

RESEARCH PAPER



Spatial contraction of demersal fish populations in a large marine ecosystem

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Abstract

Aim: The interdependencies between trophic interactions, environmental factors and anthropogenic forcing determine how species distributions change over time. Large changes in species distributions have occurred as a result of climate change. The objective of this study was to analyse how the spatial distribution of cod and flounder has changed in the Baltic Sea during the past four decades characterized by large hydrological changes.

Location: Baltic Sea

Taxon: Cod (*Gadus morhua*) and flounder (*Platichthys flesus*).

Methods: Catch per unit of effort (CPUE) data for adult and juvenile cod and for adult flounder were modelled using Delta-Generalized additive models including environmental and geographical variables between 1979 and 2016. From the annual CPUE predictions for each species, yearly distribution maps and depth distribution curves were obtained. Mean depth and the depth range were estimated to provide an indication on preferred depth and habitat occupancy.

Results: Adult and juvenile cod showed a contraction in their distribution in the southern areas of the Baltic Sea. Flounder, instead, showed an expansion in its distribution with an increase in abundance in the northern areas. The depth distributions showed a progressive shift of the mean depth of occurrence towards shallower waters for adult cod and flounder and towards deeper waters for juvenile cod, as well as a contraction of the species depth ranges, evident mainly from the late 1980s.

Main conclusions: Our study illustrates large changes in the spatial distribution of cod and flounder in the Baltic Sea. The changes in depth distribution occurred from the late 1980s are probably due to a combination of expanded areas of hypoxia in deep waters and an increase in predation risk in shallow waters. The net effect of these changes is an increased spatial overlap between life stages and species, which may amplify cod cannibalism and the interaction strength between cod and flounder.

KEYWORDS

Baltic Sea, depth preference, *Gadus morhua*, habitat contraction, *Platichthys flesus*, spatial distribution

1 | INTRODUCTION

The distribution of species is the result of the relations between the intrinsic characteristics of the populations, trophic interactions, as well as environmental and anthropogenic forcing (Layeghifard, Makarenkov, & Peres-Neto, 2015 and references therein) as shown in marine (Romagnoni, Mackinson, Hong, & Eikeset, 2015), freshwater (Bond & Jones, 2015 and references therein) and terrestrial environments (Robinson et al., 2011 and references therein). The interdependencies between these processes determine how the abundance of a species in a specific area is likely changing over time. Hence, investigating both the spatial and the temporal component of these dynamics is of primary importance to understand population dynamics. This is particularly true under climate change when large redistributions of species have been increasingly recorded (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Loarie et al., 2009).

Ecosystem-Based Fisheries Management (EBFM) is a management strategy to “plan, develop, and manage fisheries in a manner that addresses the multiple needs and desires of society without jeopardizing the options for future generations to benefit from the full range of ecosystem goods and services” (Marasco et al., 2007, pp. 929–930). In moving towards EBFM, understanding the spatiotemporal dynamics of marine ecosystems is of paramount importance (Eero et al., 2012). From a management perspective, in the latest years increasing effort has been devoted to developing spatially explicit stock assessments as well as multispecies models that can handle information such as the spatial distribution of species. These models are used to account for the spatial variability of species and their interactions through predator–prey relationships or competition, and to assess the causes and consequences of the changes in their distributions (Cadurin & Secor, 2009; Romagnoni et al., 2015). In particular, these models should take into account the environmental variability that fish populations experience in their area of distribution as well as mechanisms such as density dependence and age- or stage-dependent habitat preference (Ciannelli, Fauchald, Chan, Agostini, & Dingsør, 2008; Planque, Loots, Petitgas, Lindstrøm, & Vaz, 2011).

The Baltic Sea (Figure 1) is one of the largest brackish areas in the world and is one of the 66 Large Marine Ecosystems identified and described by the National Oceanic and Atmospheric Administration in terms of bathymetry, hydrography, productivity, and trophic relationships (Sherman & Hempel, 2009). Scarce and irregular saline water inflows from the North Sea, a water residence time of about 25–30 years, and the lack of deep water formation make the Baltic Sea particularly prone to hypoxia (Carstensen, Andersen, Gustavson, & Conley, 2014). Particularly, since the early 1990s the anoxic and hypoxic areas have increased exponentially as part of a global phenomenon of oceans' deoxygenation (Breitburg et al., 2018). This has resulted in degradation or elimination of benthic communities over vast areas of the Baltic Sea (Conley et al., 2009).

In the Baltic Sea, cod (*Gadus morhua*) and flounder (*Platichthys flesus*) are the two dominant species in the demersal fish

community (Lindegren, Möllmann, Nielsen, & Stenseth, 2009; Ustups, Müller-Karulis, Bergström, Makarchouk, & Šics, 2013), and both species are of high economic importance. The Eastern Baltic cod stock (hereafter referred to as Baltic cod) has been the focus of many studies throughout the years and information on its spatial dynamics shows that it has experienced a dramatic change in abundance and distribution throughout the last century (Bartolino et al., 2017; Eero, MacKenzie, Köster, & Gislason, 2011). Conversely no studies have investigated the long-term Baltic-wide spatiotemporal dynamics of flounder. Moreover, the potential long-term changes in vertical distribution have not been analysed, for neither cod nor flounder. Eutrophication in combination with long retention times of the deep waters of the Baltic Sea has made extensive areas of the seafloor hypoxic (Carstensen et al., 2014) and therefore unsuitable for demersal fish species (see for cod Casini et al., 2016). However, no study has shown whether and how cod and flounder have responded to these environmental changes. It may be hypothesized, for instance, that the worsened deep water oxygen conditions (Figure 1) may have promoted changes in depth distribution and caused habitat contraction of the two species.

Here, we modelled newly standardized catch data from trawl surveys conducted between 1979 and 2016 to investigate how the spatial distribution of cod and flounder has changed in the Baltic Sea in the last four decades. Specifically, we were interested in whether cod and flounder have changed their mean depth of distribution and their depth distribution range.

2 | MATERIALS AND METHODS

2.1 | Trawl survey data

Standardized catch per unit of effort (CPUE) in weight (kg/hr) of cod and flounder was obtained from data collected during the Baltic International Trawl Survey (ICES, 2014a) and during historical Swedish and Latvian trawl surveys carried out between 1979 and 2016 in ICES Subdivisions (SDs) 22–29 (Figure 1). For information about the standardization and the survey database, see Orio, Florin, et al. (2017).

We aimed at following the spatiotemporal changes of adult mature cod (≥ 30 cm, ICES, 2017a), juvenile immature cod (15–30 cm, Eero et al., 2015; ICES, 2017a), and adult mature flounder (≥ 20 cm length, ICES, 2014b; Orio, Bergström, et al., 2017). Not all hauls in the historical surveys had flounder CPUEs per length class. However, based on the analyses and conclusions published in Orio, Florin, et al. (2017), we also assumed that the spatiotemporal changes in the total flounder CPUEs would reliably represent the trends of the spawning part of the population. In the case of juvenile cod, our analyses rely on the assumption we made when defining the length of this life stage. From around 2005, the mean length at first maturity of cod has decreased to values lower than 30 cm (Köster et al., 2016) and therefore we probably have a mix of mature and immature fish in our juvenile cod group, which could blur some

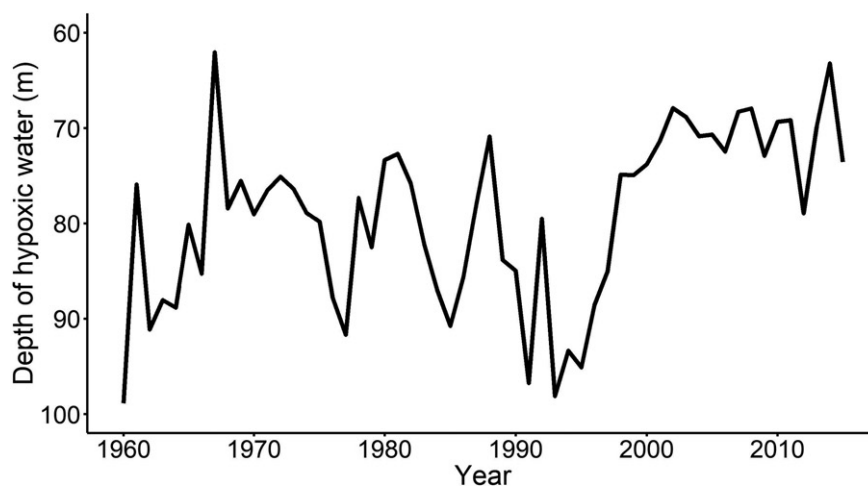
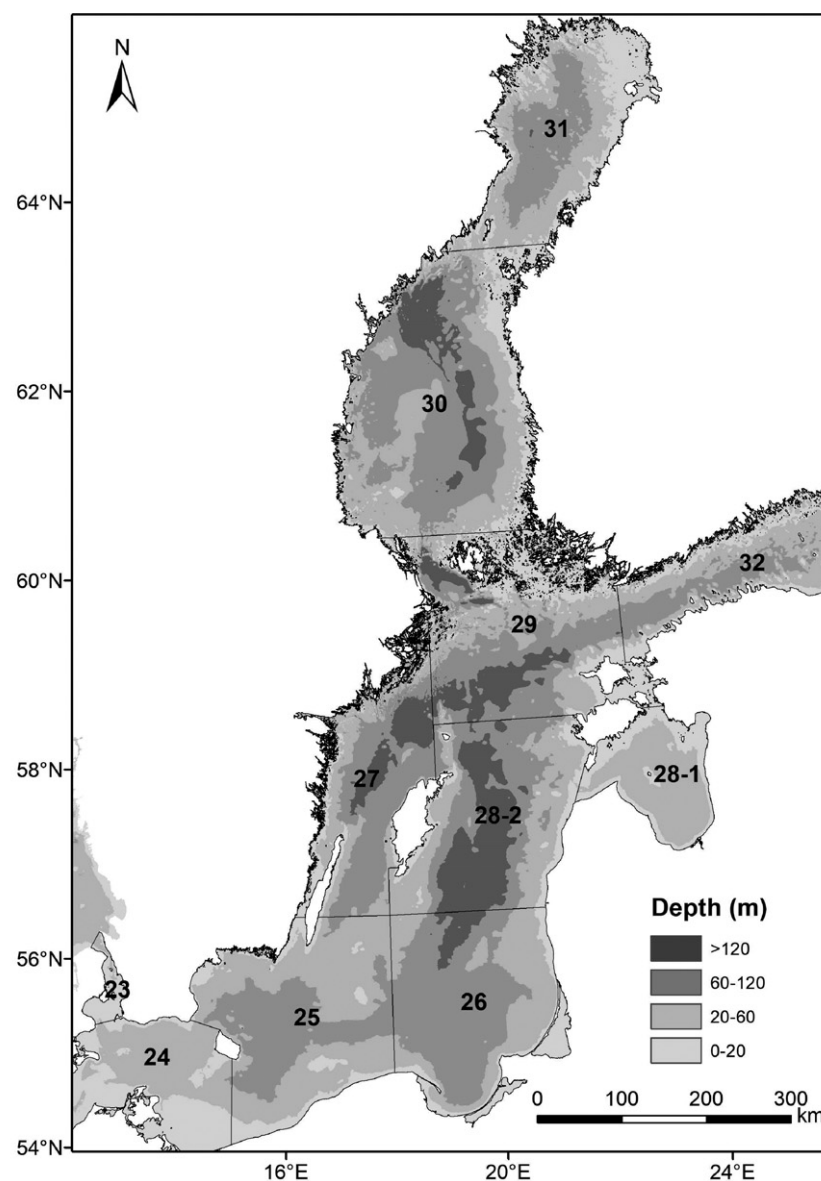


FIGURE 1 Map of the Baltic Sea divided in ICES Subdivisions and time series of the average depth of hypoxic water (oxygen concentration <1 ml/L) in the Baltic Sea between October and December in the years 1960–2015

of the juveniles' specific signals. However, we decided to use the same length for juvenile immature cod that is used in stock assessment (Eero et al., 2015; ICES, 2017a) assuming that the major dynamics of the juvenile cod would still be reflected.

We included in the analyses all the hauls in SDs 24–28, excluding the Gulf of Riga (SD 28-1), in quarter 1 and 4 with depths between 20 and 120 m because of good spatial and temporal coverage. We excluded from the analyses all the hauls in SD 27 north of 58° latitude and in SD 24 west of 12.5° longitude as these areas were not consistently covered by the bottom trawl surveys during the period analysed.

2.2 | Environmental data

To increase the predictive power of our models (see section below) and also because these variables have been shown to be important in explaining the distribution of both gadoids and flatfishes (Able, Neuman, & Wennhage, 2005; Hinrichsen, Kraus, Böttcher, & Köster, 2009), we included bottom temperature, salinity and oxygen in the analyses. Based on the location and time of the hauls, we matched all the CPUE data with the environmental variables. Data on bottom salinity, temperature and oxygen were monthly averages of the selected years extracted from the hydrodynamic Kiel Baltic Sea Ice-Ocean Model (Lehmann, Hinrichsen, Getzlaff, & Myrberg, 2014; Lehmann, Krauss, & Hinrichsen, 2002).

2.3 | Delta-Generalized additive model

The CPUEs of cod and flounder were modelled using Generalized additive models (GAM) in a delta modelling approach framework as in Orio, Florin, et al. (2017). This approach has been used to analyse zero-inflated data (Maunder & Punt, 2004), to estimate the spatial distribution of marine organisms at large spatial scales (Grüss, Drexler, & Ainsworth, 2014; Lauria, Vaz, Martin, Mackinson, & Carpentier, 2011; Loots, Vaz, Planque, & Koubbi, 2010; Parra et al., 2016), and to standardize CPUE data and indices of abundance (Cosgrove, Sheridan, Minto, & Officer, 2014; Thorson & Ward, 2014).

This modelling approach consists of two steps: the first involves modelling the presence/absence of the species using a binomial error distribution with a logit link function, while in the second step only the positive CPUE records are modelled, in our case log-transformed data, using a Gaussian error distribution with an identity link function (Parra et al., 2016). The predicted probability of presence, resulting from the binomial model, was then multiplied by the log CPUE prediction, resulting from the Gaussian model, to obtain the final CPUEs predictions.

The full binomial model for presence/absence and the full Gaussian model for the positive CPUE values were formulated as follows:

$$\begin{aligned} \text{presence/absence} = & \beta(\text{quarter}) + s(\text{long, lat}) + te_1(\text{depth, year}) \\ & + f_1(\text{year}) + f_2(\text{depth}) + f_3(\text{lat}) + f_4(\text{long}) \\ & + f_5(\text{temperature}) + f_6(\text{salinity}) + f_7(\text{oxygen}) + \varepsilon \end{aligned}$$

$$\begin{aligned} \log(\text{CPUE}) = & \beta(\text{quarter}) + s(\text{long, lat}) + te_1(\text{depth, year}) \\ & + te_2(\text{long, year}) + te_3(\text{lat, year}) + f_1(\text{year}) + f_2(\text{depth}) \\ & + f_3(\text{lat}) + f_4(\text{long}) + f_5(\text{temperature}) + f_6(\text{salinity}) \\ & + f_7(\text{oxygen}) + \varepsilon \end{aligned}$$

where β is an overall intercept different for each quarter, s is an isotropic smoothing function (thin-plate regression spline; Wood, 2003), te_i are tensor product smoothing functions used for representing interaction terms, f_i are natural cubic splines and ε are error terms. The interactions were introduced to take into account the changes in the spatiotemporal distribution of the species over the long time period analysed.

Model selection for both models was done through a backward stepwise elimination process based on statistical significance (Wood, 2006) following Orio, Florin, et al. (2017). To obtain ecologically significant models and to avoid overfitting, we set a limit to the maximum degrees of freedom (number of knots, k) allowed to the smoothing functions of the variables latitude, longitude, depth, temperature, salinity and oxygen ($k = 4$) and of the interaction between latitude and longitude ($k = 20$).

2.4 | Mapping CPUEs

The final models were used to predict the annual CPUEs over a regular grid of 0.02×0.01 degrees for quarter 1 and quarter 4. The same areas and depths removed from the data used for modelling were removed from the prediction grid. The environmental data associated to the grids were the averages of the first 3 months of each year for quarter 1 (January–March) and the last three for quarter 4 (October–December).

2.5 | Reconstructing the changes in depth distribution

From the annual CPUE spatial predictions, we calculated the percentage of each species (and life stage for cod) in every 5 m depth stratum from 20 to 120 m, for each quarter and SD. From this calculation, we obtained a different depth distribution curve for every year, quarter and SD. We then estimated the mean depth and the depth range calculated as the interquartile range (75th quantile–25th quantile) of each depth distribution. The mean depth was considered to be an indication of the preferred depth for each species (and life stage for cod) while the depth range an indication on the habitat occupancy.

All the analyses were performed using R software and the `MGCv` and `GGPLOT2` libraries of R (R Core Team, 2017; Wickham, 2016; Wood, 2011).

3 | RESULTS

As the environmental variables (in particular oxygen; Supporting Information Figure S1 and Table S1) show higher variability in the

TABLE 1 Summary statistics of the Delta-GAMs used to model the CPUE of different life stages of cod and flounder. Only the variables retained in the final models are shown

Species	Model	n	edf	Variables retained	Dev%
Adult cod	Binomial	9969	48.4	Latitude:Longitude, Depth:Year, Longitude, Oxygen, Temperature, Year (as linear effect), Quarter	32.3
	Gaussian	8550	88.4	Latitude:Longitude, Latitude:Year, Longitude:Year, Depth:Year, Depth, Oxygen, Salinity, Temperature, Year	45.6
Juvenile cod	Binomial	9969	50.0	Latitude:Longitude, Depth:Year, Oxygen, Salinity, Temperature, Year (as linear effect), Quarter	30.6
	Gaussian	8550	83.0	Latitude:Longitude, Latitude:Year, Longitude:Year, Depth:Year, Depth, Oxygen, Salinity, Temperature, Year, Quarter	35.5
Flounder	Binomial	9764	47.4	Latitude:Longitude, Depth:Year, Latitude, Oxygen, Temperature, Year, Quarter	31.6
	Gaussian	8317	95.6	Latitude:Longitude, Latitude:Year, Longitude:Year, Depth:Year, Latitude, Oxygen, Salinity, Temperature, Year, Quarter	40.7

n = numbers of stations used in the models; edf = effective degrees of freedom; Dev% = explained deviance.

first quarter, due to the presence of inflows from the North Sea in late autumn and winter (Mohrholz, Naumann, Nausch, Krüger, & Gräwe, 2015), and also because the major patterns are similar between the two quarters, only the results from the first quarter of the year are presented here.

The final models for adult and juvenile cod and for flounder are presented in Table 1. The deviance explained by the models used for producing the distribution maps was between 31% and 46%. The high degree of unexplained variation, which is common in large-scale fish models (Grüss et al., 2014; Parra et al., 2016), probably originates from noise introduced by the fish sampling method and the use of modelled environmental data, in combination with stochasticity in fish distributions. Thus, we believe that the models still captured general patterns in the data. No multicollinearity between explanatory variables was found in the models as the variance inflation factors calculated with the *usdm* library of R (Naimi, Hamm, Groen, Skidmore, & Toxopeus, 2014) were 3 or lower (Zuur, Ieno,

Walker, Saveliev, & Smith, 2009). Visual inspection of the residuals revealed, in some cases, slight departures from the model assumptions and signs of temporal autocorrelation especially in the first part of the time series with a lower number of observations, but we considered the overall quality of the residuals to be satisfactory (Supporting Information Figures S2–S7). Spatial autocorrelation of the residuals of the models was inspected using spline correlograms plotted with the *NCF* library of R (Bjørnstad, 2018). No significant spatial autocorrelation was detected, based on 95% pointwise bootstrap confidence intervals.

In both the binomial and Gaussian models, all the interactions were retained in the final models. Regarding the variables not in interactions, only year, oxygen and bottom temperature were retained in all models. The partial effects of the binomial and Gaussian models are presented in the Supporting Information Figures S8–S13.

The changes in spatial prediction of adult cod, juvenile cod and flounder CPUEs over time are presented in Figure 2.

Adult cod showed widespread high CPUEs in the first part of the time series. At the beginning of the 1990s, the CPUE started to decline in the north-eastern areas. This contraction continued throughout the study period. Since the mid-2000s, however, the CPUE started to increase again in the southern part of the study area. Juvenile cod showed a similar dynamic with a progressive contraction of their distribution towards the southern areas. Flounder showed widespread low CPUEs up to the mid-1980s and thereafter, during the 1990s, the CPUEs started to increase in the study area, especially in the northern parts. In the more recent period, high CPUE values were found also in the westernmost areas corresponding to SDs 24 and 25.

Depth distribution curves were calculated from the CPUE predictions (Figure 3) and the time series of average depth and depth range are shown in Figure 4.

The average depth and depth range in SD 24 of both adult and juvenile cod and flounder appeared to be quite stable with a progressive slight displacement towards deeper waters and reduced depth range during the period investigated. In SD 25, the average depth of adult cod increased from around 50 m to around 60 m. In SDs 26–28, the temporal development of the average depth is U-shaped with a maximum (~80 m) in the early 1990s and minima in the early 1980s and in the most recent years (~60 m). The depth range of adult cod decreased in SDs 25–28 from the beginning of the 1990s. In general, juvenile cod was found at shallower depths and showed a more stable mean depth compared to adult cod, oscillating around 60 m, although a slight overall shift towards deeper waters was observed over the whole study period. Also the depth range appeared to be generally more stable than for adult cod, but in SDs 26–28 a decline (from 30 m to ~15 m) was evident during the study period. The trend in average depth of flounder is similar to that of adult cod for all SDs, but the maximum average depth appeared earlier, at the end of the 1980s. In SDs 26–28, the average depth for flounder was ~85 m at the end of 1980s and reached the minimum in the most recent years (~60 m). The depth range for flounder in SD 25 is quite stable throughout the entire time series,

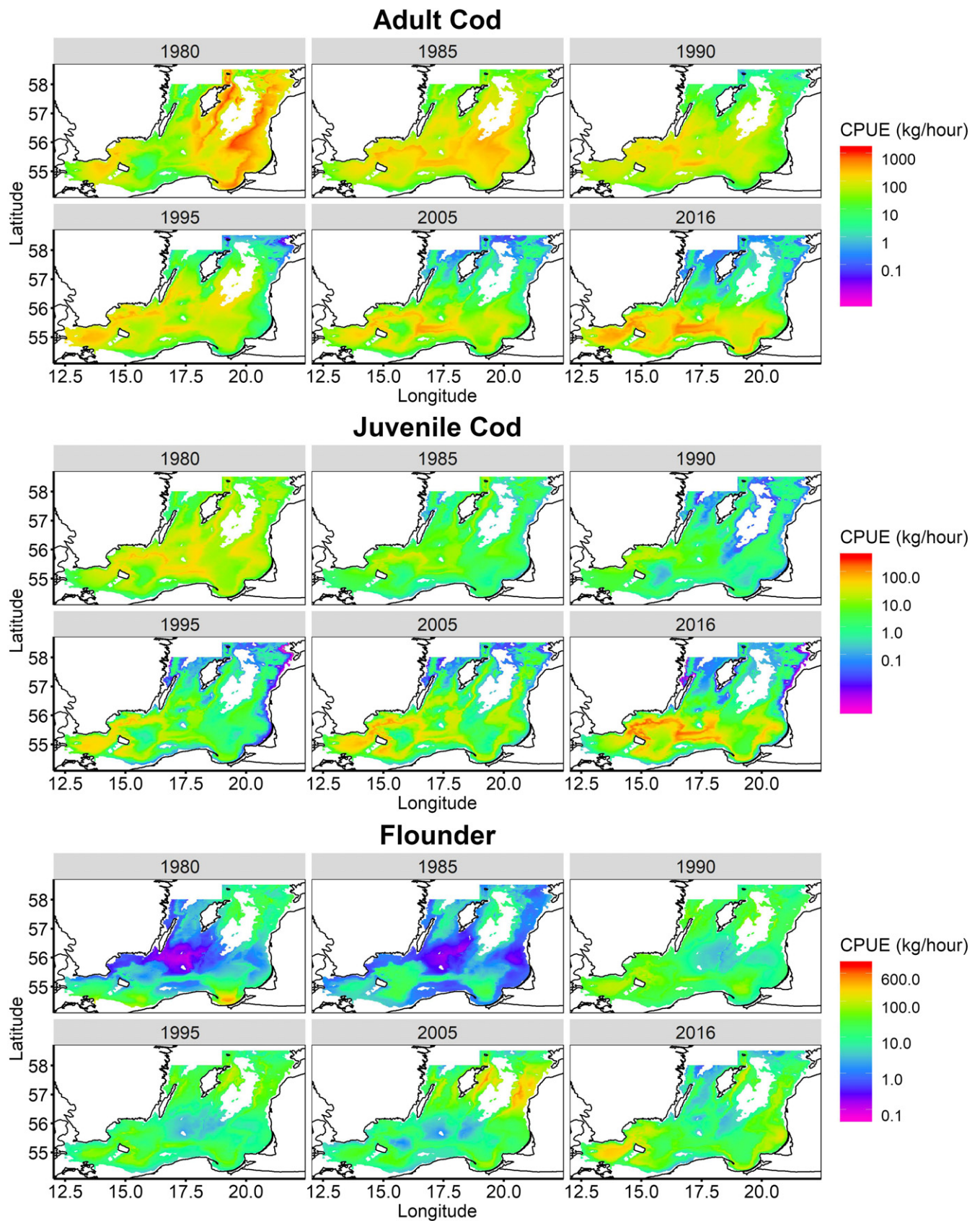


FIGURE 2 Predictions of the distribution of adult cod, juvenile cod and flounder CPUEs (kg/hr) in the first quarter of different years in the Baltic Sea [Colour figure can be viewed at wileyonlinelibrary.com]

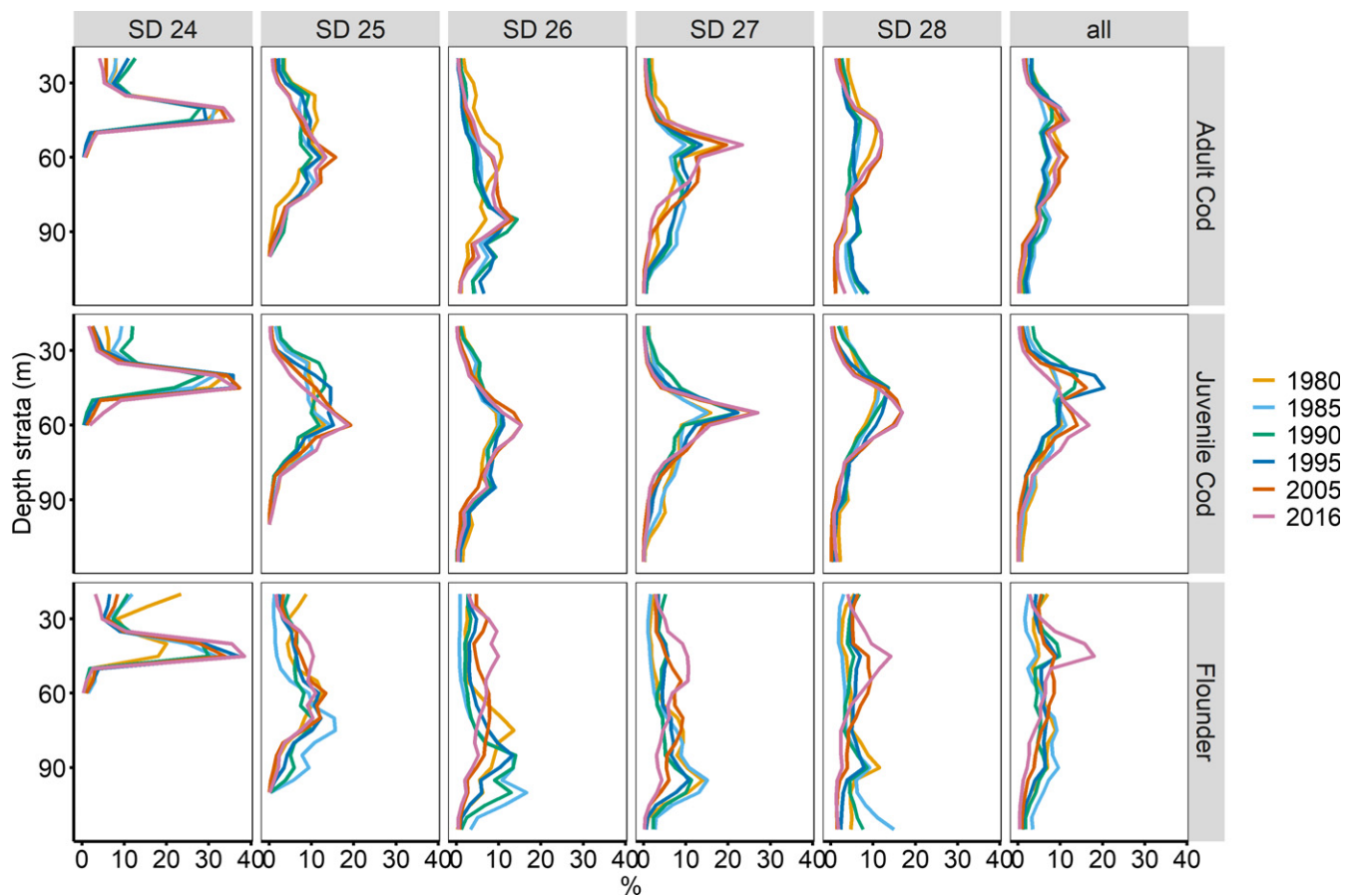


FIGURE 3 Depth distribution curves (in percentage) of adult cod, juvenile cod and flounder in the different SDs of the Baltic Sea in the first quarter of different years [Colour figure can be viewed at wileyonlinelibrary.com]

in SD 26 the range increased, while in SDs 27 and 28 the trend is dome-shaped with the maximum at the end of the 1980s (~50 m) and a minimum in the most recent years (~30 m). Cod and flounder have shown large variations in maximum individual size during the period investigated (Orio, Florin, et al. 2017). Therefore, to exclude the possibility that the observed changes in depth distribution were simply due to size-specific depth preferences, we ran also a GAM using only cod sizes of 40–45 cm and flounder sizes of 30–35 cm. The results were very similar to the original models, confirming that the changes in adult cod and flounder depth distribution were related to a real shift in area occupation.

4 | DISCUSSION

4.1 | Spatial distribution

Both adult and juvenile cod show widespread high abundances in the beginning of the 1980s followed by a contraction to the southern Baltic and a recent increase in abundance in the southern areas without re-expansion into the north. Flounder show low abundances at the beginning of the study period and then, from the beginning of the 1990s, an increase in the whole study area but especially in the north and, in later years, also in the southwest.

The changes in spatial distribution of adult cod are in line with Bartolino et al. (2017) even if the CPUE data used in the historical part (i.e. before 1991) of our analyses, as well as the environmental data and the modelling framework are different. The results of our models also reveal a recent increase in abundance of adult cod in the southern areas. In the literature, the spatiotemporal dynamics of cod have been linked to the 'ideal-free distribution' theory and to 'density-dependent habitat selection' (Bartolino, Ciannelli, Bachelier, & Chan, 2011 and references therein). According to these theories, cod should expand/contract its distribution areas during periods of high/low abundance, respectively, to maximize its fitness. In particular, three different models that link local density, total abundance and distribution have been proposed (Petitgas, 1998): the proportional density model, the constant density model, and the basin model. In the first half of our time series, the changes in spatial distribution of cod seem to follow the basin model, according to which there is an expansion in the distribution when total abundance increases and all the different areas show an increase in local abundances. In the second half of our time series, cod abundances show an increase only in the most suitable southern areas and the proportional density model thus seems to better reflect the recent dynamics of cod. This result could be an indication that the regime shift that occurred in the Baltic between the end of the 1980s and the beginning of the 1990s

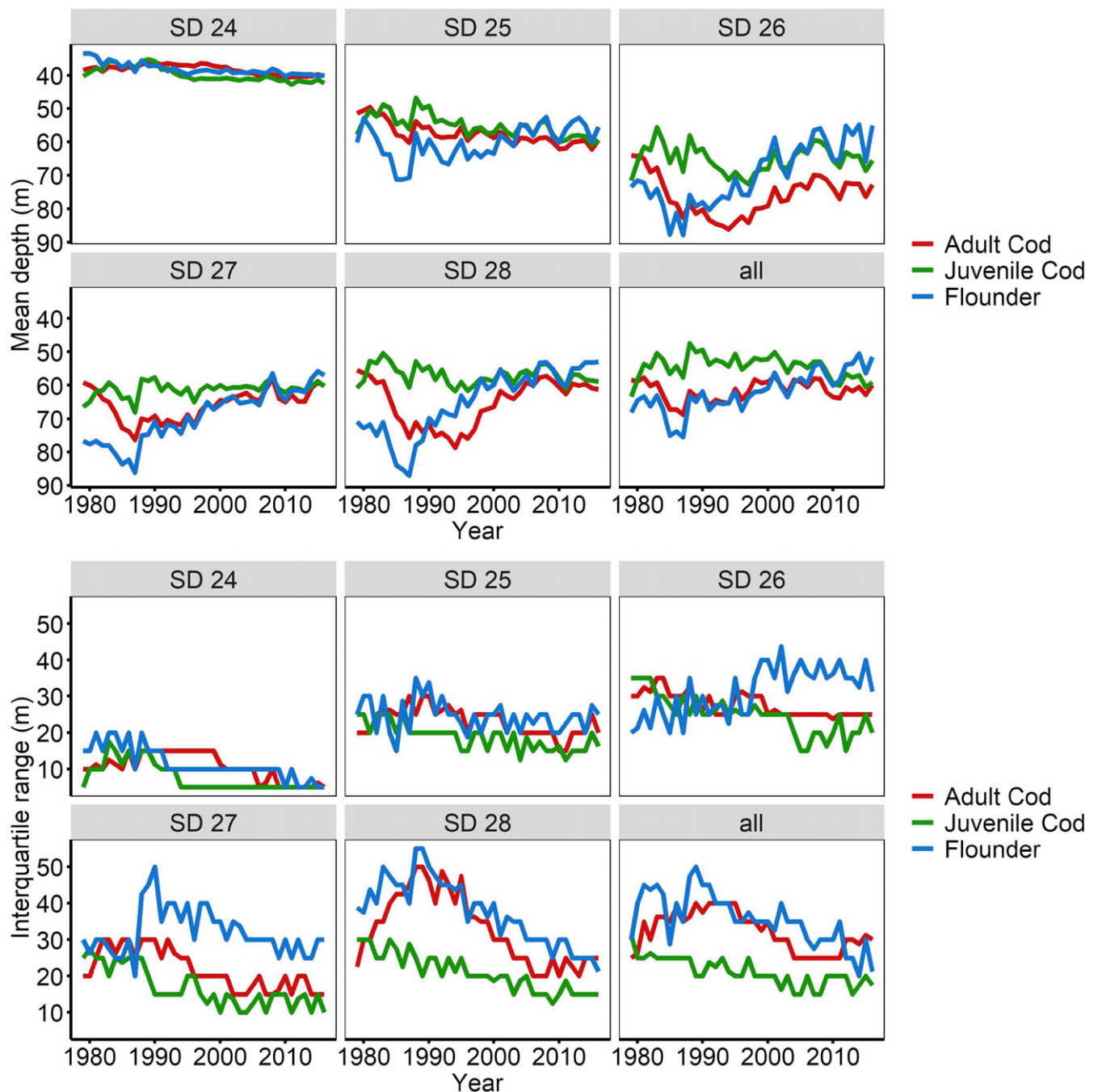


FIGURE 4 Time series of mean depth (top panels) and depth range (calculated as the interquartile range of each predicted depth distribution; bottom panels) of adult cod, juvenile cod and flounder in the different SDs of the Baltic Sea in the first quarter [Colour figure can be viewed at wileyonlinelibrary.com]

(Möllmann et al., 2009) has disrupted the relationships between local density, total abundance and the distribution area that were governing the spatial dynamics of cod. One potential explanation could be the extensive decrease of available spawning areas in the eastern part of the Baltic due to the decrease in bottom oxygen (Hinrichsen, Lehmann, et al. 2016). Therefore, it is possible that cod, in the current ecosystem state, will not be able to re-expand in the northern areas even if its abundance will further increase.

The long-term changes in distribution of juvenile cod have not been shown before and represent an important source of

information to better understand the population dynamics of Baltic Sea cod. The general trend of the juvenile cod looks similar to the one of adult cod. However, juveniles clearly prefer shallower waters compared to the adults, as also shown previously (Nielsen, Lundgren, Kristensen, & Bastardie, 2013). Another interesting feature shown by our model is the signal of re-expansion of the juveniles in the northern areas around the mid-2000s that disappears in the 2010s simultaneously with the increase in density in the southern areas. This increase in juvenile cod during the mid-2000s in the Gotland Basin has also been shown by Plikshs et al. (2015), who observed in that



period an increase of cod of age 1 that was related to environmental conditions suitable for egg development.

Our analyses on flounder reveal almost opposite spatial dynamics compared to cod. When cod reaches the highest abundances in the mid-1980s, flounder abundance is low in almost all the central Baltic Sea. Thereafter, when cod abundance decreases and contracts in the southern areas, flounder increase both its distribution and abundance, particularly in the northern areas where cod almost disappeared. This spatiotemporal pattern supports the hypothesis of a negative interaction between cod and flounder as suggested by Orio, Florin, et al. (2017). In the most recent period, flounder shows its highest abundance in the south-western part of the Baltic. One possible explanation is the increase in availability of high quality spawning habitat in SDs 24–25 that occurred between the 1990s and the mid-2010s (Orio, Bergström, et al. 2017) but also the high survival of flounders eggs in those areas due to favourable oxygen and salinity conditions (Hinrichsen, Petereit, et al. 2016). On the contrary, in the northern parts of the study area the increase in flounder abundance can be potentially explained by other mechanisms. In the northern Baltic Sea, two sympatric flounder ecotypes (or potentially two species according to Momigliano, Denys, Jokinen, & Merilä, 2018) are present with different physiological adaptation and spawning behaviour (Orio, Bergström, et al., 2017). The pelagic spawning flounder spawns pelagic eggs in deep waters and requires higher salinity for successful reproduction, while the demersal spawning flounder spawns demersal eggs in coastal shallow water and has lower salinity requirements (Nissling, Westin, & Hjerne, 2002). Therefore, the increase in flounder abundance in the northern areas could potentially be explained by a change in the dominance of the two ecotypes with an increase of the demersal ecotype and a decrease of the pelagic one.

4.2 | Depth distribution

Beside the overall changes in the horizontal distributions, our analyses revealed that large changes in depth distributions have also occurred for both cod and flounder in the last decades. In particular, adult cod and flounder in the beginning of the 1990s displayed a larger separation in terms of depth distribution while in the recent years they are both concentrating at depths around 60 m. Moreover, in the beginning of the 1990s both species showed a depth range of 40–50 m while in the recent years this value has dropped to around 20–30 m. Most of these depth changes could be attributed to the variations in the extent of hypoxic areas in the Baltic Sea (Carstensen et al., 2014). In particular, the shift of average depth towards shallower areas and the compression of the depth range of distribution from the beginning of the 1990s corresponds to the massive contraction of the species' suitable habitat as a result of deoxygenation (Casini et al., 2016; Orio, Bergström, et al., 2017; Figure 2). Hypoxic waters can affect organisms through direct mortality, alteration of metabolism and growth, forced migration, habitat contraction, increased susceptibility to predation or changes in prey availability (Diaz & Rosenberg, 2011; Levin, 2018). In the case of

mobile organisms, such as fish, the effects of hypoxic water are mostly indirect and connected to habitat contraction and changes in spatial distribution (Bijma, Pörtner, Yesson, & Rogers, 2013; Chu & Tunnicliffe, 2015). Decrease in habitat availability and changes in spatial distribution of species, due to climate change- and eutrophication-induced hypoxia, have been shown for many species: tropical pelagic fishes (Stramma et al., 2012), tunas (Mislán, Deutsch, Brill, Dunne, & Sarmiento, 2017), croaker (Eby, Crowder, McClellan, Powers, & Peterson, 2005), rockfish (McClatchie, Goericke, Cosgrove, Auad, & Vetter, 2010), crabs (Eby & Crowder, 2002) and shrimps (Craig & Crowder, 2005). Similar vertical shifts (i.e. elevational range shifts) in animal distribution in terrestrial environment caused by climate change have been reported for insects (Chen et al., 2011; Colwell, Brehm, Cardelús, Gilman, & Longino, 2008), birds (Chen et al., 2011; Sekercioglu, Schneider, Fay, & Loarie, 2008) and mammals (Büntgen et al., 2017; Chen et al., 2011).

In the case of juvenile cod, we also observe a habitat contraction but towards slightly deeper areas, which correspond to the average depths of adult cod in the latest years. One potential explanation of this pattern is an increased risk of seal and bird predation in shallow waters. Seal and cormorant populations in the Baltic Sea have increased exponentially in the last decades with a consequent increase in predation on fishes (Hansson et al., 2017). In particular, seals in the Baltic appear to prefer shallow coastal areas with depth less than around 30–40 m for feeding and to avoid areas deeper than 50 m (Oksanen, Ahola, Lehtonen, & Kunasranta, 2014), while cormorants usually feed in waters shallower than 10 m but can dive more than 30 m (Nelson, 2005). Therefore, by moving towards deeper areas, juvenile cod could decrease the risk of seal and bird predation. In the Gulf of St. Lawrence, it has been shown that the increase in seal population caused changes in spatial distribution and habitat selection in many fish populations, including cod, which could be explained by active risk avoidance from seal predation (Swain, Benoit, & Hammill, 2015). It has to be noted that both seals and cormorants in the Baltic Sea predate on juvenile cod but also on adult cod and flounder (ICES, 2017b; Lundström, Hjerne, Alexandersson, & Karlsson, 2007; Östman, Boström, Bergström, Andersson, & Lunnerød, 2013). Therefore, the contraction of the depth range of adult cod and flounder in the latest period could also be a response to predation avoidance when the populations moved into more shallow areas due to hypoxia.

The concentration of cod and flounder in more similar depths and the contraction of the area occupied in the most recent period, as revealed by our study, could have increased intra- and interspecific competition for benthic resources causing density-dependent effects. One such effect could be the significant decrease in maximum length observed for both cod and flounder in the last two decades (Orio, Florin, et al. 2017). Another density-dependent effect could be the recorded drop in cod condition since the mid-1990s, which in literature has been statistically linked to the increase in hypoxic zones and the resulting reduction in suitable areas (Casini et al., 2016; Hinrichsen, von Dewitz, Lehmann, Bergström, & Hüsey, 2017). Our study provides unique and new evidence of an actual

contraction of cod depth distribution supporting the hypothesis that hypoxia-driven compression in cod spatial distribution has contributed to the condition decline (Casini et al., 2016). However, more studies on the diet overlap between cod and flounder from the same areas will be needed in order to quantify the effect of the decrease in habitat availability on the competitive interactions between the two species. In addition, the hypothesis that the increasing overlap between adult and juvenile cod could have increased intraspecific competition is supported by cod stomachs data, which show an increase in cod cannibalism in the recent period in the areas where cod is concentrating (i.e. SD 25; ICES, 2016).

5 | CONCLUSIONS

Our study illustrates large changes in the spatial and depth distribution of cod and flounder in the Baltic Sea in the last four decades, which have not been reported before. We show that from the late 1980s the mean depth of both adult cod and flounder distributions has decreased, while that of juvenile cod has increased, and that the depth ranges have contracted, probably due to a combination of hypoxia in deep waters and increase in predation risk in shallow waters. The net effect of these changes is that adult cod, juvenile cod and flounder overlap more, which may increase the intra- and interspecific interactions. This information is highly relevant both for marine spatial planning and for EBFM as it can be implemented, for example, in spatially explicit stock assessment or multispecies models. More studies are needed in order to disentangle the different causes of the changes observed, but this study provides a step towards describing and understanding the spatiotemporal dynamics of keystone species of the Baltic Sea and shows the importance of taking into consideration changes both in the horizontal and vertical distribution when analysing the spatiotemporal dynamics of marine organisms.

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DATA ACCESSIBILITY

All the data used for the modelling are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.kb2f352>.

REFERENCES

- Able, K. W., Neuman, M. J., & Wennhage, H. (2005). Ecology of juvenile and adult stages of flatfishes: Distribution and dynamics of habitat associations. In R. N. Gibson (Ed.), *Flatfishes. Biology and exploitation* (pp. 164–184). Oxford, UK: Blackwell Publishing.
- Bartolino, V., Ciannelli, L., Bacheler, N. M., & Chan, K. S. (2011). Ontogenetic and sex-specific differences in density-dependent habitat selection of a marine fish population. *Ecology*, 92, 189–200. <https://doi.org/10.1890/09-1129.1>
- Bartolino, V., Tian, H., Bergström, U., Jounela, P., Aro, E., Dieterich, C., ... Casini, M. (2017). Spatio-temporal dynamics of a fish predator: Density-dependent and hydrographic effects on Baltic Sea cod population. *PLoS ONE*, 12, e0172004. <https://doi.org/10.1371/journal.pone.0172004>
- Bijma, J., Pörtner, H. O., Yesson, C., & Rogers, A. D. (2013). Climate change and the oceans — What does the future hold? *Marine Pollution Bulletin*, 74, 495–505. <https://doi.org/10.1016/j.marpolbul.2013.07.022>
- Bjornstad, O. N. (2018). ncf: Spatial covariance functions. R package version 1.2-5. Retrieved from <https://CRAN.R-project.org/package=ncf>
- Bond, M. J., & Jones, N. E. (2015). Spatial distribution of fishes in hydropeaking tributaries of Lake Superior. *River Research and Applications*, 31, 120–133. <https://doi.org/10.1002/rra.2720>
- Breitburg, D. L. (2002). Effects of hypoxia and the balance between hypoxia and enrichment, on coastal fishers and fisheries. *Estuaries*, 25, 767–781. <https://doi.org/10.1007/BF02804904>
- Breitburg, D., Levin, L. A., Oschlies, A., Grégoire, M., Chavez, F. P., Conley, D. J., ... Zhang, J. (2018). Declining oxygen in the global ocean and coastal waters. *Science*, 359(6371), eaam7240. <https://doi.org/10.1126/science.aam7240>
- Büntgen, U., Greuter, L., Bollmann, K., Jenny, H., Liebhold, A., Galván, J. D., ... Myrsterud, A. (2017). Elevational range shifts in four mountain ungulate species from the Swiss Alps. *Ecosphere*, 8(4), e01761. <https://doi.org/10.1002/ecs2.1761>
- Cadrin, S. X., & Secor, D. H. (2009). Accounting for spatial population structure in stock assessment: Past, present and future. In R. J. Beamish, & B. J. Rothschild (Eds.), *The future of fisheries science in North America* (pp. 405–425). New York, NY: Springer. <https://doi.org/10.1007/978-1-4020-9210-7>
- Carstensen, J., Andersen, J. H., Gustavson, B. G., & Conley, D. J. (2014). Deoxygenation of the Baltic Sea during the last century. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 5628–5633. <https://doi.org/10.1073/pnas.1323156111>
- Casini, M., Käll, F., Hansson, M., Plikshs, M., Baranova, T., Karlsson, O., Lundström, K., ... Hjelm, J. (2016). Hypoxic areas, density-dependence and food limitation drive the body condition of a heavily exploited marine fish predator. *Royal Society Open Science*, 3, 160416. <https://doi.org/10.1098/rsos.160416>
- Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333, 1024–1026. <https://doi.org/10.1126/science.1206432>
- Chu, J. W., & Tunnicliffe, V. (2015). Oxygen limitations on marine animal distributions and the collapse of epibenthic community structure during shoaling hypoxia. *Global Change Biology*, 21, 2989–3004. <https://doi.org/10.1111/gcb.12898>
- Ciannelli, L., Fauchald, P., Chan, K. S., Agostini, V. N., & Dingsør, G. E. (2008). Spatial fisheries ecology: Recent progress and future prospects. *Journal of Marine Systems*, 71, 223–236. <https://doi.org/10.1016/j.jmarsys.2007.02.031>
- Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C., & Longino, J. T. (2008). Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, 322, 258–261. <https://doi.org/10.1126/science.1162547>
- Conley, D. J., Björck, S., Bonsdorff, E., Carstensen, J., Destouni, G., Gustafsson, B. G., ... Zillen, L. (2009). Hypoxia-related processes in the Baltic Sea. *Environmental Science & Technology*, 43, 3412–3420. <https://doi.org/10.1021/es802762a>
- Cosgrove, R., Sheridan, M., Minto, C., & Officer, R. (2014). Application of finite mixture models to catch rate standardization better represents



- data distribution and fleet behavior. *Fisheries Research*, 153, 83–88. <https://doi.org/10.1016/j.fishres.2014.01.005>
- Craig, J. K., & Crowder, L. B. (2005). Hypoxia-induced habitat shifts and energetic consequences in Atlantic croaker and brown shrimp on the Gulf of Mexico shelf. *Marine Ecology Progress Series*, 294, 79–94. <https://doi.org/10.3354/meps294079>
- Diaz, R. J., & Rosenberg, R. (2011). Introduction to environmental and economic consequences of hypoxia. *International Journal of Water Resources Development*, 27, 71–82. <https://doi.org/10.1080/07900627.2010.531379>
- Eby, L. A., & Crowder, L. B. (2002). Hypoxia-based habitat compression in the Neuse River Estuary: Context-dependent shifts in behavioral avoidance thresholds. *Canadian Journal of Fisheries and Aquatic Sciences*, 59, 952–965. <https://doi.org/10.1139/f02-067>
- Eby, L. A., Crowder, L. B., McClellan, C. B., Powers, M. J., & Peterson, C. H. (2005). Habitat degradation from intermittent hypoxia: Impacts on juvenile fishes. *Marine Ecology Progress Series*, 291, 249–262. <https://doi.org/10.3354/meps291249>
- Eero, M., Hjelm, J., Behrens, J., Buchmann, K., Cardinale, M., Casini, M., ... Kirkegaard, E. (2015). Eastern Baltic cod in distress: Biological changes and challenges for stock assessment. *ICES Journal of Marine Science*, 72, 2180–2186. <https://doi.org/10.1093/icesjms/fsv109>
- Eero, M., MacKenzie, B. R., Köster, F. W., & Gislason, H. (2011). Multi-decadal responses of a cod (*Gadus morhua*) population to human-induced trophic changes, fishing, and climate. *Ecological Applications*, 21, 214–226. <https://doi.org/10.1890/09-1879.1>
- Eero, M., Vinther, M., Haslob, H., Huwer, B., Casini, M., Storr-Poulsen, M., & Köster, F. W. (2012). Spatial management of marine resources can enhance the recovery of predators and avoid local depletion of forage fish. *Conservation Letters*, 5, 486–492. <https://doi.org/10.1111/j.1755-263X.2012.00266.x>
- Grüss, A., Drexler, M., & Ainsworth, C. H. (2014). Using delta generalized additive models to produce distribution maps for spatially explicit ecosystem models. *Fisheries Research*, 159, 11–24. <https://doi.org/10.1016/j.fishres.2014.05.005>
- Hansson, S., Bergström, U., Bonsdorff, E., Härkönen, T., Jepsen, N., Kautsky, L., ... Sendek, D. (2017). Competition for the fish – Fish extraction from the Baltic Sea by humans, aquatic mammals, and birds. *ICES Journal of Marine Science*, 75, 999–1008.
- Hinrichsen, H. H., Kraus, G., Böttcher, U., & Köster, F. (2009). Identifying eastern Baltic cod nursery grounds using hydrodynamic modelling: Knowledge for the design of marine protected areas. *ICES Journal of Marine Science*, 66, 101–108.
- Hinrichsen, H. H., Lehmann, A., Peterait, C., Nissling, A., Ustups, D., Bergström, U., & Hüsey, K. (2016). Spawning areas of eastern Baltic cod revisited: Using hydrodynamic modelling to reveal spawning habitat suitability, egg survival probability, and connectivity patterns. *Progress in Oceanography*, 143, 13–25. <https://doi.org/10.1016/j.pocean.2016.02.004>
- Hinrichsen, H. H., Peterait, C., Nissling, A., Wallin, I., Ustups, D., & Florin, A.-B. (2016). Survival and dispersal variability of pelagic eggs and yolk-sac larvae of central and eastern Baltic flounder (*Platichthys flesus*): Application of biophysical models. *ICES Journal of Marine Science*, 74, 41–55.
- Hinrichsen, H. H., von Dewitz, B., Lehmann, A., Bergström, U., & Hüsey, K. (2017). Spatio-temporal dynamics of cod nursery areas in the Baltic Sea. *Progress in Oceanography*, 155, 28–40. <https://doi.org/10.1016/j.pocean.2017.05.007>
- ICES. (2014a). Report of the Baltic International Fish Survey Working Group (WGBIFS), 24–28 March 2014, Gdynia, Poland. ICES CM 2014/SSGESST:13. Copenhagen, Denmark: ICES.
- ICES. (2014b). Report of the Benchmark Workshop on Baltic Flatfish Stocks (WKBALFLAT), 27–31 January 2014, Copenhagen, Denmark. ICES CM 2014/ACOM:39. Copenhagen, Denmark: ICES.
- ICES. (2016). Report of the Workshop on Spatial Analyses for the Baltic Sea (WKSPATIAL), 3–6 November 2015, Rome, Italy. ICES CM 2015/SSGIEA. Copenhagen, Denmark: ICES.
- ICES. (2017a). Report of the Baltic Fisheries Assessment Working Group (WGBFAS), 19–26 April 2017, Copenhagen, Denmark. ICES CM 2017/ACOM:11. Copenhagen, Denmark: ICES.
- ICES. (2017b). Report of the workshop on biological input to Eastern Baltic Cod Assessment (WKBEBCA), 1–2 March 2017, Gothenburg, Sweden. ICES CM 2017/SSGEPD:19. Copenhagen, Denmark: ICES.
- Köster, F. W., Huwer, B., Hinrichsen, H. H., Neumann, V., Makarchouk, A., Eero, M., ... Plikshs, M. (2016). Eastern Baltic cod recruitment revisited—Dynamics and impacting factors. *ICES Journal of Marine Science*, 74, 3–19.
- Lauria, V., Vaz, S., Martin, C. S., Mackinson, S., & Carpentier, A. (2011). What influences European plaice (*Pleuronectes platessa*) distribution in the eastern English Channel? Using habitat modelling and GIS to predict habitat utilization. *ICES Journal of Marine Science*, 68, 1500–1510. <https://doi.org/10.1093/icesjms/fsr081>
- Layeghifard, M., Makarenkov, V., & Peres-Neto, P. R. (2015). Spatial and species compositional networks for inferring connectivity patterns in ecological communities. *Global Ecology and Biogeography*, 24, 718–727. <https://doi.org/10.1111/geb.12293>
- Lehmann, A., Hinrichsen, H. H., Getzlaff, K., & Myrberg, K. (2014). Quantifying the heterogeneity of hypoxic and anoxic areas in the Baltic Sea by a simplified coupled hydrodynamic-oxygen consumption model approach. *Journal of Marine Systems*, 134, 20–28. <https://doi.org/10.1016/j.jmarsys.2014.02.012>
- Lehmann, A., Krauss, W., & Hinrichsen, H. H. (2002). Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. *Tellus A: Dynamic Meteorology and Oceanography*, 54, 299–316. <https://doi.org/10.1034/j.1600-0870.2002.00289.x>
- Levin, L. A. (2018). Manifestation, drivers, and emergence of open ocean deoxygenation. *Annual Review of Marine Science*, 10, 229–260. <https://doi.org/10.1146/annurev-marine-121916-063359>
- Lindgren, M., Möllmann, C., Nielsen, A., & Stenseth, N. C. (2009). Preventing the collapse of the Baltic cod stock through an ecosystem-based management approach. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 14722–14727. <https://doi.org/10.1073/pnas.0906620106>
- Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackery, D. D. (2009). The velocity of climate change. *Nature*, 462(7276), 1052. <https://doi.org/10.1038/nature08649>
- Loots, C., Vaz, S., Planque, B., & Koubbi, P. (2010). What controls the spatial distribution of the North Sea plaice spawning population? Confronting ecological hypotheses through a model selection framework. *ICES Journal of Marine Science*, 67, 244–257. <https://doi.org/10.1093/icesjms/fsp238>
- Lundström, K., Hjerne, O., Alexandersson, K., & Karlsson, O. (2007). Estimation of grey seal (*Halichoerus grypus*) diet composition in the Baltic Sea. *NAMMCO Scientific Publications*, 6, 177–196. <https://doi.org/10.7557/3.2733>
- Marasco, R. J., Goodman, D., Grimes, C. B., Lawson, P. W., Punt, A. E., & Quinn, T. J. II (2007). Ecosystem-based fisheries management: Some practical suggestions. *Canadian Journal of Fisheries and Aquatic Sciences*, 64, 928–939. <https://doi.org/10.1139/f07-062>
- Maunder, M. N., & Punt, A. E. (2004). Standardizing catch and effort data: A review of recent approaches. *Fisheries Research*, 70, 141–159. <https://doi.org/10.1016/j.fishres.2004.08.002>
- McClatchie, S., Goericke, R., Cosgrove, R., Auad, G., & Vetter, R. D. (2010). Oxygen in the Southern California Bight: Multidecadal trends

- and implications for demersal fisheries. *Geophysical Research Letters*, 37. <https://doi.org/10.1029/2010gl044497>
- Mislán, K. A., Deutsch, C. A., Brill, R. W., Dunne, J. P., & Sarmiento, J. L. (2017). Projections of climate driven changes in tuna vertical habitat based on species-specific differences in blood oxygen affinity. *Global Change Biology*, 23, 4019–4028. <https://doi.org/10.1111/gcb.13799>
- Mohrholz, V., Naumann, M., Nausch, G., Krüger, S., & Gräwe, U. (2015). Fresh oxygen for the Baltic Sea—An exceptional saline inflow after a decade of stagnation. *Journal of Marine Systems*, 148, 152–166. <https://doi.org/10.1016/j.jmarsys.2015.03.005>
- Möllmann, C., Diekmann, R., Müller-Karulis, B., Kornilovs, G., Plikshs, M., & Axe, P. (2009). Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: A discontinuous regime shift in the Central Baltic Sea. *Global Change Biology*, 15, 1377–1393. <https://doi.org/10.1111/j.1365-2486.2008.01814.x>
- Momigliano, P., Denys, G. P., Jokinen, H., & Merilä, J. (2018). *Platichthys solemdali* sp. nov. (Actinopterygii, Pleuronectiformes): A new flounder species from the Baltic Sea. *Frontiers in Marine Science*, 5, 225. <https://doi.org/10.3389/fmars.2018.00225>
- Naimi, B., Hamm, N. A., Groen, T. A., Skidmore, A. K., & Toxopeus, A. G. (2014). Where is positional uncertainty a problem for species distribution modelling? *Ecography*, 37, 191–203. <https://doi.org/10.1111/j.1600-0587.2013.00205.x>
- Nelson, J. B. (2005). *Pelicans, Cormorants and their relatives*. Oxford, UK: Oxford University Press.
- Nielsen, J. R., Lundgren, B., Kristensen, K., & Bastardie, F. (2013). Localisation of nursery areas based on comparative analyses of the horizontal and vertical distribution patterns of juvenile Baltic cod (*Gadus morhua*). *PLoS ONE*, 8, e70668. <https://doi.org/10.1371/journal.pone.0070668>
- Nissling, A., Westin, L., & Hjerne, O. (2002). Reproductive success in relation to salinity for three flatfish species, dab (*Limanda limanda*), plaice (*Pleuronectes platessa*), and flounder (*Pleuronectes flesus*), in the brackish water Baltic Sea. *ICES Journal of Marine Science*, 59, 93–108. <https://doi.org/10.1006/jmsc.2001.1134>
- Oksanen, S. M., Ahola, M. P., Lehtonen, E., & Kunnasranta, M. (2014). Using movement data of Baltic grey seals to examine foraging-site fidelity: Implications for seal-fishery conflict mitigation. *Marine Ecology Progress Series*, 507, 297–308. <https://doi.org/10.3354/meps10846>
- Orio, A., Bergström, U., Casini, M., Erlandsson, M., Eschbaum, R., Hüsey, K., ... Florin, A.-B. (2017). Characterizing and predicting the distribution of Baltic Sea flounder (*Platichthys flesus*) during the spawning season. *Journal of Sea Research*, 126, 46–55. <https://doi.org/10.1016/j.seares.2017.07.002>
- Orio, A., Florin, A.-B., Bergström, U., Šics, I., Baranova, T., & Casini, M. (2017). Modelling indices of abundance and size-based indicators of cod and flounder stocks in the Baltic Sea using newly standardized trawl survey data. *ICES Journal of Marine Science*, 74, 1322–1333. <https://doi.org/10.1093/icesjms/fsx005>
- Östman, Ö., Boström, M. K., Bergström, U., Andersson, J., & Lunneryd, S. G. (2013). Estimating competition between wildlife and humans – A case of cormorants and coastal fisheries in the Baltic Sea. *PLoS ONE*, 8(12), e83763. <https://doi.org/10.1371/journal.pone.0083763>
- Parra, H. E., Pham, C. K., Menezes, G. M., Rosa, A., Tempera, F., & Morato, T. (2016). Predictive modeling of deep-sea fish distribution in the Azores. *Deep Sea Research Part II: Topical Studies in Oceanography*, 145, 49–60.
- Petitgas, P. (1998). Biomass-dependent dynamics of fish spatial distributions characterized by geostatistical aggregation curves. *ICES Journal of Marine Science*, 55, 443–453. <https://doi.org/10.1006/jmsc.1997.0345>
- Planque, B., Loots, C., Petitgas, P., Lindström, U., & Vaz, S. (2011). Understanding what controls the spatial distribution of fish populations using a multi-model approach. *Fisheries Oceanography*, 20, 1–17. <https://doi.org/10.1111/j.1365-2419.2010.00546.x>
- Plikshs, M., Hinrichsen, H. H., Elferts, D., Šics, I., Kornilovs, G., & Köster, F. W. (2015). Reproduction of Baltic cod, *Gadus morhua* (Actinopterygii: Gadiformes: Gadidae), in the Gotland Basin: Causes of annual variability. *Acta Ichthyologica Et Piscatoria*, 45, 247–258. <https://doi.org/10.3750/AIP>
- R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Robinson, L. M., Elith, J., Hobday, A. J., Pearson, R. G., Kendall, B. E., Possingham, H. P., & Richardson, A. J. (2011). Pushing the limits in marine species distribution modelling: Lessons from the land present challenges and opportunities. *Global Ecology and Biogeography*, 20, 789–802. <https://doi.org/10.1111/j.1466-8238.2010.00636.x>
- Romagnoni, G., Mackinson, S., Hong, J., & Eikeset, A. M. (2015). The eco-space model applied to the North Sea: Evaluating spatial predictions with fish biomass and fishing effort data. *Ecological Modelling*, 300, 50–60. <https://doi.org/10.1016/j.ecolmodel.2014.12.016>
- Sekercioglu, C. H., Schneider, S. H., Fay, J. P., & Loarie, S. R. (2008). Climate change, elevational range shifts, and bird extinctions. *Conservation Biology*, 22, 140–150. <https://doi.org/10.1111/j.1523-1739.2007.00852.x>
- Sherman, K., & Hempel, G. (2009). The UNEP large marine ecosystem report: A perspective on changing conditions in LMEs of the world's regional seas. UNEP Regional Seas Reports and Studies, vol. 182. Nairobi, Kenya: United Nations Environment Programme.
- Stramma, L., Prince, E. D., Schmidtke, S., Luo, J., Hoolihan, J. P., Visbeck, M., ... Körtzinger, A. (2012). Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. *Nature Climate Change*, 2, 33–37. <https://doi.org/10.1038/nclima1304>
- Swain, D. P., Benoît, H. P., & Hammill, M. O. (2015). Spatial distribution of fishes in a Northwest Atlantic ecosystem in relation to risk of predation by a marine mammal. *Journal of Animal Ecology*, 84, 1286–1298. <https://doi.org/10.1111/1365-2656.12391>
- Thorson, J. T., & Ward, E. J. (2014). Accounting for vessel effects when standardizing catch rates from cooperative surveys. *Fisheries Research*, 155, 168–176. <https://doi.org/10.1016/j.fishres.2014.02.036>
- Ustups, D., Müller-Karulis, B., Bergström, U., Makarchouk, A., & Šics, I. (2013). The influence of environmental conditions on early life stages of flounder (*Platichthys flesus*) in the central Baltic Sea. *Journal of Sea Research*, 75, 77–84. <https://doi.org/10.1016/j.seares.2012.05.001>
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. New York, NY: Springer-Verlag. <https://doi.org/10.1007/978-3-319-24277-4>
- Wood, S. N. (2003). Thin-plate regression splines. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 65, 95–114. <https://doi.org/10.1111/1467-9868.00374>
- Wood, S. N. (2006). *Generalized additive models: An introduction with R*. Boca Raton, FL: Chapman and Hall. <https://doi.org/10.1201/9781420010404>
- Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 73, 3–36. <https://doi.org/10.1111/j.1467-9868.2010.00749.x>
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York, NY: Springer. <https://doi.org/10.1007/978-0-387-87458-6>



BIOSKETCH

Alessandro Orio is a PhD student who studies the spatiotemporal dynamics of fish species in the Baltic Sea. His research focuses on spatial and habitat modelling, on stock assessment and on species interactions.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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