdmark *et al.*, 2015). As these larger prey become available to fisheries, predation may facilitate fisheries catches (Huss *et al.*, 2014). However, in order to check for that possibility in the current model, intra- and interspecific competition between herring and sprat, as well as the effect of competition on their growth and body condition, would need to be accounted for in the model structure, and estimated given enough supporting data. This analysis, however, is outside current possibilities and aims of this study and the model.

A decline in cod abundance and a drastic decrease of cod condition in the Baltic (Eero *et al.*, 2015; Casini *et al.*, 2016) have called for more actions towards rebuilding the Baltic cod stock. The pinnacle of these measures has been the recent zero catch advice for the Baltic cod (ICES, 2019f) and cod fishing ban in the southern Baltic (EC, 2019). Moreover, in an attempt to halt the low condition of cod, ICES recommended that sprat catches in the main distribution area of cod should be restricted (ICES, 2018b). Although sprat represents one of the main prey of cod, and the measure appears as a first rational choice, our results on the cod size preference for sprat and the overlap with the fisheries suggest that such measures might

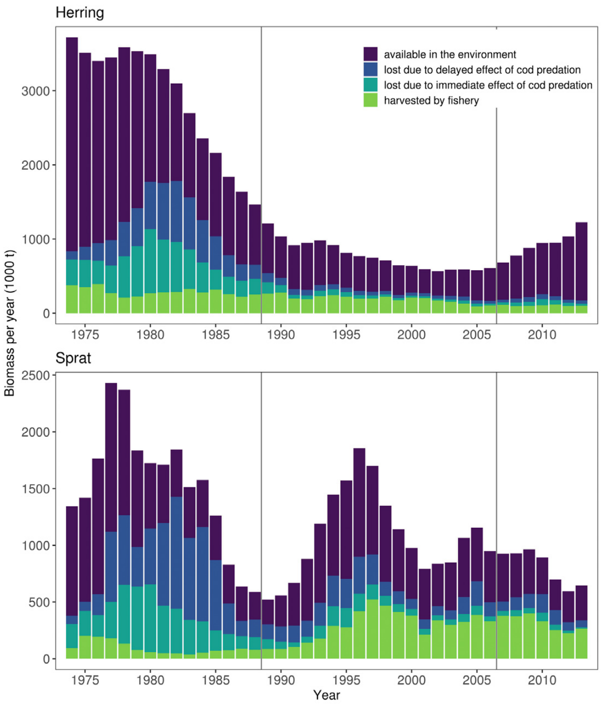

Figure 5. Temporal variability in the potential competition between cod and fisheries for herring (upper panel) and sprat (lower panel) from the fisheries perspective. Biomass harvested by the fishery is compared to the biomass of prey with a size $\geq l_{50}$ (i.e. harvestable size for fisheries), which is consumed by cod (i.e. immediate effect of competition with cod), and the biomass of prey at l_{50}, to which $<l_{50}$ consumed prey would have grown in the absence of cod (i.e. delayed effect of competition with cod). The biomasses of herring and sprat of harvestable for fisheries size that survived until the end of the year ("available in the environment"), i.e. after all predation and harvesting events, are also shown for comparison.

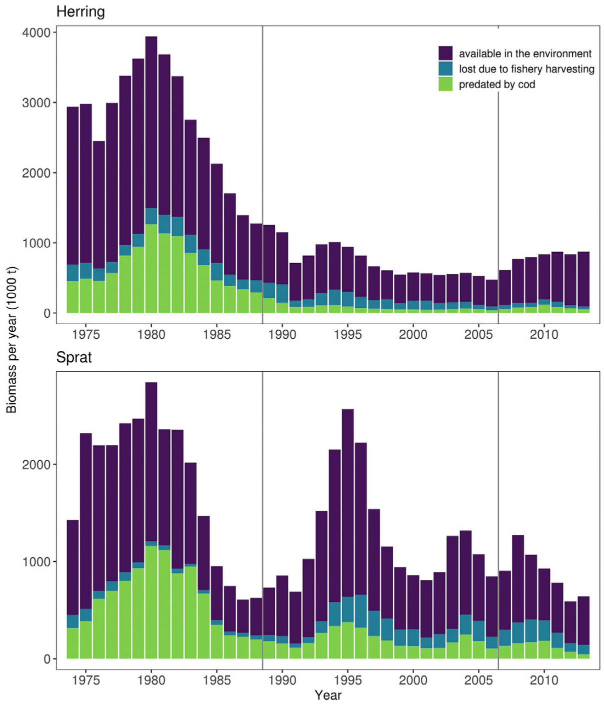

Figure 6. Temporal variability in the potential competition between cod and fisheries for herring (upper panel) and sprat (lower panel) from the cod perspective. Biomass predated by cod is compared to the biomass of prey that is harvested by the fisheries but of a suitable size for cod predation, as well as clupeids of size suitable for cod that have survived until the end of the year ("available in the environment").

not be as effective as previously thought. Our study suggests that only ~30% of sprat length ranges preferred by cod overlap with the sprat length ranges that are selected by the fisheries. Cod is mainly eating smaller sprat than those caught by the fisheries, thus causing a mismatch in the sprat caught by fisheries and required as the prey for cod.

Further steps in the analysis of predator–prey interactions between cod, herring, and sprat may also include investigating the bottom-up effect of sprat and herring on cod by linking cod growth to consumption. The current model covers 1974–2013; thus to make predictions on cod recovery as well as future impacts of cod predation on prey and implications for the fishery, the model needs to be updated.

Most studies that evaluate the competition between fisheries and predators compare only prey biomasses harvested by fisheries and eaten by the predator. Even if that provides the idea of relative influence of the predator and fisheries on prey, the impact on the structure and demography of prey population remain hidden. We, instead, compared the lengths of prey selected by the predator and fisheries. The overlap between those lengths causes the immediate effect of potential competition between fisheries and predator (and corresponds to biomasses compared by other studies). It is, however, quite often that the predator (as for example cod that we have studied) predates on smaller prey than those harvested by fisheries. This causes the delayed effect of competition, since those prey could have grown into size suitable for fisheries if they had survived. We have shown that in some years the delayed effect of competition was close in value to the immediate effect, thus doubling the total effect of competition. Besides providing a more complete evaluation of effects of competition between Baltic cod and the pelagic fisheries on herring and sprat, our study can be used to outline the prey lengths that are more relevant for fisheries and the predator; thus, if the management objective is to recover the predator population, instead of a total ban or suggested decrease in forage fish fisheries, gear measures can be evaluated, so more small prey remain available for the predator. The model could also serve as a basis for an MSE to evaluate a cod recovery plan.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Data availability statement

The data underlying this article will be shared on reasonable request to the corresponding author.

Acknowledgements

We thank Ulrika Beier and Hakan Wennhage for their valuable comments on an earlier version of the manuscript and during analysis discussions. We also thank Ken H. Andersen and three anonymous reviewers for their constructive feedback on the manuscript. We are grateful to all the colleagues and experts that participated in collecting and standardizing diverse data used in this study. This study has received funding from the European Union's Seventh Framework Programme for research, technological development and demonstration under grant agreement No. 613571 for the project MareFrame (Co-creating ecosystem-based fisheries management solutions).

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Handling editor: Ken Andersen