Understanding ontogenetic and temporal variability of Eastern Baltic cod diet using a multispecies model and stomach data

Nataliia Kulatska[a,*], Stefan Neuenfeldt[b], Ulrika Beier[a,c], Bjarki Þór Elvarsson[d], Håkan Wennhage[a], Gunnar Stefansson[e], Valerio Bartolino[a]

[a] Swedish University of Agricultural Sciences, Department of Aquatic Resources, Turistgatan 5, 453 30 Lysekil, Sweden
[b] Technical University of Denmark, National Institute of Aquatic Resources, Kemitorvet, Building 201, 2800 Kgs. Lyngby, Denmark
[c] Wageningen Marine Research, P.O. Box 68, 1970 AB IJmuiden, the Netherlands
[d] Marine and Freshwater Research Institute, Skulagata 4, 121 Reykjavik, Iceland
[e] University of Iceland, Science Institute, Dunhagi 5, 107 Reykjavik, Iceland

ARTICLE INFO

ABSTRACT

Size of predator and prey determines, to a large extent, predator-prey interactions in aquatic systems. Understanding the relationship between predator and prey size in the individual predator's food selection process is a cornerstone of ecological modelling. Stomach content data are used to inform such models, as they provide prey species specific information about the predator diet in the wild. These data are strongly relevant as direct observations of species trophic interactions, but they have limitations, and are costly. Our objective was to develop and test a model which is able to predict changes in the Baltic cod diet by reconstructing the dynamics of cod and its prey, herring and sprat, populations, their length distributions, and parametrizing trophic interactions between them. We analysed time-series of cod stomach data and built an age-length structured multispecies model using Gadget. Both observed and predicted diets of smaller (juvenile) cod consisted mainly of benthos, while larger cod fed mostly on fishes (herring and sprat). Our model could predict the main patterns in species and length composition of cod diet. We also identified important knowledge gaps, especially on benthos dynamics and processes affecting prey availability and predator preference.

1. Introduction

Size of predator and prey determines, to a large extent, predator-prey interactions in aquatic systems. Larger predators move at higher speed and are more successful in catching prey (Lundvall et al., 1999; Webb, 1976). Prey, on the other hand, may escape predation by either becoming faster as they grow (Folkvord and Hunter, 1986; Lundvall et al., 1999), or by growing beyond the size threshold of what predator can consume (limited by predator gape size; Scharf et al., 2000). In addition, to avoid direct competition between life stages, many predators experience partition of food resources into ontogenetic niches, switching dietary preferences from one prey type to another during life history (Schoener, 1974; Werner and Gilliam, 1984).

Understanding the relationship between predator and prey size in the individual predator's food selection process is a cornerstone of ecological modelling and it is a fundamental step for the development of analytical multispecies models in support of an ecosystem based fisheries management (FAO, 2008). In combination with quantifying

the functional response (Holling, 1959; Solomon, 1949), this knowledge allows to predict predation rates based on predator and prey abundances and length distributions. Stomach content data are used to inform such models, as they provide prey species-specific information about the predator diet in the wild. These data are among the most relevant direct observations of species trophic interactions, but they have limitations. What is found in a stomach is a snapshot of what the predator has consumed recently. Moreover, the evacuation time of each prey in the stomach, and consequently the detection probability, is directly related to prey-specific digestion rates, the presence of hard parts in the prey body and temperature. In addition, it is possible for predators to consume prey in the fishing gear during the sampling process, known as net feeding (Hopkins and Baird, 1975). However, corrected for these potential biases and integrated across a large number of observations in space and time, the individual snapshots may combine into a slideshow that provides an informative picture of the predator diet. To fulfil that purpose, stomach data have to be collected with sufficient spatial coverage over extended periods. As extensive

---

* Corresponding author.
  E-mail address: nataliia.kulatska@slu.se (N. Kulatska).

collection of stomach data is costly it is highly desirable to reliably model predator diet to allow inference on species trophic interactions also in periods when stomach content data are missing.

Atlantic cod (*Gadus morhua*) is a top predator feeding on various fish and invertebrate species (Link and Garrison, 2002) and thus a key species of ecosystems in the northern part of the Atlantic Ocean (Bogstad and Mehl, 1997; Daan, 1973; Hansson et al., 1996; Rudstam et al., 1994). A series of trophic cascades with increases in prey populations following the collapse of the cod populations were described for most of the areas that cod inhabits: Labrador, northern Newfoundland, Flemish Cap, northern Gulf of St. Lawrence, Iceland, Barents Sea (Worm and Myers, 2003), eastern Scotian Shelf (Frank et al., 2005), North Sea (Alheit et al., 2005) and Baltic Sea (Alheit et al., 2005; Casini, 2013; Österblom et al., 2007). During its development process cod switches dietary preferences from one prey type to another (Bagge et al., 1994; Link and Garrison, 2002; van Leeuwen et al., 2013), experiencing ontogenetic shifts typical for many fishes and other animals (Werner and Gilliam, 1984). Juvenile cod prefers small benthic organisms; as it grows, the size of its prey increases; medium size cod starts to include small fishes, like sprat (*Sprattus sprattus*), capelin (*Mallotus villosus*), herring (*Clupea harengus*), into its diet; and large cod eats even bigger fish, like flounder (*Platichthys flesus*) and smaller cod (Bagge et al., 1994; Garrison and Link, 2000; Link and Garrison, 2002; Uzars, 1975).

Besides the importance for ecosystems, cod is also vital for humans as a food and even a livelihood source for many. Even though global cod catches are merely a third of their maximum during the last 65 years (FAO, 2017), cod remain among the top 15 fish species that yielded the highest catches (FAO, 2016).

Water bodies that cod inhabits differ in their diversity of resources: the Baltic Sea has low biodiversity (Elmgren and Hill, 1997; MacKenzie et al., 2007), compared to other areas, for example the North Sea, the Celtic Sea or Icelandic waters. That narrows down the prey choice for the Baltic Sea cod and may potentially increase the strength of predator-prey interactions (May, 1972).

Stomach data of Baltic Sea cod have been well documented for the 1960's-1980's (Uzars, 1994, 1975). However, major changes has happened since that period: sprat has become more abundant, while the cod population has declined severely (Alheit et al., 2005; Casini, 2013; Österblom et al., 2007). Furthermore, body condition of cod has declined (Casini et al., 2016; Eero et al., 2012) with potential implications for predation success. Moreover, predator and prey spatial overlap has changed during 2000s: cod has concentrated mainly in the south-western part of the Baltic Sea (Eero et al., 2015; Bartolino et al., 2017), while herring and sprat densities have increased in the north-eastern part (Casini et al., 2011; Eero et al., 2012). In addition only a portion of sprat is in the same part of the water column as cod (Neuenfeldt and Beyer, 2003).

A newly compiled Baltic cod stomach database covering 1964–2014 (ICES, 2014a) allows to investigate ontogenetic and temporal changes in the cod predation on the commercially important clupeids herring and sprat, while at the same time evaluating a model of predator diet using unique long-term observational data.

Trophic interactions can have noticeable impact on fisheries management of both predator and prey populations. Multispecies models showed that predation mortalities of forage (prey) fish in the North Sea were much higher than previously thought and highly variable in time (Pope, 1991). Underestimating predation mortality and its variability may lead to biased estimates and projections of fish biomass and yield (Tyrrell et al., 2011). At the same time, overfishing of forage fish species may decrease their availability to the predator and consequently affect predator abundance. Pikitch et al. (2012) found that the diet of 16% of the predator species in 72 studied systems consisted of 50 or more percent forage fish. These effects are even stronger in systems like the Baltic Sea, where predators have few alternative prey species. In addition, size selectivity of predator as well as size distribution of both predator and prey need to be taken into consideration in an ecosystem

based fisheries management, as predators and fisheries may compete for the same prey size (Link, 2002).

The long tradition of multispecies modelling in the Baltic Sea is reflected in a wide range of models which span across a broad gradient of applications from tactical to strategic. Many include trophic interactions between cod, herring and sprat in the central Baltic, with marked differences in their approach to species interactions. Tactical models include the Stochastic multispecies model (SMS, ICES, 2012) and the Multispecies virtual population analysis (MSVPA, ICES, 2005). They both account for the length and species prey suitability (Andersen and Ursin, 1977) and average daily ration of cod. However, both SMS and MSVPA are age-structured models and, thus, they convert both predator and prey from age groups into size groups prior to estimation of consumption, and then back to ages. A simplified approach is applied by Multispecies production models (MSPM, Horbowy, 2005) where age groups of all species are replaced with life stages. For all three models, consumption was parametrised using stomach data with a very limited temporal and spatial coverage compared to the present study. Implementations of more strategic models for the central Baltic Sea include Ecopath with Ecosim (EwE; Bauer et al., 2018; Tomczak et al., 2012) and more recently Atlantis (Bossier et al., 2018). Contrary to age-structured models, EwE simplifies the modelled populations into few life-stages, and trophic interaction is based on the "foraging arena" theory (Ahrens et al., 2012; Walters and Juanes, 1993) where vulnerability of prey populations to predation is related to spatial and temporal restrictions of prey and predator activities. The predation parameters of the EwE model used for the integrated assessment of the Baltic Sea (ICES, 2016) were also derived from a sparse, old set of cod stomach data. That model was recently re-parameterized using the newly compiled database of cod stomachs as in our study, but the model was limited to the period 2004–2013 (Bauer et al., 2018), providing little insight into the long-term trophodynamics of cod and clupeids. A more mechanistic approach to trophic interaction is implemented by the Atlantis model, where predator consumption depends on various predator characteristics, such as growth and consumption rate, gape size, functional response, and on a prey availability parameter. SMS and EwE were, however, used to inform dietary patterns of the Atlantis model for the Baltic Sea, which has 2005 as initial year (Bossier et al., 2018).

Our study aims to implement a quantitative model to reconstruct the ontogenetic and main temporal changes in the diet of Baltic cod during the last four decades by modelling the dynamics of cod, herring and sprat populations, their size structures, and trophic interactions. For the first time coupling a model to observations from a unique Baltic dataset on cod stomach content, we compared diet compositions in the periods of major changes in the Baltic system: 1) prior to the ecosystem shift in 1989, which is characterised by high cod and herring abundances and low sprat abundance (Alheit et al., 2005; Casini, 2013; Möllmann et al., 2004); 2) in the period 1989–2007, when cod and herring populations declined and sprat increased; and 3) after 2007, when the cod population increased but was concentrated in the Southern Baltic Sea (Eero et al., 2012). The Globally applicable Area Disaggregated General Ecosystem Toolbox (Gadget; Begley, 2017) was used in this study, as it offers a suitable modelling framework to integrate stomach data into size structured population dynamic models of both cod and clupeids, and represents a valid tool with potential for both tactical and strategic applications.

2. Materials and methods

2.1. Study area and species

The Baltic Sea is a large semi-enclosed brackish water body with strong salinity and temperature gradients (Elmgren, 1984; Leppäkoski et al., 2002). Its salinity is below levels preferred by marine organisms and above levels preferred by freshwater organisms and, thus, induces

physiological stress to both groups. In addition, the Baltic Sea is a geologically young basin, i.e., time for species to invade and adapt has been limited. These are the main reasons for the low biodiversity (Elmgren, 1984; Hammer et al., 2008). As a result the same three species (cod, herring and sprat) are both the bulk of commercial catches (comprising together about 95% of them; ICES, 2013) and the key species of the Baltic Sea ecosystem (Lindegren et al., 2014; Rudstam et al., 1994; Sparholt, 1994).

Cod (Sick, 1965) and herring (Jørgensen et al., 2005; Ojaveer, 1988; Parmanne et al., 1994) each have more than one population in the Baltic Sea. Only Eastern Baltic cod and Central Baltic herring are subjects of the current study. Baltic sprat is described as a single population (Rechlin, 1986). For simplicity, the populations mentioned above will be referred to as cod, herring and sprat in this study. The distribution of these three populations differs, with sprat occupying most of the Baltic Sea while cod and herring just parts of it. Their spatial distributions has also changed in the past few decades, with cod concentrating progressively towards the south-western part of the central Baltic Sea (mostly ICES subdivision (SD) 25 and partly 26; Fig. 1) and the two clupeids
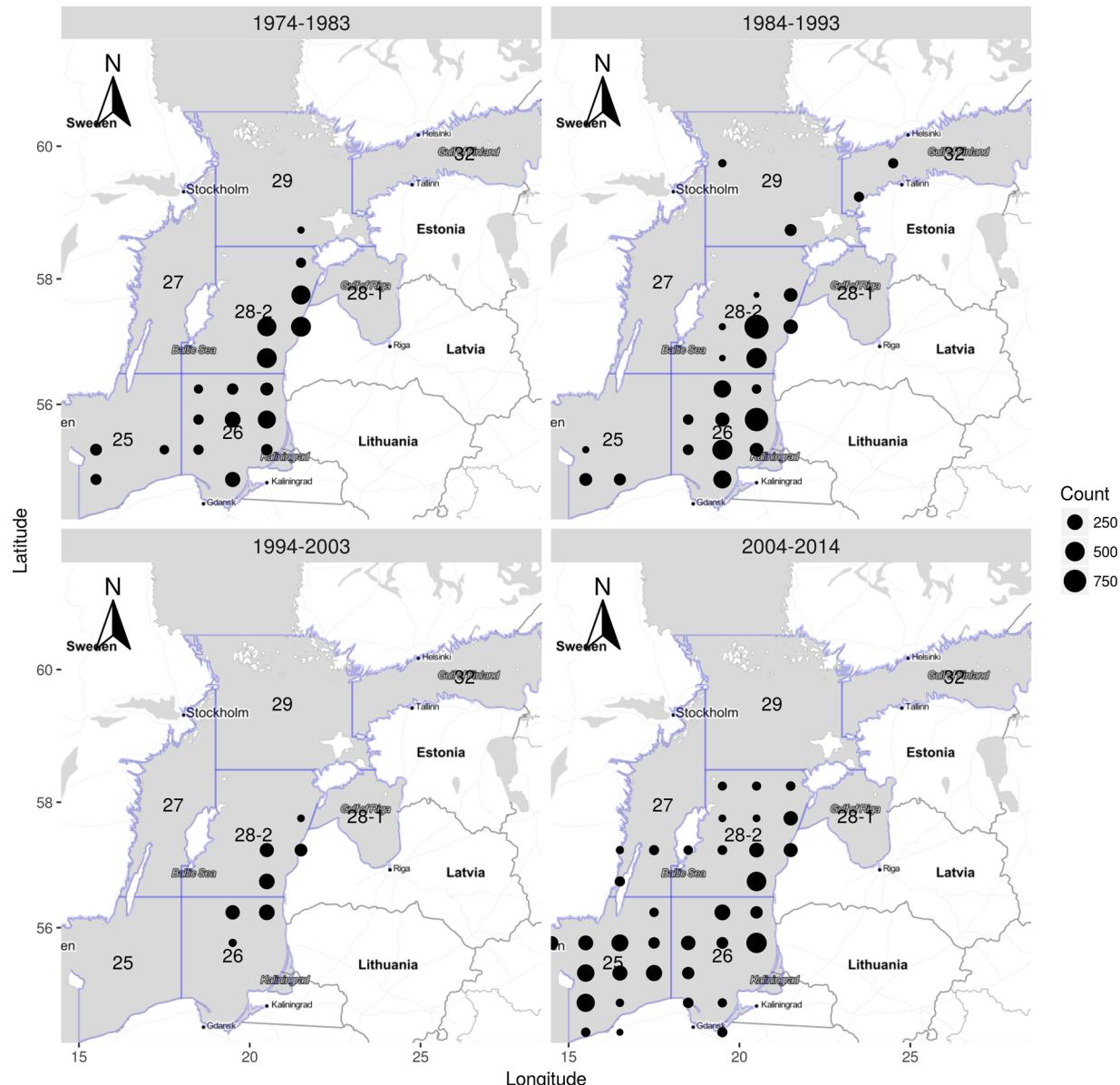
increasing their densities towards the north-eastern part (mostly SD 28–32; Casini et al., 2011; Eero et al., 2012)

2.2. Empirical analysis

2.2.1. Stomach data

A comprehensive dataset of cod stomach data from the Baltic Sea for the period 1964-2014 has been recently prepared under the EU tender No MARE/2012/02 and made available by ICES (Huwer et al., 2014; ICES, 2014a). Data were collected during various national sampling programs of Baltic countries as well as Baltic international trawl survey (BITS, ICES, 2014b). Our analyses cover the time period 1974–2013 (Fig. 1), with gaps in the cod stomach data in the 1975–1979 due to missing cod length measurements (Table A1).

We explored two aspects of cod diet composition in the stomach analysis: species composition and prey size selection. Only full stomachs were used for this purpose. In addition, daily rations of individual cod, including cod with empty and full stomachs, were used to calculate the average consumption of the cod population (see Section

Fig. 1. Spatio-temporal distribution of cod stomach samples in Quarter 1. The size of the circles corresponds to sample size, while location corresponds to the centre of the ICES rectangle (ICES, 1977), where sample was taken. Numbers 25–32 are ICES sub-divisions (ICES, 1969).

2.3.5 "Evacuation models and average consumption"). Seasonal differences in the diet of Baltic cod have been reported by Uzars (1975), especially between the first and second halves of the year. Stomach data had quarterly resolution which was expected to capture such seasonal variation in the diet. Only stomachs from quarters one and four were sampled for a sufficient number of years (Table A1) and were used to parameterize the model. Stomach data for cod smaller than 16 cm were excluded because they have not been consistently sampled for the entire time series. Stomachs from the Gulf of Riga (SD 28-1) were also excluded from the analysis because a different population of herring inhabits this area.

Data comprised of digestion stages 0–2, which represent a gradual increase in level of digestion of prey items with 0 being intact prey, 1 – partly digested prey, and 2 – skeletal material. The 0 digestion stage was excluded from further analysis as it, with high probability, is represented by prey that cod have eaten in the trawl during sampling (Hopkins and Baird, 1975).

2.2.2. Prey species composition of the diet

Sprat, herring, Saduria (*Saduria enthomon*) and mysids (*Mysis* spp., but mainly *Mysis mixta*) comprised most (about 80%) of the cod's diet and were used individually in the analysis, while the remaining food types (about 50 taxonomic groups) were grouped together as "other food".

In order to identify predator length groups with sufficiently similar diet composition, reflecting ontogenetic shifts, we performed hierarchical cluster analysis. We grouped cod into length categories with 5 cm bins and for cod larger than 60 cm with 10 cm bins to have sufficiently large sample size. For each cod length category the weight ratios r_w of the prey species were calculated as:

$$r_w = \frac{w_i}{\sum_{preys} w} \qquad (1)$$

which is the ratio between the weight of all prey of species i (w_i) in the stomachs of the specific cod length category and the total weight of all prey in the stomachs of that cod length category.

Species ratios in the cod stomachs were then compared between the categories using a Bray–Curtis dissimilarity index (Faith et al., 1987, calculated with the package Vegan for R, Oksanen et al., 2018):

$$d_{jk} = \frac{\sum_i |x_{ij} - x_{ik}|}{\sum_i (x_{ij} + x_{ik})}, \qquad (2)$$

which compares the ratio of prey species i in the stomachs of two cod size groups j and k. The index ranges between 0 (identical prey composition) and 1 (no prey is shared) and corresponds to proportional difference between prey composition of two cod size groups (Ricotta and Podani, 2017).

A dissimilarity index of 0.2 or larger was chosen to separate cod length groups. This hierarchical cluster analysis suggested five cod length groups: 16–25, 25–35, 35–60, 60–80 and 80–112 cm. The stomach data were therefore aggregated according to these length groups for further analysis and included as a likelihood component in the multispecies model. Initial analysis showed that 20 stomachs per length group/time-step combination were sufficient to represent species composition of the diet. That is why we limited our analysis to length group/time-step combinations with 20 or more stomachs sampled. For each of the selected length groups prey weight ratios were estimated using Eq. (1) for quarter 1 and 4 in each of the study periods 1974–1988, 1989–2006, and 2007–2013. In addition, to inform the model (see Section 2.3.1) we made the same calculations for each year, respectively.

2.2.3. Length composition of fish prey in the diet

For prey length analysis the same cod length groups as for the species composition were used. Prey items longer than the cod that had consumed them (comprising about 5% of all prey items) were excluded

from analysis, being likely a measurement error. Screening of the available cod stomach data revealed that information on the individual weight of prey with measured lengths was available only for a limited number (about 70%) of samples. To reduce potential biases, the presence ratio (i.e., frequency of occurrence, Hyslop, 1980) was considered as a better indicator of the predator-prey size relationship compared to weight ratio or number ratio, under the assumption that the proportion of stomachs in a cod length group with a prey of a certain size relates to the prey abundance. A benefit of using the presence ratio estimator is that it does not rely on the measurements of individual weights or numbers of prey, both of which may be biased, due to measurement challenges or errors. The presence ratio r_p was calculated as:

$$r_p = \frac{p_{il}}{\sum p}, \qquad (3)$$

which is the ratio between the number of stomachs of the specific cod length category containing prey species i of length l and total number of stomachs of that cod length category.

2.3. Modelling

To reconstruct population dynamics of cod, herring and sprat, their trophic interactions and the effect of fisheries, we built an age-length structured model using Gadget (Globally applicable Area Disaggregated General Ecosystem Toolbox). Gadget models represent biological processes like growth, maturation, reproduction, consumption, etc. in the form of functions, which are often length-based, as well as various components of the ecosystem: interactions between species, impact of environmental variables, impact of fisheries, etc. (Begley, 2017; see also Pérez-Rodríguez et al., 2017; Taylor and Stefansson, 2004; Trenkel et al., 2004 for multispecies model examples).

Gadget was run using the Rgadget package (Elvarsson, 2015) for R (R Core Team, 2016). A database for the model was built and queried using the MFDB package (Lentin, 2014)

The modelling process to estimate unknown parameters in Gadget can be outlined in three steps. First, provided with initial parameter values, Gadget runs a forward projection model. Then it compares obtained predictions to observed values and calculates likelihood scores (negative log-likelihood) to represent goodness of fit. As the last step, Gadget re-adjusts parameter values and re-runs the model until optimum parameter values are found, which produce the overall best fit of the model to multiple data components (Begley, 2017).

The optimization process in steps two and three uses three algorithms: first, a wide area search simulated annealing (Corana et al., 1987) to reach the general area of a solution, followed by a local search Hooke and Jeeves algorithm (Hooke and Jeeves, 1961) to rapidly find a local solution and then Boyden-Fletcher-Goldfarb-Shanno algorithm (BFGS, Bertsekas, 1999) to fine-tune the optimization. This procedure is repeated several times to prevent converging to a local optimum.

Our model used 21 datasets to estimate the parameters (see Table A2). The nature of these datasets is different (length distribution, survey indices, etc), thus, an appropriate function for each data type (called likelihood component) is used to calculate a likelihood score during the optimization. Scores of individual likelihood components are then combined into an overall likelihood score (objective function; Begley, 2017). In order to prevent some likelihood components from dominating the objective function and reduce the impact of low quality data iterative re-weighting is used (ICES, 2014c; Stefánsson, 2003; Taylor et al., 2007):

$$l = \sum_i w_i l_i, \qquad (4)$$

where l is objective function, l_i and w_i are respectively the likelihood score and weight assigned to a likelihood component i.

The iterative re-weighing approach is based on assigning the inverse variance of the fitted residuals as component weights. The variances,

and thus the final weights, are calculated as follows:

1) The initial variance (usually sums of squares, SS) are calculated using the initial parametrization for all likelihood components. The inverse SS (1/SS) are assigned as the initial weights for each likelihood component (initial score multiplied by weight will be 1 for each component).

2) For each likelihood component in a sequence, an optimization run is done where the initial weight is multiplied by 10 000 while weights of other components are multiplied by 1 until the minimum negative log-likelihood score is found. The residual variance is then estimated by dividing the resulting SS of that component by the degrees of freedom (*df*):

$$\sigma^2 = \frac{SS}{df},$$ (5)

3) After the series of optimization runs final weight for each component is set as the inverse of the estimated variance from the step above (weight = $1/\sigma^2$).

2.3.1. Modelling procedure

The time frame for the model was set to 1974–2013, based on stepwise calculations for each quarter (year) and using the whole Baltic Sea (ICES sub-divisions 25–32) as one single area.

We first built the single-species models for cod, herring and sprat (see Table A2 for a summary of data-sources used in the models, and Table A3 for parameter values). Some parameters are highly correlated, e.g., k and L_{inf} in the von Bertalanffy growth function, and thus hard to estimate simultaneously. In those cases, groups of parameters were estimated in different phases. We evaluated goodness of fit of each model based on visual inspection (where we evaluated whether predicted values had similar magnitude and trends as observed values) and by estimating overall and individual components likelihood scores. When satisfactory single-species models were parametrised, they have been linked into a multi-species implementation with cod feeding on both herring and sprat. In addition to herring and sprat which are dynamically represented in the model, Saduria, mysids and "other food" were added as constant prey groups available for cod.

2.3.2. Consumption

Consumption of each prey in the model was a function of both predator (*L*) and prey length (*l*), and related to prey availability, predator requirements and preference for the different preys as follows:

$$C_p(l, L) = \frac{N_L M_L S B_{p,l}}{\sum_{preys} S B_{p,l}}$$ (6)

First, the model estimated the biomass B of prey species p and length l (for sprat and herring, while biomass of Saduria, mysids and "other food" was assumed to be always available and constant through time). Then this biomass was multiplied by a suitability function S, which estimated the probability that the prey would be caught by the predator based on the lengths of predator (*L*) and prey (*l*). In the next step, the model estimated the proportion of biomass of this specific prey p to the total biomass of all suitable preys, $\sum_{preys} p S B_{p,l}$. This proportion was then multiplied by the average consumption (M_L; see 2.3.5 for more details) for the predator of length (*L*) to satisfy its dietary requirements, and multiplied by the number of predator individuals of that length (N_L).

2.3.3. Prey species composition

The selection of prey by predator was determined in the model by a suitability function S. The selection was prey specific, and determined by the shape of the relation between the ratios of the prey and the size of cod that consumed it, as observed in the stomach data.

An exponential suitability function, which logarithmically depends on the size of the predator (*L*), was used to represent the selection of mysids:

$$S(L) = \frac{d\delta}{1 + e^{(-\alpha - \gamma L)}}$$ (7)

The Andersen-Ursin suitability function (Andersen and Ursin, 1977; Ursin, 1973), where suitability depends on the ratio between predator (*L*) and prey (*l*) lengths was used to represent the selection of Saduria (prey length was constant), herring and sprat:

$$S(l, L) = \begin{cases} d e^{-\frac{\left(\ln\frac{L}{l} - p_1\right)^2}{p_4}}, & if \ln\frac{L}{l} \le p_1 \\ d e^{-\frac{\left(\ln\frac{L}{l} - p_1\right)^2}{p_3}}, & if \ln\frac{L}{l} > p_1 \end{cases}$$ (8)

A constant suitability function was used to represent the selection of "other food" as it is independent on both the sizes of predator and prey:

$$S(L) = d$$ (9)

In all three functions the parameter d was used to represent the prey species preference by cod. This parameter was estimated by the model separately for the first and second half of the year, informed by weight ratios estimated from stomach data (see Section 2.2.2; also 2.3.7 in Supplementary material). All the other parameters of the suitability (except for sprat and herring; see Section 2.3.4) were fixed to values estimated from stomach data outside the model.

To compare predicted diet composition to observed we used Bray–Curtis dissimilarity index (Eq. (2); Section 2.2.2, approach similar to Tarnecki et al., 2016).

2.3.4. Prey length composition

Herring and sprat length in predicted cod diet resulted from applying an Andersen-Ursin suitability function (Eq. (8), Andersen and Ursin, 1977; Ursin, 1973) on reconstructed length distributions of cod, herring and sprat. The function was simplified by assuming that $p_3 = p_4$, i.e. the suitability function is symmetrical and not skewed. Parameters $p_{1,3}$ in the suitability function were estimated by the model in different runs informed by prey length composition from stomach data (see Section 2.2.3; also 2.3.7 in Supplementary material), with initial values estimated outside the model from stomach data of cod lengths with sufficient sample size: 39–57 cm cod for herring suitability and 35–50 cm cod for sprat.

2.3.5. Evacuation models and average consumption

The food requirement of cod was represented by its average consumption and expressed as an exponential function of the predator length (*L*):

$$M(L) = m_0 L^{m_1}$$ (10)

Evacuation models and bioenergetic models are two commonly used methods to convert stomach content into daily rations (Hansson et al., 1996). Several of these models were developed for cod in different regions. In this study we used the model of evacuation rate (*R*) developed by (Jones, 1978) in an experimental setting with the North Sea and Faroe cod (Fig. 6):

$$R = 0.16 \left(\frac{L}{40}\right)^{1.4} W^{0.46} 24,$$ (11)

where L is the cod length and W is the weight of its stomach content, $(L/40)^{1.4}$ is length correction, $W^{0.46}$ is weight correction; 0.16 corresponds to digestion rate of fish prey at temperature 8-10°, 24 is for hours in a day.

Stomach data used for this estimation process included empty stomachs to account for individual variation and to estimate an average consumption that is representative of the whole population. We discarded the stomachs that were marked as regurgitated, as well as

stomachs of cod larger than 80 cm, because their daily rations were too variable as a result of limited sample size (Fig. 6).

The amount of food consumed per day was assumed to be equal to the average daily evacuation, so that the parameters m_0 and m_1 of the equation 10 were directly estimated using the cod stomach data and scaled up to represent the consumption in the Gadget model.
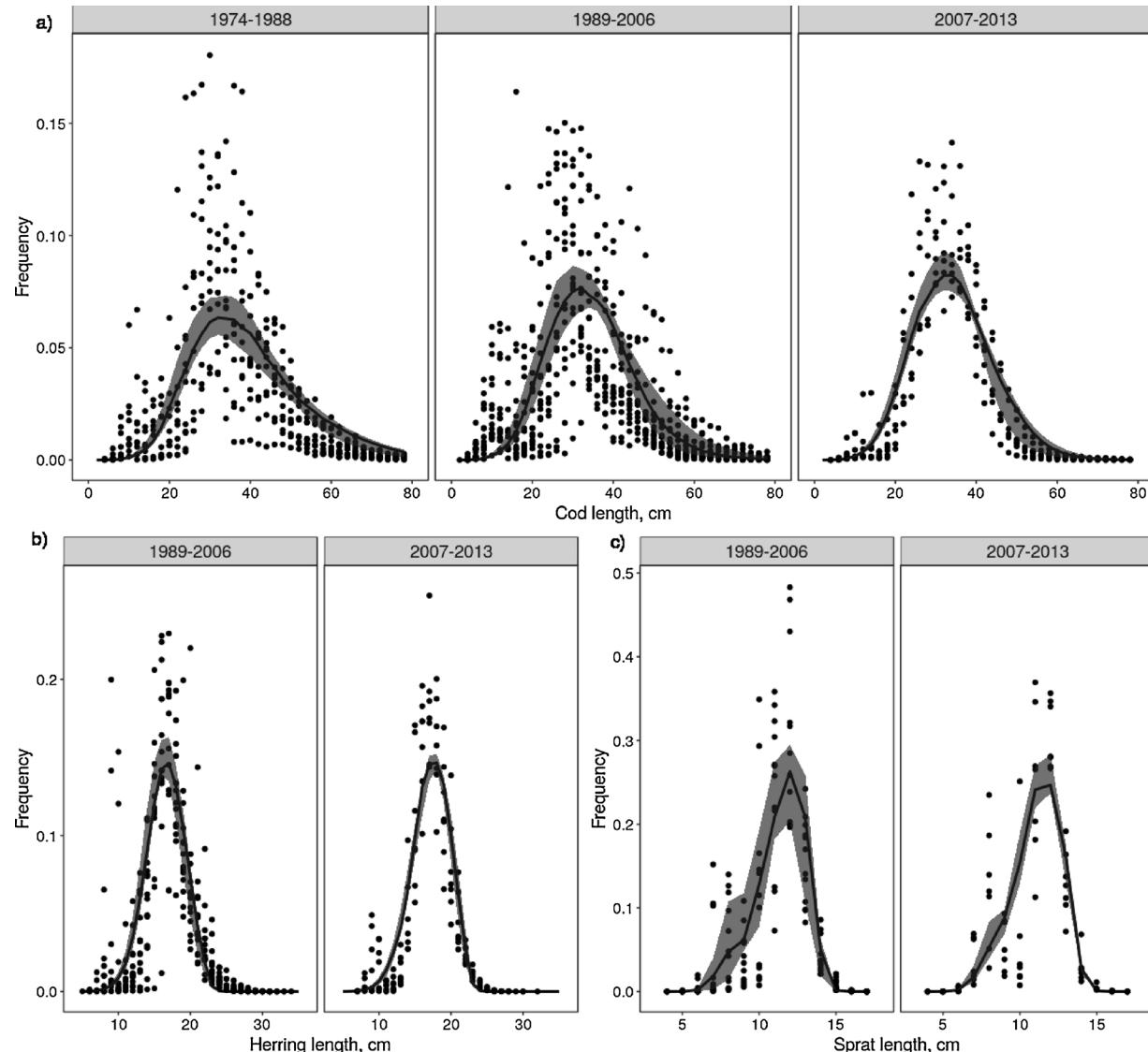
3. Results

To interpret the predicted diet, it is important to evaluate model performance in predicting the underlying abundances and length structures of the predator and prey populations. The model reproduced the general trends observed in the data (Fig. 2, A4-10). The only exceptions were the abundance of cod in the third period (2007–2013), which was lower in the model compared to the survey (Figure A4), abundance of cod larger than 60 cm in the first period (1974–1988), which was higher in the model compared to the survey (Figure A4) and cod and herring length distribution from the survey in certain years (e.g. 1991, 1995 on Figure A7; 1991, 1992 on Figure A8).
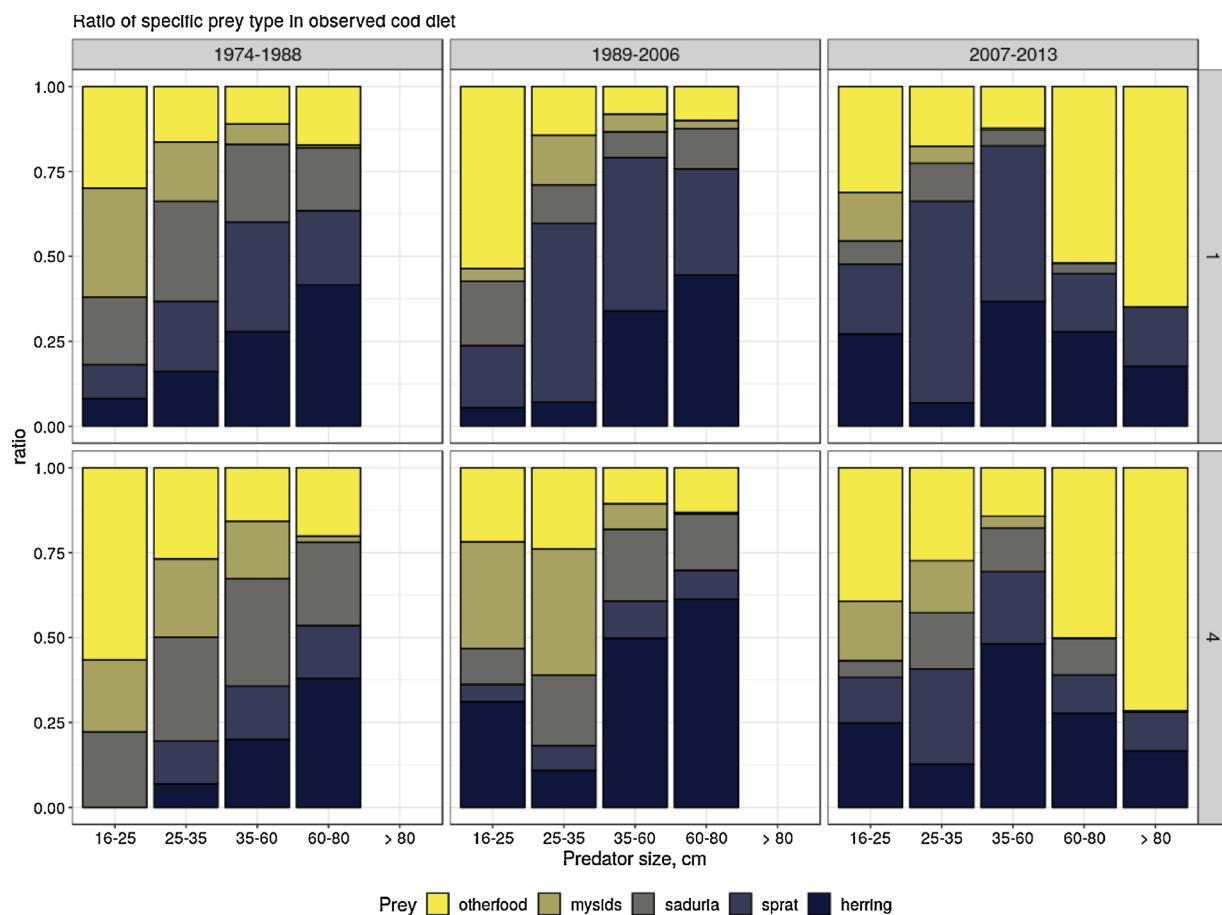
3.1. Prey species composition

The cod stomachs showed marked differences in the ratios of different prey types for cod of different sizes (Fig. 3; bars from left to right). The herring ratio was small in the first two cod length groups, it increased in cod of 35–60 cm, peaked for cod of 60–80 cm (except for the third period) and decreased when cod grew beyond 80 cm. Sprat ratio was the highest for cod of 25–35 cm and gradually decreased as cod grew beyond 35 cm. The ratios of both Saduria and mysids decreased with cod size, though Saduria was an important prey in all cod length groups.

A large portion of the cod diet consisted of sprat in quarter 1 and of herring and benthos in quarter 4 (except for 1974–1988, when cod diets between quarters were similar). In quarter 4 in 1989–2006 and both quarters in 2007–2013 herring ratio in the diet of the smallest cod (16–25 cm) were higher than that of small cod (25–35 cm).

Sprat ratios in quarter 1 increased in all cod groups from 1974–1988 to 1989–2006, but remain stable after that. Sprat ratios in quarter 4 decreased in all cod groups from 1974-1988 to 1989-2006 (except the smallest cod), but increased in 2007–2013. Herring ratios were quite stable in the quarter 1, but in quarter 4 increased in 1989–2006 and declined a bit in 2007–2013. Ratios of mysids and Saduria declined

Fig. 2. Comparison of observed (points) and predicted (line corresponds to 50%, while shaded area to 5% and 95% percentiles of distribution) length distribution for cod (a), herring (b) and sprat (c) catches in scientific surveys in different periods.

Fig. 3. Observed species composition of cod diet with respect to ontogenetic niches and temporal shifts. Three vertical panels correspond to three contrasting periods in the dynamics of cod, herring and sprat: 1) 1974–1989, which is characterised by high cod and herring and low sprat abundance; 2) 1989–2007, when cod and herring populations declined and sprat increased; and 3) 2007–2013, when cod population increased but concentrated in the Southern Baltic. Two horizontal panels correspond to year quarters (1 and 4). Five vertical bars in each sub-panel from left to right are length groups of cod representing ontogenetic niches (see Introduction for more details). Main prey groups of cod (with "other food" gathering all prey items not represented in the other four groups) are colour-coded (see legend). Colour in online version.

with time in all cod groups (except for quarter 4 in the second period for smallest and small cod), especially in the last time-period (2007–2013).

The model was able to represent the general ontogenetic shifts in predicted cod diet (Fig. 4). The proportion of clupeids increased with cod growth and eventually declined when cod reached more than 80 cm in length, while the proportion of mysids and Saduria progressively declined. However, the model systematically underestimated ratio of herring in the cod diet (except for 16–25 cm cod in 1974–1988) and sprat in the diet of smaller cod (< 35 cm), but overestimated ratio of sprat in the diet of larger cod (> 35 cm).

The proportion of sprat slightly increased with time, while the proportion of herring was highest in the first period. The proportion of herring and sprat in quarter 1 was predicted slightly higher than in quarter 4.

The dissimilarity index between the observed and predicted diet composition was in the range 0.08-0.28 during the first period (1974–1988), while it ranged between 0.24 and 0.52 during the second (1989–2006) and third (2007–2013) suggesting a better fitting of the stomach data for all the length groups during the first part of the time series.

3.2. Prey length composition

The length ranges of sprat and herring overlap in both predicted and observed cod diet (i.e. 35–60 cm at Fig. 5), with herring showing a peak at 15–16 cm and sprat at 10 cm.

The size of herring with the highest occurrence in the predicted cod diet was slightly lower than in the observed diet in the second period. Estimated optimal sprat size (cf. p_1 in Eq. (5)) was 19% of cod size, while optimal herring size was 28% of cod size (represented in Fig. 5 as the peaks in the estimated prey length ranges).
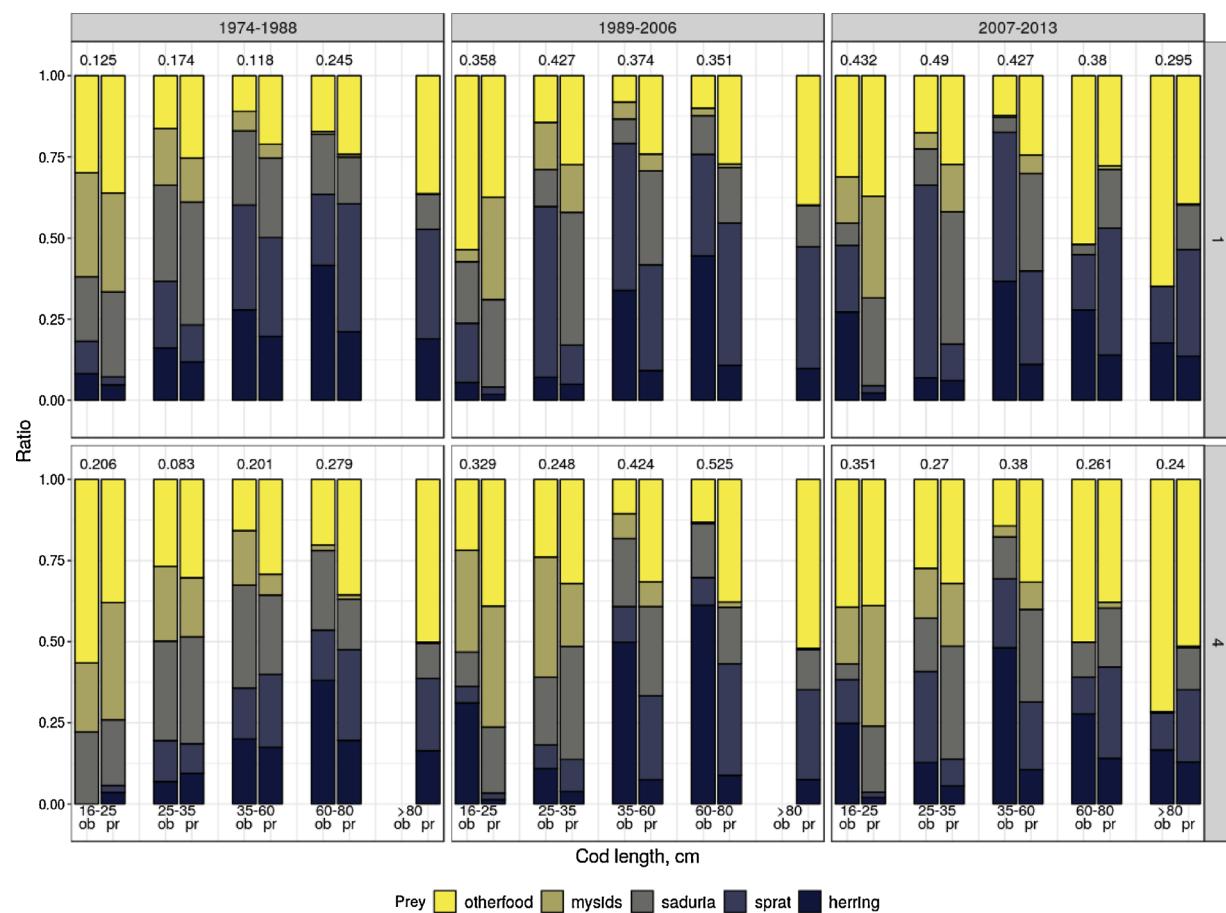
3.3. Consumption

Individual daily consumption reconstructed from stomach content using Jones evacuation model (Eq. (11) in Section 2.3.5) was found to be variable, but showed a general exponential relation to cod size (Fig. 6).
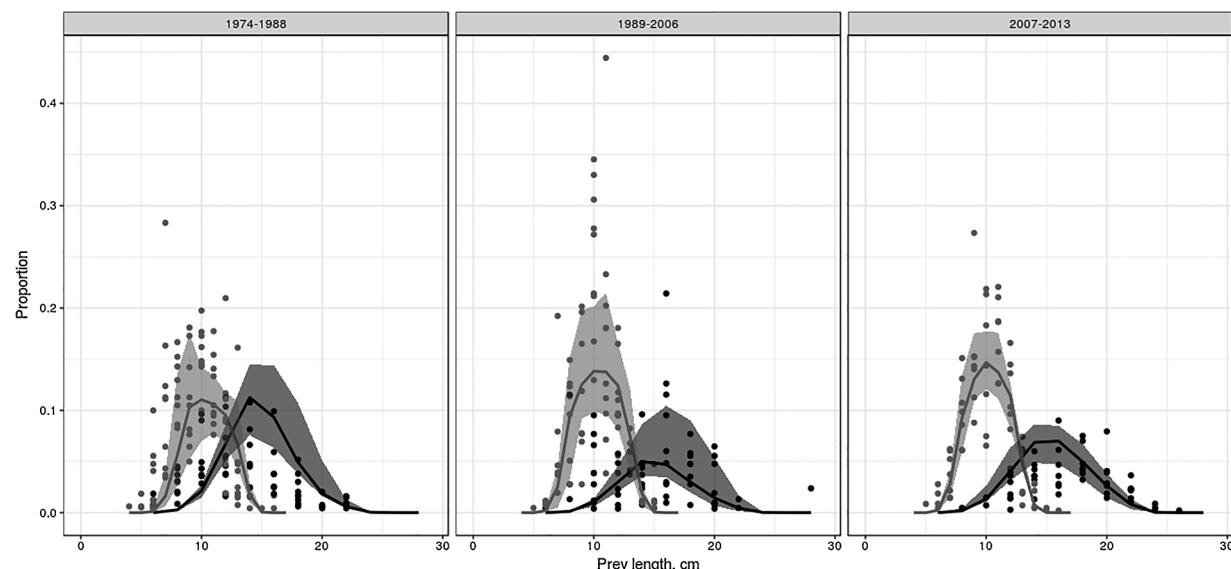
Parameters of average consumption function (see Eq. (10) in Section 2.3.5) fitted to individual daily consumption were: $m_0 = 3.167e-4$ and $m_1 = 2.66$. These values suggest that 22 cm cod consumes on average 1.2 g/day, which increases to 8 g/day for 45 cm cod and 50 g/day for 90 cm cod.
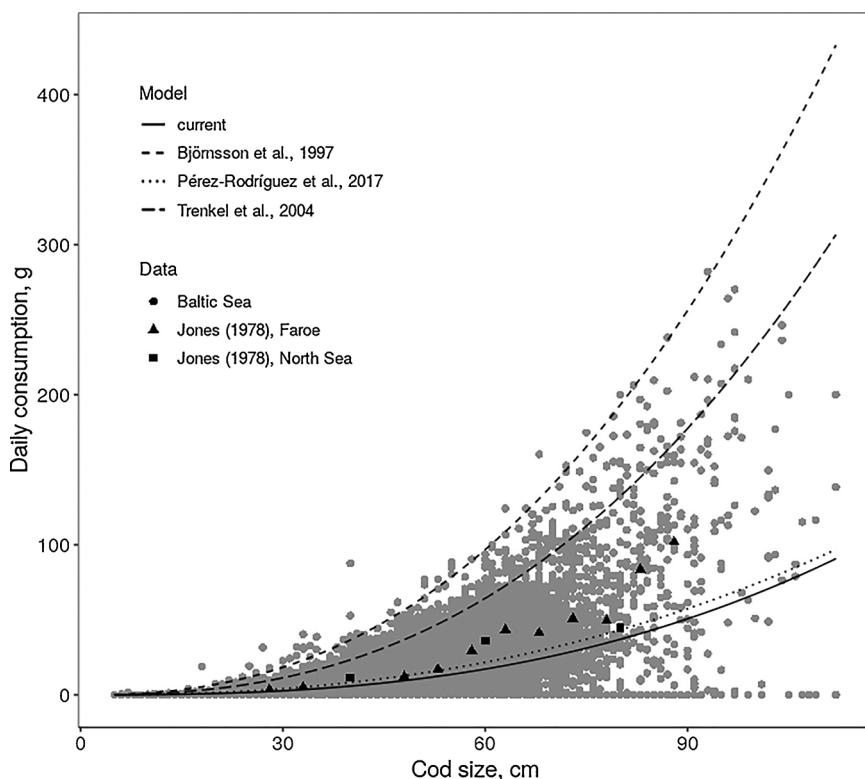
4. Discussion

In this study we aimed to develop a model to represent ontogenetic and temporal changes observed in the cod diet. Our model reproduced the general ontogenetic shifts in the species composition of the cod diet, but represented temporal patterns in diet composition better for the period 1974–1988, when cod was more abundant and more stomachs were sampled. The model predicted similar prey length distributions to

Fig. 4. Comparison between observed (ob) and predicted (pr) species composition of cod diet with respect to ontogenetic niches and temporal shifts. Three vertical panels correspond to three contrasting periods in the dynamics of cod, herring and sprat: 1) 1974–1989, which is characterised by high cod and herring and low sprat abundance; 2) 1989–2007, when cod and herring populations declined and sprat increased; and 3) 2007–2013, when cod population increased but concentrated in the Southern Baltic. Two horizontal panels correspond to year quarters (Q1 and Q4). The bars in each sub-panel represent the diet composition observed (ob) and predicted by the model (pr) for different cod length groups. Numbers above vertical bars correspond to proportional difference between observed and predicted composition as calculated from the Bray–Curtis dissimilarity index. Colour in online version.

Fig. 5. Observed (points) and predicted (line corresponds to 50%, while shaded area to 5% and 95% percentiles of distribution)) prey (herring - black and sprat – light grey) length composition in the diet of 35–60 cm cod in Quarter 1 in different periods.

Fig. 6. Estimation of average consumption (line) based on daily consumption (points) reconstructed by evacuation rate model from content of individual cod stomachs. Average consumption is a function of cod length (see eq. 10 in section 2.3.5). Data points (circles) with daily consumption of 0 g are empty stomachs, while those above 0 g contain food. Other point types represent evacuation rates from laboratory experiments of Jones (1978). Other lines compare model estimates to similar cod models, where model of Pérez-Rodríguez et al. (2017) and current model used average consumption while models of Björnsson et al. (1997) and Trenkel et al. (2004) used maximum consumption. Consumption in the models of Pérez-Rodríguez et al. (2017) and Björnsson et al. (1997) is dependent on temperature, which is 8 °C and 2 °C respectively.

those observed in the stomach content.

Both observed and predicted diets of smaller (juvenile) cod consisted mainly of benthos, while larger cod fed mostly on fishes (herring and sprat). The same ontogenetic development has also been observed for the Georges Bank and the northeast US continental shelf (Garrison and Link, 2000; Link and Garrison, 2002).

The proportion of sprat in the stomachs was larger in 1989–2013, probably due to an increase in sprat abundance observed during this period. On the contrary, the proportion of herring in the stomachs show no clear trend over the whole time period investigated, despite a declining abundance of herring. This pattern in the diet implies that cod preference for herring had increased at decreasing herring abundance, a phenomenon described as 'negative switching' (Chesson, 1984; Neuenfeldt and Beyer, 2006). 'Negative switching' is when the proportion of a prey type in a predator's diet decreases slower than its proportion in total prey abundance. This has been suggested to cause destabilisation of prey populations, as the impact of a predator on a prey with decreasing abundance is over-proportionally high (Chesson, 1984). However, this phenomenon can also be observed as an artefact of variable predator-prey spatial overlap (Neuenfeldt and Beyer, 2006), which was not accounted for in this study.

The stomach data suggest that the proportion of herring decreased over time in the diet of small cod, while it increased in the diet of the smallest cod. This can be a consequence of changes in the spatial distribution of herring and cod. A relevant knowledge gap, however, exists here on how the spatial distribution for the different sizes of cod and herring has changed which may have resulted in the reduced availability of prey of the appropriate size for certain size groups of cod but not for others.

Changes in prey abundances alone are insufficient to explain the complex temporal patterns observed in the cod stomachs, and there are at least two major assumptions of the model that may contribute to deviations between model results and observations, which would deserve future investigation.

First, biomasses of mysids, Saduria and other food were assumed to be constant in the model which is not supported by the decline of

benthos in the observed cod's diet. Little is known on the dynamics of the Baltic Sea benthic communities. However, the abundance of many benthic species is expected to be limited by oxygen concentration in the water (Diaz and Rosenberg, 2008, 1995; Karlson et al., 2002; Mulicki, 1957). The observed decline of mysids and Saduria in the cod diet during 2007–2013 coincides with the observed increase in hypoxic and anoxic areas (Carstensen et al., 2014).

Second, both the model and to some extent also the spatio-temporal coverage of stomach sampling assume that the spatial overlap between cod and its prey is stable over time. The spatial distribution of cod has considerably contracted south-west towards the central Baltic and Bornholm Basin during the 1990s and 2000s (Bartolino et al., 2017; Eero et al., 2012). At the same time, the distribution of both herring and sprat have shifted in an opposite direction towards the north-east (Casini et al., 2011; Eero et al., 2012) generating a possible partial mismatch between cod and its prey.

Modelled consumption was assumed constant over the time period investigated, which is a simplification, given also indications on the decline in body condition of cod in recent years (Casini et al., 2016; Eero et al., 2012). An alternative approach would be to introduce a feeding level parameter, expressing consumption rate as time-variable fraction of the maximum possible long-term consumption rate. This could be derived from the stomach data.

The predicted length distributions of consumed preys were consistent with those observed in the stomach data. Length distributions of herring and sprat in the population may be expected to be better represented since the early-mid 1990s with the beginning of the scientific surveys and the availability of the first length information used by the model. Optimal sprat size at 19% and herring size at 28% of cod size are comparable to the results of similar multispecies models from other areas, where optimal size of capelin for Icelandic cod is 25% of cod size (Björnsson et al., 1997), and 29% for the fish prey of Celtic cod (Trenkel et al., 2004).

The analytical stock assessment of Eastern Baltic cod has not been accepted since 2014 (ICES, 2014d). The main reason is large inconsistency in data mainly due to changes in the cod biology. The growth

of Baltic cod has changed considerably during the time period investigated by the model and both cod weight and length at age showed temporal shifts. This issue was accounted for by using three time-blocks, each one with a specific growth, but could potentially also be addressed by expanding the model we propose here and accounting for the influence of prey abundance on predator growth. One possible reason for the recent decrease in the condition of Baltic cod, expressed in decreased weight and hepatosomatic index and increased amount of cod with empty stomachs, is thought to be the decreased amount of prey available for cod (Eero et al., 2015, 2012).

The recent decrease in cod growth could have affected the selectivity by the commercial fisheries, as slimmer young fish may escape through the cod end of the trawl. At the same time finer mesh size used by scientific survey may have increased selectivity of the older cod. These together are possible causes of inconsistency in abundance indices from commercial catches and scientific survey observed from 2007 (ICES, 2014d). Aware of these issues we decided to estimate catches based on fishing effort (from 2004, when the effort data became available from STECF; Supplementary 2.3.5) rather than to assume them being without error. Trade-off between commercial catches and survey indices were observed also in the model.

Cannibalism has been reported in cod and other gadoids (Bogstad and Mehl, 1997; Daan, 1973; Folkvord and Otteraa, 1993; Mehl, 1988; Uzars and Plikshs, 2000). In exceptional cases cannibalism may account for a large part of total mortality causing challenges for stock assessment and management (Folkvord, 1997). For example, after the decline of capelin, the main prey of cod in the Barents Sea, in the mid-1980s, observed cannibalism of cod increased, accounting for up to 85% of the mortality of age 1–3 cod (Mehl, 1988). The level of cannibalism in Baltic Sea cod seems lower; during 1963–1989 in samples from the Gotland and Gdansk basins (Subdivision 26) and the coastal areas of Subdivision 28, cod was found in up to 4% of stomachs of cod > 35 cm, with value not exceeding 0.5% in most years (Uzars and Plikshs, 2000). Current models can further be improved by including cod cannibalism as we observed it in the stomach data (not presented here). However, it is particularly challenging as the intensity of cannibalism will affect the abundance of the predator directly. In addition, cannibalistic behaviour is typical only for large cod, for which stomach samples are rather limited.

The model presented here was fitted to a large number of various data components (21; see Table A2). Combing information from different sources is expected to provide a more complete picture of the multiple processes and dimensions that characterize fish populations, but at the cost of fitting different types of data with apparently conflicting information (Stefánsson, 2003). The objective function used in this study by Gadget is, essentially, a weighted sum of squares. This objective function provides reasonable point estimates, while inferences may be unreliable. This is also an issue with many of the commonly used methods. Length distributions (Hrafnkelsson and Stefánsson, 2004; Stefánsson, 2003) and abundance indices (Stefánsson, 2003) are challenging to fit using classical likelihood approaches (based on multinomial or Dirichlet distributions), as they underestimate the strong intra-haul correlations between length groups. Spatial bootstrapping approach (Elvarsson et al., 2014), which allows to evaluate uncertainty of estimated parameters and derived quantities, has been developed to provide inferences. However this approach is outside the scope of this paper.

In spite of the limitations of the current model formulation (i.e., fixed abundance of benthos, temperature independent consumption, lack of cannibalism or variable spatial overlap between cod and clupeids) and technical issues in fitting to some of the data components (i.e., trade-off between recent cod catches and survey indices, potential pending issues with the ageing of cod, gaps in spatial and temporal coverage of stomach and other data), the model presented here predicted general patterns in the species and length composition of the cod diet with respect to ontogenetic and partly temporal changes.

Therefore, with proper consideration of its limits and assumptions, the model could be used for further applications, such as, exploring cod-clupeid interactions in the central Baltic Sea, and to evaluate the short- and medium-term consequences of alternative fishing regimes or gear regulations on the trophodynamics of the system.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.fishres.2018.11.023.

References

Ahrens, R.N.M., Walters, C.J., Christensen, V., 2012. Foraging arena theory. Fish Fish. 13, 41–59. https://doi.org/10.1111/j.1467-2979.2011.00432.x.

Alheit, J., Möllmann, C., Dutz, J., Kornilovs, G., Loewe, P., Mohrholz, V., Wasmund, N., 2005. Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. ICES J. Mar. Sci. 62, 1205–1215. https://doi.org/10.1016/j.icesjms.2005.04.024.

Andersen, K.P., Ursin, E., 1977. A multispecies extentsion of the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. Meddelelser fra Danmarks Fisk. og Havundersøgelser 7, 319–435.

Bagge, O., Thurow, F., Steffensen, E., Bay, J., 1994. The Baltic cod. Dana 10, 1–28.

Bartolino, V., Tian, H., Bergström, U., Jounela, P., Aro, E., Dieterich, C., Markus Meier, H.E., Cardinale, M., Bland, B., Casini, M., 2017. Spatio-temporal dynamics of a fish predator: Density-dependent and hydrographic effects on Baltic Sea cod population. PLoS One 12, 1–17. https://doi.org/10.1371/journal.pone.0172004.

Bauer, B., Meier, H.E.M., Casini, M., Hoff, A., Margoński, P., Orio, A., Saraiva, S., Steenbeek, J., Tomczak, M.T., 2018. Reducing eutrophication increases spatial extent of communities supporting commercial fisheries: a model case study. ICES J. Mar. Sci. doi. https://doi.org/10.1093/icesjms/fsy003.

Begley, J., 2017. Gadget User Guide, Marine Research Institute Report Series.

Bertsekas, D., 1999. Nonlinear Programming, 2nd ed. Athena Scientific.

Björnsson, H., Stefánsson, H.N., Pálsson, Ó.K., Vilhjálmsson, H., Stefánsson, G., 1997. General ecology of cod. In: Stefánsson, G., Pálsson, Ó.K. (Eds.), Bormicon. A Boreal Migration and Consumption Model. Marine Research Institute Report p. 223.

Bogstad, B., Mehl, S., 1997. Interactions between Atlantic cod (*Gadus morhua*) and its prey species in the Barents Sea. Forage Fishes Mar. Ecosyst. Am. Fish. Soc. 591–615.

Bossier, S., Palacz, A.P., Nielsen, J.R., Christensen, A., Hoff, A., Maar, M., Gislason, H., Bastardie, F., Gorton, R., Fulton, E.A., 2018. The Baltic Sea Atlantis: an integrated end-to-end modelling framework evaluating ecosystem-wide effects of human-induced pressures. PLoS One. https://doi.org/10.1371/journal.pone.0199168.

Carstensen, J., Conley, D.J., Bonsdorff, E., Gustafsson, B.G., Hietanen, S., Janas, U., Jilbert, T., Maximov, A., Norkko, A., Norkko, J., Reed, D.C., Slomp, C.P., Timmermann, K., Voss, M., 2014. Hypoxia in the Baltic Sea: biogeochemical cycles, benthic fauna, and management. Ambio 43, 26–36. https://doi.org/10.1007/s13280-013-0474-7.

Casini, M., 2013. Spatio-temporal ecosystem shifts in the Baltic Sea: top-down control and reversibility potential. In: Daniels, J.A. (Ed.), Advances in Environmental Research, Vol. 28. Nova Science Publishers Inc, Hauppauge NY.

Casini, M., Kornilovs, G., Cardinale, M., Möllmann, C., Grygiel, W., Jonsson, P., Raid, T., Flinkman, J., Feldman, V., 2011. Spatial and temporal density dependence regulates the condition of central Baltic Sea clupeids: compelling evidence using an extensive international acoustic survey. Popul. Ecol. 53, 511–523. https://doi.org/10.1007/s10144-011-0269-2.

Casini, M., Käll, F., Hansson, M., Plikshs, M., Baranova, T., Karlsson, O., Lundström, K., Neuenfeldt, S., Gårdmark, A., Hjelm, J., 2016. Hypoxic areas, density-dependence and food limitation drive the body condition of a heavily exploited marine fish

predator. R. Soc. Open Sci. 3. https://doi.org/10.1098/rsos.160416.

Chesson, P.L., 1984. Variable predators and switching behavior. Theor. Popul. Biol. 26, 1–26. https://doi.org/10.1016/0040-5809(84)90021-2.

Corana, A., Marchesi, M., Martini, C., Ridella, S., 1987. Minimizing multimodal functions of continuous variables with the "Simulated Annealing" algorithm. ACM Trans. Math. Softw. 13, 262–280. https://doi.org/10.1145/29380.29864.

Daan, N., 1973. A quantitative analysis of the food intake of North Sea cod, *Gadus morhua*. Netherlands J. Sea Res. 6, 479–517. https://doi.org/10.1016/0077-7579(73)90002-1.

Diaz, R.J., Rosenberg, R., 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. In: Ansell, A.D., Gibson, R.N., Barnes, M. (Eds.), Oceanography and Marine Biology: An Annual Review. UCL Press, London, pp. 245–304.

Diaz, R.J., Rosenberg, R., 2008. Spreading dead zones and consequences for marine ecosystems. Science 321, 926–929. https://doi.org/10.1126/science.1156401.

Eero, M., Vinther, M., Haslob, H., Huwer, B., Casini, M., Storr-Paulsen, M., Köster, F.W., 2012. Spatial management of marine resources can enhance the recovery of predators and avoid local depletion of forage fish. Conserv. Lett. 5, 486–492. https://doi.org/10.1111/j.1755-263X.2012.00266.x.

Eero, M., Hjelm, J., Behrens, J., Buchmann, K., Cardinale, M., Horbowy, J., Hüssy, K., Casini, M., Gasyukov, P., Kirkegaard, E., Oeberst, R., Plikshs, M., Kornilovs, G., Krumme, U., Köster, F.W., Radtke, K., Raid, T., Schmidt, J., Tomczak, M., Vinther, M., Zimmermann, C., Storr-Paulsen, M., 2015. Eastern Baltic cod in distress: biological changes and challenges for stock assessment. ICES J. Mar. Sci. https://doi.org/10.1093/icesjms/fsv109.

Elmgren, R., 1984. Trophic dynamics in the enclosed, brackish Baltic Sea. Rapp. P.-v. Reun. Cons. int. Explor. Mer. 183, 152–169.

Elmgren, R., Hill, C., 1997. Ecosystem function at low biodiversity - the Baltic example. In: Ormond, R.G., Gage, J.D., Angel, M.V. (Eds.), Marine Biodiversity – Patterns and Processes. Cambridge University Press, Cambridge, pp. 319–336.

Elvarsson, B.T., 2015. RGadget: A R–package for Development, Testing and Analysis of Gadget Models. ICES C. 2015/A37. pp. 2–4.

Faith, D.P., Minchin, P.R., Belbin, L., 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69, 57–68. https://doi.org/10.1007/bf00038687.

FAO, 2008. Fisheries Management. 2. The Ecosystem Approach to Fisheries 2.1. Best Practices in Ecosystem Modelling for Informing an Ecosystem Approach to Fisheries, FAO. Technical Guidelines for Responsible Fisheries. FAO Fisheries Technical Guidelines for Responsible Fisheries. No. 4, Suppl. 2, Add. 1. FAO, Rome. https://doi.org/10.1002/9780470015902.a0003252.pub3.

FAO, 2016. The State of World Fisheries and Aquaculture 2016. Contributing to Food Security and Nutrition for All. Rome. .

FAO, 2017. Fishery Statistics. [WWW Document]. URL. http://www.fao.org/figis/servlet/SQServlet?file=/work/FIGIS/prod/webapps/figis/temp/hqp_1420115122316191519.xml&outtype=html.

Folkvord, A., 1997. Ontogeny of cannibalism in larval and juvenile fishes with special emphasis on Atlantic cod. In: Chambers, R.C., Trippel, E. (Eds.), Early Life History and Recruitment in Fish Populations. pp. 251–278.

Folkvord, A., Hunter, J.R., 1986. Size-specific vulnerability of northern anchovy, *Engraulis mordax*, larvae to predation by fishes. Fish. Bull. 84, 859–869.

Folkvord, A., Otteraa, H., 1993. Effect of initial size distribution, day length, and feeding frequency on growth, survival, and cannibalism in juvenile Atlantic cod (*Gadus morhua* L.). Aquaculture 11, 243–260.

Frank, K.T., Petrie, B., Choi, J.S., Leggett, W.C., 2005. Trophic cascades in a formerly cod-dominated ecosystem. Science 308, 1621–1623. https://doi.org/10.1126/science.1113075.

Garrison, L.P., Link, J.S., 2000. Fishing effects on spatial distribution and trophic guild structure of the fish community in the Georges Bank region. ICES J. Mar. Sci. 57, 723–730. https://doi.org/10.1006/jmsc.2000.0713.

Hammer, C., Dorrien, C., Ernst, P., Gröhsler, T., Köstner, F., Mackenzie, B., Möllmann, C., Wegner, G., Zimmermann, C., 2008. Fish stock developement under hydrographic and hydrochemical aspects, the history of Baltic Sea fisheries and its management. In: Feistel, R., Nausch, G., Wasmund, N. (Eds.), State and Evolution of the Baltic Sea, 1952-2005. John Wiley & Sons, Inc, pp. 543–582.

Hansson, S., Rudstam, L.G., Kitchell, J.F., Johnson, B.L., Peppard, P.E., 1996. Predation rates by North Sea cod (*Gadus morhua*) – predictions from models on gastric evacuation and bioenergetics. ICES J. Mar. Sci. 53, 107–114.

Holling, C.S., 1959. Some characteristics of simple types of predation and parasitism-abstract. Can. Entomol. 91, 385–398.

Hooke, R., Jeeves, T.A., 1961. Direct search solution of numerical and statistical problems. J. ACM 8, 212–229.

Hopkins, T.L., Baird, R.C., 1975. Net feeding in mesopelagic fishes. Fish. Bull. U.S. 73, 908–914.

Horbowy, J., 2005. The dynamics of Baltic fish stocks based on a multispecies stock production model. J. Appl. Ichthyol. 21, 198–204. https://doi.org/10.1111/j.1439-0426.2005.00596.x.

Hrafnkelsson, B., Stefánsson, G., 2004. A model for categorical length data from groundfish surveys. Can. J. Fish. Aquat. Sci. 61, 1135–1142. https://doi.org/10.1139/f04-049.

Huwer, B., Neuenfeldt, S., Rindorf, A., Andreasen, H., Levinsky, S.-E., Storr-Paulsen, M., Dalmann, R.S., Haslund, O.H., Horbowy, J., Pachur, M., Pawlak, J., Ustups, D., Kruze, E., Sics, I., Uzars, D., Velasco, A., Kempf, A., Eberle, S., Floeter, J., Temming, A., van Hal, R., de Boois, I., Pennock, I., Hoek, R., Pinnegar, J., Hunter, E., Plirö, A., Casini, M., Belgrano, A., 2014. Study on Stomach Content of Fish to Support the Assessment of Good Environmental Status of Marine Food Webs and the Prediction of MSY After Stock Restoration.

Hyslop, E.J., 1980. Stomach contents analysis—a review of methods and their application. J. Fish Biol. 17, 411–429. https://doi.org/10.1111/j.1095-8649.1980.tb02775.x.

ICES, 1969. Fishery Statistical Notes: North-east Atlantic Statistical Area. ICES C. 1969/D6. .

ICES, 1977. ICES Statistical Rectangle Coding System. ICES C. 1977/Gen3. .

ICES, 2005. Report of the Study Group on Multispecies Assessment in the Baltic (SGMAB). 13-17 June 2005, Riga, Latvia. ICES CM 2005/H:06. .

ICES, 2012. Report of the Workshop on integrated/multispecies Advice for Baltic Fisheries (WKMULTBAL). 6–8 March 2012, Charlottenlund, Denmark. ICES CM 2012/ACOM:40. .

ICES, 2013. Report of the Baltic Fisheries Assessment Working Group 2013 (WGBFAS). 10-17 April 2013, ICES Headquarters, Copenhagen. ICES CM 2013/ACOM:10 747. .

ICES, 2014a. Report of the Study Group on Spatial Analysis for the Baltic Sea (SGSPA-TIAL). 4–6 November 2014, Gothenburg, Sweden. ICES CM 2014/SSGRSP:08.

ICES, 2014b. Manual for the Baltic International Trawl Surveys (BITS). Series of ICES survey protocols SISP 7 - BITS. 71 pp.

ICES, 2014c. Report of the working group on biology and assessment of deep-sea fisheries resources (WGDEEP). 4–11 April 2014, Copenhagen, Denmark . ICES CM 2014/ACOM:17.

ICES, 2014d. Report of the Baltic Fisheries Assessment Working Group (WGBFAS). 3-10 April 2014 , Copenhagen, Denmark. ICES C. 2014/ACOM:10 932.

ICES, 2016. Report of the Workshop on Developing Integrated Advice for Baltic Sea Ecosystem-based Fisheries Management (WKDEICE). 18-21 April 2016, Helsinki, Finland. ICES CM 2016/SSGIEA:13. .

Jørgensen, H.B.H., Hansen, M.M., Bekkevold, D., Ruzzante, D.E., Loeschcke, V., 2005. Marine landscapes and population genetic structure of herring (*Clupea harengus* L.) in the Baltic Sea. Mol. Ecol. 14, 3219–3234. https://doi.org/10.1111/j.1365-294X.2005.02658.x.

Jones, R., 1978. Estimates of the food consumption of haddock (*Melanogrammus aeglefinus*) and cod (*Gadus morhua*). J. Cons. Int. Explor. Mer 38, 18–27.

Karlson, K., Rosenberg, R., Bonsdorff, E., 2002. Temporal and spatial large-scale effects on eutrophication and oxygen deficiency on bentic fauna in Scandinavian and Baltic waters - a review. Oceanogr. Mar. Biol. an Annu. Rev. 40, 427–489.

Lentin, J., 2014. MFDB: MareFrame DB Querying Library. R package version 6.0-0. .

Leppäkoski, E., Olenin, S., Gollasch, S., 2002. The Baltic Sea – a field laboratory for invasion biology. In: Leppäkoski, E., Gollasch, S., Olenin, S. (Eds.), Invasive Aquatic Species of Europe. Distribution, Impacts and Management. Springer Netherlands, Dordrecht, pp. 253–259. https://doi.org/10.1007/978-94-015-9956-6_27.

Lindegren, M., Andersen, K.H., Casini, M., Neuenfeldt, S., 2014. A Metacommunity Perspective on Source – Sink Dynamics and Management : the Baltic Sea As a Case Study 24. pp. 1820–1832.

Link, J.S., 2002. Ecological considerations in fisheries management: When does it matter? Fisheries 27, 10–17. https://doi.org/10.1577/1548-8446(2002)027<0010.

Link, J.S., Garrison, L.P., 2002. Trophic ecology of Atlantic cod *Gadus morhua* on the northeast US continental shelf. Mar. Ecol. Prog. Ser. 227, 109–123. https://doi.org/10.3354/meps227109.

Lundvall, D., Svanbäck, R., Persson, L., Byström, P., 1999. Size-dependent predation in piscivores: interactions between predator foraging and prey avoidance abilities. Can. J. Fish. Aquat. Sci. 56, 1285–1292. https://doi.org/10.1139/f99-058.

MacKenzie, B.R., Gislason, H., Möllmann, C., Köster, F.W., 2007. Impact of 21st century climate change on the Baltic Sea fish community and fisheries. Glob. Chang. Biol. 13, 1348–1367. https://doi.org/10.1111/j.1365-2486.2007.01369.x.

May, R.M., 1972. Will a large complex system be stable? Nature 238, 413–414. https://doi.org/10.1038/238413a0.

Mehl, S., 1988. The Northeast Arctic cod stock's consumption of commercially exploited prey species in 1984-1986. Rapp. Proces-verbaux des Reun. Cons. Int. Pour l'Exploration la Mer 185–205.

Möllmann, C., Kornilovs, G., Fetter, M., Köster, F.W., 2004. Feeding ecology of central Baltic Sea herring and sprat. J. Fish Biol. 65, 1563–1581. https://doi.org/10.1111/j.1095-8649.2004.00566.x.

Mulicki, Z., 1957. Ecology of the more important Baltic invertebrates. Pr. Morsk. Inst. Ryb. Gdyni 9, 313–379.

Neuenfeldt, S., Beyer, J.E., 2003. Oxygen and salinity characteristics of predator-prey distributional overlaps shown by predatory Baltic cod during spawning. J. Fish Biol. 62, 168–183. https://doi.org/10.1046/j.1095-8649.2003.00013.x.

Neuenfeldt, S., Beyer, J.E., 2006. Environmentally driven predator–prey overlaps determine the aggregate diet of the cod *Gadus morhua* in the Baltic Sea. Mar. Ecol. Prog. Ser. 310, 151–163. https://doi.org/10.3354/meps310151.

Ojaveer, E., 1988. Baltic Herrings. Agropromisdat, Moskow.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2018. Vegan: Community Ecology Package. R package version 2.5-3. https://CRAN.R-project.org/package=vegan.

Österblom, H., Hansson, S., Larsson, U., Hjerne, O., Wulff, F., Elmgren, R., Folke, C., 2007. Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. Ecosystems 10, 877–889. https://doi.org/10.1007/s10021-007-9069-0.

Parmanne, R., Rechlin, O., Sjöstrand, B., 1994. Status and future of herring and sprat stocks in the Baltic Sea. Dana 10, 29–59.

Pérez-Rodríguez, A., Howell, D., Casas, M., Saborido-Rey, F., Ávila-De Melo, A., 2017. Dynamic of the Flemish Cap commercial stocks: use of a Gadget multispecies model to determine the relevance and synergies among predation, recruitment, and fishing. Can. J. Fish. Aquat. Sci. 74, 582–597. https://doi.org/10.1139/cjfas-2016-0111.

Pikitch, E., Boersma, P.D., Boyd, I.L., Conover, D.O., Cury, P., Essington, T., Heppell, S.S., Houde, E.D., Mangel, M., Pauly, D., Plagányi, É., Sainsbury, K., Steneck, R., 2012. Little Fish, Big Impact: Managing a Crucial Link in Ocean Food Webs. Lenfest Ocean

Program, Washington, DC.

Pope, J.G., 1991. The ICES multispecies assessment working group: evolution, insights, and future problems. ICES Mar. Sci. Symp, vol. 193, 22e33.

R Core Team, 2016. R: a Language and Environment for Statistical Computing. R foundation for statistical computing.

Rechlin, O., 1986. Remarks on Baltic Sea Sprat Assessment in Relation to Stock Identity. ICES C. 1986/J16 1–6. .

Ricotta, C., Podani, J., 2017. On some properties of the Bray–Curtis dissimilarity and their ecological meaning. Ecol. Complex. 31, 201–205.

Rudstam, L.G., Aneer, G., Hildén, M., 1994. Top-down control in the pelagic Baltic ecosystem. Dana 10, 105–129.

Scharf, F.S., Juanes, F., Rountree, R.A., 2000. Predator size - prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Mar. Ecol. Prog. Ser. 208, 229–248. https://doi.org/10.3354/meps208229.

Schoener, T.W., 1974. Resource partitioning in ecological communities. Science 185 (4145), 27–39. http://www.jstor.org/stable/1738612.

Sick, K., 1965. Haemoglobin polymorphism of cod in the Baltic and the Danish Belt Sea. Hereditas 54, 19–43.

Solomon, M.E., 1949. The natural control of animal populations. J. Anim. Ecol. 18, 585–610. https://doi.org/10.1111/J.1365-2745.2008.01361.X.

Sparholt, H., 1994. Fish species interactions in the Baltic Sea. Dana 10, 131–162.

Stefánsson, G., 2003. Issues in multispecies models. Nat. Resour. Model. 16, 415–437. https://doi.org/10.1111/j.1939-7445.2003.tb00121.x.

Tarnecki, J., Wallace, A., Simons, J., Ainsworth, C., 2016. Progression of a Gulf of Mexico food web supporting Atlantis ecosystem model development. Fish. Res. 179, 237–250. https://doi.org/10.1016/j.fishres.2016.02.023.

Taylor, L., Stefansson, G., 2004. Gadget models of cod–capelin–shrimp interactions in Icelandic waters. ICES CM 2004/FF:29.

Taylor, L., Begley, J., Kupca, V., Stefansson, G., 2007. A simple implementation of the statistical modelling framework Gadget for cod in Icelandic waters. Afr. J. Mar. Sci. 29, 223–245. https://doi.org/10.2989/AJMS.2007.29.2.7.190.

Tomczak, M.T., Niiranen, S., Hjerne, O., Blenckner, T., 2012. Ecosystem flow dynamics in the Baltic Proper—using a multi-trophic dataset as a basis for food–web modelling. Ecol. Modell. 230, 123–147. https://doi.org/10.1016/j.ecolmodel.2011.12.014.

Trenkel, V.M., Pinnegar, J.K., Blanchard, J.L., Tidd, A.N., 2004. Can Multispecies Models Be Expected to Provide Better Assessments for Celtic Sea Groundfish Stocks? ICES C. 2004/FF05. pp. 1–26.

Tyrrell, M.C., Link, J.S., Moustahfid, H., 2011. The importance of including predation in fish population models : implications for biological reference points. Fish. Res. 108, 1–8. https://doi.org/10.1016/j.fishres.2010.12.025.

Ursin, E., 1973. On the prey size preferences of cod and dab. Meddelelser fra Danmarks Fisk. og Havundersøgelser 7, 85–98.

Uzars, D., 1975. Peculiarities of Feeding and Quantitative Food Consumption of Eastern Baltic Cod. ICES C. 1975 F. .

Uzars, D., 1994. Feeding of cod (*Gadus morhua callarias* L.) in the Central Baltic in relation to environmental changes. ICES Mar. Sci Symp 198, 612–623.

Uzars, D., Plikshs, M., 2000. Cod (*Gadus morhua* L.) cannibalism in the Central Baltic: interannual variability and influence of recruit abundance and distribution. ICES J. Mar. Sci. 57, 324–329.

van Leeuwen, A., Huss, M., Gårdmark, A., Casini, M., Vitale, F., Hjelm, J., Persson, L., de Roos, A.M., 2013. Predators with multiple ontogenetic niche shifts have limited potential for population growth and top-down control of their prey. Am. Nat. 182, 53–66. https://doi.org/10.1086/670614.

Walters, C.J., Juanes, F., 1993. Recruitment limitation as a consequence of natural-selection for use of restricted feeding habitats and predation risk-taking by juvenile fishes. Can. J. Fish. Aquat. Sci. 50, 2058–2070. https://doi.org/10.1139/f93-229.

Webb, P.W., 1976. The effect of size on the fast-start performance of rainbow trout *Salmo gairdneri*, and a consideration of piscivorous predator-prey interactions. J. Exp. Biol. 65, 157–177.

Werner, E.E., Gilliam, J.F., 1984. The ontogenetic niche and species interactions in size-structured populations. Annu. Rev. Ecol. Syst. 15, 393–425. https://doi.org/10.1146/annurev.soc.30.012703.110553.

Worm, B., Myers, R.A., 2003. Meta-analysis of cod–shrimp interactions reveals top-down control in oceanic food webs. Ecology 84, 162–173.