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Original Article

Spatio-temporal dynamics and behavioural ecology of a "demersal" fish population as detected using research survey pelagic trawl catches: the Eastern Baltic Sea cod (*Gadus morhua*)

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Cod is usually monitored for scientific purposes using bottom trawl surveys, although its regular pelagic occurrence is well documented. Here we analysed, using Generalized Additive Models, the spatio-temporal changes in the Eastern Baltic cod adult population using pelagic catches from an acoustic survey covering 37 years and the whole central Baltic Sea. Our analysis shows that in the northern areas cod catch per unit effort (CPUE, kg h^{-1}) was high in the early 1980s whereas it dropped and remained very low thereafter. Conversely, in the southernmost area CPUE largely oscillated after the early 1990s. Our model was able to capture key ecological features of the Baltic cod such as preferred depth of occurrence and response to hypoxic conditions. The model also revealed a clear daily cycle of CPUEs, indicating diel vertical migrations at the population level. The temporal trends of pelagic CPUEs generally followed those from the bottom trawl surveys, although differences were observed especially in the recent years with a relative decline in the cod occurring in the pelagic waters. Our results point to the great potential of acoustic survey trawl catches to complement bottom trawl surveys for investigating the spatio-temporal population dynamics and behaviour of the Baltic cod.

Keywords: acoustic survey, behavioural ecology, demersal species, Generalized Additive Models, pelagic occurrence, spatial and temporal dynamics.

Introduction

Cod (*Gadus morhua*) is a key species in the whole North Atlantic, from both an ecological and socio-economic perspective (Hamilton and Butler, 2001; Casini *et al.*, 2012). While early life stages of cod are pelagic (Lough *et al.*, 1989; Hallfredsson and Pedersen, 2007), larger individuals are typically dwelling in the demersal habitat. However, adult fish often migrate into pelagic layers in search of food, for spawning, due to population demography or because of environmental constraints in deeper layers (Godø and Wespestad, 1993; Strand and Huse, 2007 and references therein).

Pelagic occurrence is particularly well recognized for the Eastern Baltic Sea cod (hereafter referred to as Baltic cod). This behaviour, beside the general reasons explained above, is in the Baltic Sea to a large extent related to the often low oxygen content of the deep water masses (Tomkiewicz *et al*., 1998; Neuenfeldt, 2002; Neuenfeldt *et al*., 2009). Accordingly, high concentrations of cod can be found in the water column above anoxic and hypoxic layers, as demonstrated by acoustic experimental studies performed in the southern Baltic Sea (ICES, 2008; Schaber *et al*., 2009, 2012). In the Baltic Sea, moreover, pelagic trawling is regularly used by the commercial fishery to target cod (Madsen *et al*., 2010).

In the Baltic Sea, the Baltic International Trawl Survey (BITS; ICES, 2017a), coordinated by the International Council for the Exploration of the Sea (ICES), is used to monitor the cod density. Catch per unit effort (CPUE) data from this bottom-trawl survey have been used as tuning indices in analytical stock assessment until 2013 (ICES, 2017b). Since then the CPUEs from the BITS [mainly covering the ICES Subdivisions (SDs) 25–28; Figure 1] have been used directly to follow the changes in the density of large fish and have constituted the only source of information to provide management advice by ICES (2017b). Another opportunity to regularly monitor the Baltic cod population is given by another currently ICES-coordinated survey, the Baltic International Acoustic Survey (BIAS; ICES, 2017a), which covers nearly the whole Baltic Sea. However, this survey so far has been mainly used to estimate the abundance and age composition of the target species, i.e. herring (*Clupea harengus*) and sprat (*Sprattus sprattus*), and has been largely underemployed for the investigation of the long-term dynamics of other species, such as cod (but see Bergström *et al*., 2015 for three-spined sticklebacks, *Gasterosteus aculeatus*).

In this paper, the temporal and spatial changes in the Baltic cod population were reconstructed for the first time using 37 years of pelagic trawl catches from autumn acoustic surveys. The objectives of this study were (i) to collate and standardize the available information on the pelagic trawl catches from the acoustic surveys collected during the past four decades in the Baltic Sea; (ii) to use these data to model the spatio-temporal dynamics of the Eastern Baltic cod over the whole central Baltic Sea, using Generalized Additive Models; (iii) to compare the temporal trends in the catches of the cod sampled in the acoustic surveys with those from the bottom trawl surveys usually employed to monitor cod; (iv) to generally reveal the potentialities of these pelagic data for cod monitoring and scientific purposes.

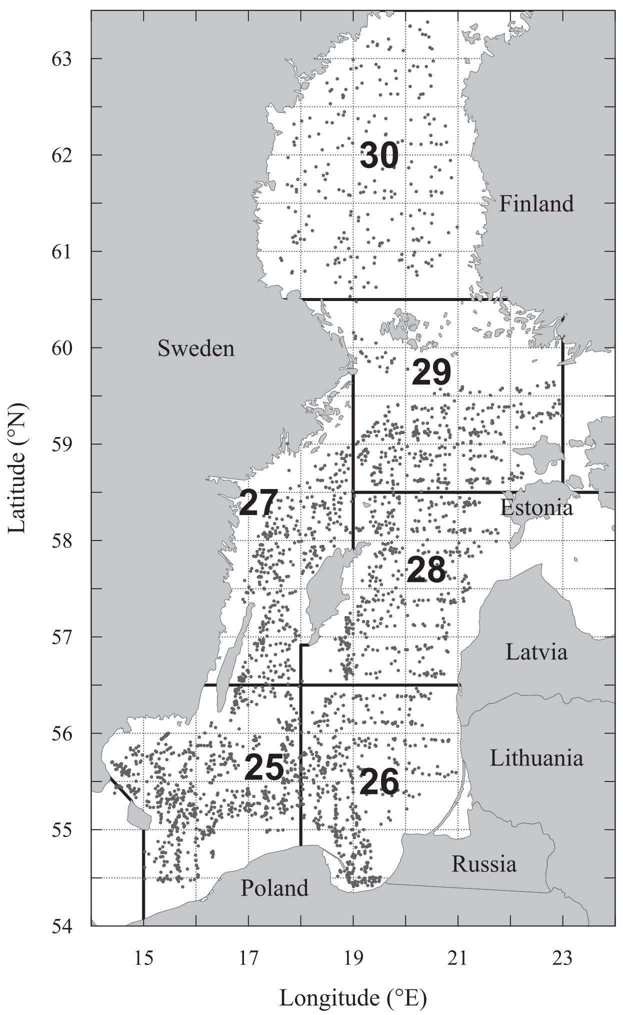

Figure 1. Map of the Baltic Sea divided into the analysed ICES SDs (delimited by bold lines). Thin lines demark ICES statistical rectangles. Black dots show the location of all the pelagic trawl hauls swept during the period 1979–2015.

Material and methods

Fish sampling

Acoustic surveys have been conducted in the Baltic Sea in autumn since the late 1970s. The surveys have been typically performed in September–October in the open areas of the Baltic Sea. The ICES SDs 25–29 (Figure 1) have been consistently covered, while the Bothnian Sea (SD 30) was infrequently monitored in the early times, but continuously with high spatial coverage since 2007. The survey is internationally coordinated by ICES since 1998 (BIAS; ICES, 2017a) and has the aim to estimate the abundances of herring and sprat to be used as tuning indices in the annual analytical stock assessment of these pelagic species (ICES, 2017b). During the survey, trawling is typically performed in correspondence of dense fish concentrations for the determination of the species composition and for the collection of biological parameters of the target species. According to the survey design (two trawl hauls for each ICES statistical rectangle as minimum, Figure 1) fishing can however also occur in areas of low fish concentrations. Fishing is carried out using mid-water trawls in the pelagic zone and occasionally near the bottom layers, depending on the fish vertical distribution detected by the echosounder (ICES, 2017a). For each trawl haul, CPUE (kg h^{-1}) is typically estimated for each species caught and length-class. In this paper, we used the CPUEs of cod sampled during the acoustic surveys in the period 1979–2015. We limit our analyses on cod larger than 30 cm, corresponding to the size at which cod start to be piscivorous (Huwer *et al*., 2014) and start to spawn (Radtke and Grygiel, 2013; ICES, 2017b).

Data analysis

No complete international database currently exists for the BIAS raw catch data. Data of cod CPUEs by length-class were therefore collated from Sweden, Poland, Latvia, Lithuania, and Estonia, Supplementary Table S1). During the acoustic surveys, different gears have been employed. Sweden has typically employed a Fotö trawl (mean mouth opening of 240 m^2), although during the period 1998–2006 a Macro trawl (mean mouth opening of 395 m^2)

was used. Poland and Latvia have employed a WP53/64 × 4 trawl (mean mouth opening of 714 m^2), Lithuania an OTM trawl (mean mouth opening of 840 m^2) and Estonia the EPT1, EPT2, EPT3 trawls (mean mouth opening between 375 m^2 and 1000 m^2) and WP53/64 × 4 trawls in different years. However, no cod catches from the EPT1, EPT2, and EPT3 trawls were recorded. Since the Swedish Fotö trawl has been used for the highest number of trawl hauls and years, and it is still in use, we standardized all the CPUEs to the opening of the Fotö trawl. This was done by dividing the CPUEs from Macro trawl by 1.6 (the ratio of mean mouth opening between Macro and Fotö trawls), and likewise the CPUEs from the WP53/64 × 4 by 3 and the CPUEs from the OTM trawl by 3.5. The CPUEs were also standardized to a trawling speed of 3.4 knots (corresponding to a distance of 6.3 km when trawling 1 h), which is the mean trawling speed used during the five most recent years (2011–2015). Therefore, all hauls were standardized to a mean swept volume of 1.51×10^{-3} km^3. This method is equivalent to the swept area standardization applied for bottom trawls (Rijnsdorp and Millner, 1996; Daan *et al.*, 2005). The standardized CPUEs for each SD, and for the whole central Baltic Sea, are shown in Figure 2. Time-series of trawling depth and trawling distance from the sea floor, together with histograms of trawl durations, are shown in Supplementary Figure S1. Time-series of trawling depth and trawling distance from the sea floor for the hauls in which cod ≥30 cm was caught, together with histograms of CPUE of cod ≥30 cm, are shown in Supplementary Figure S2. These figures show that all hauls, and also the hauls with cod catches, were swept in average at a distance from the seafloor between 25 and 50 m with a slight declining trend during the study period. We estimated that in average, considering the trawl distance from the sea floor and the vertical opening of the trawls, only between 10 and 30% of the pelagic hauls with cod ≥30 cm catch have been swept annually at a depth interval that would vertically overlap, even partially, with the ordinary bottom trawl survey BITS (Supplementary Figure S3a). Moreover, we estimated that in average around 30–40% of the pelagic hauls with cod ≥30 cm catch have been swept in locations with hypoxic conditions at the seafloor, which the bottom-trawl survey BITS would not sample, assuming 0-catches (ICES, 2017a) (Supplementary Figure S3b).

To model the spatio-temporal changes in cod CPUE, we used General Additive Models (GAMs; Wood, 2006). GAMs are able to account for unbalanced design in the sampling among years, latitudes, longitudes, and depths (see Maunder and Punt, 2004

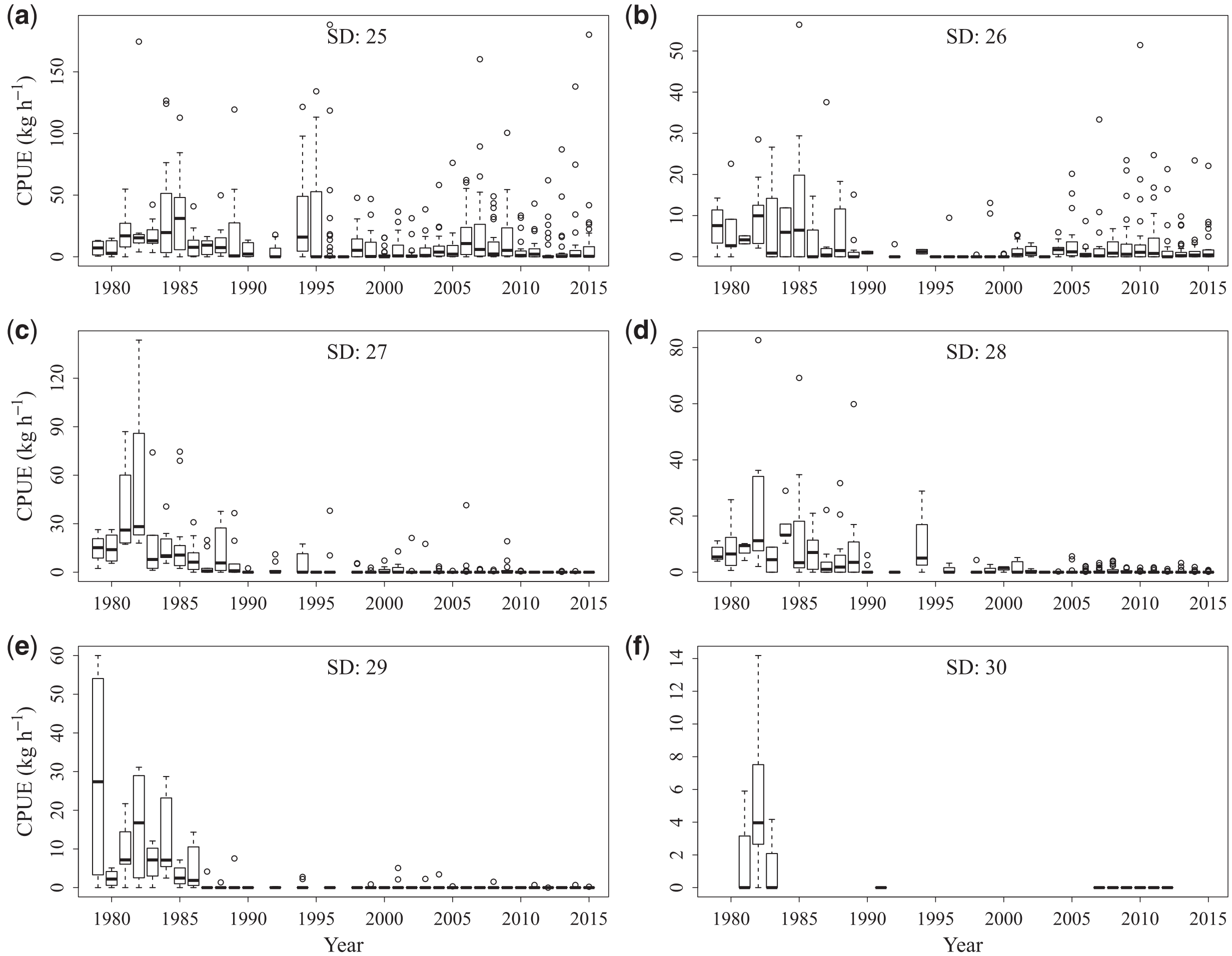

Figure 2. Cod CPUE (kg h^{-1}, cod length ≥30 cm) from the acoustic surveys conducted in ICES SDs 25–30 (a–f) during the period 1979–2015. The thick horizontal lines show the median of each year, and the lower and upper edges of the box the 25th and 75th percentiles. Whiskers span from the smallest to the largest non-outlier observations. Note the different scale on the *y*-axis.

for a useful review of different standardization approaches). In our analysis we used the following model formulation:

$$\text{CPUE} = s(\text{Lat}, \text{Long}, \text{Year}) + s(\text{Ttime}) + s(\text{Tdepth}, \text{Odepth}) + \varepsilon,$$

where *s*(Lat, Long, Year) fits the year-specific cod spatial distribution, accounting for the fact that cod horizontal distribution may vary in different years (Casini *et al.*, 2012). Ttime is the trawling starting time, and was included in the model because of the potential difference in cod catchability in the pelagic waters depending on the fishing time. In fact, in other areas cod has been shown to perform diel vertical migrations (DVM) in the water column (McQuinn *et al.*, 2005; Strand and Huse, 2007), generally concentrating close to the bottom at day-time and more dispersed in pelagic waters at night-time. Tdepth is the mean trawling depth (i.e. the mean depth of the trawl headrope) and was included in the model because of the potentially different catchability of cod at different depth (e.g. due to the demersal nature of the cod, we expected higher catches closer to the seafloor). Cod in the Baltic has been shown however to avoid oxygen concentrations below 1 ml l^{-1} (Schaber *et al.*, 2012), and therefore we used Odepth (depth at which oxygen was 1 ml l^{-1} at the trawl haul location) as interactive effect with Tdepth. In the case the whole water column was well oxygenated (i.e. no Odepth was present), Odepth was set equal to bottom depth. *s* is the smoothing functions and ε is the error term. We used a thin-plane regression spline to model the interaction between year and geographic coordinates. We used a cyclic cubic regression spline to smooth the Ttime predictor because it forces the estimated effect to have the same value (and up to second derivative) at its start and end points (Wood, 2006).

The model was fitted using a negative-binomial distribution, which assumes a quadratic relationship between mean and variance of the samples (variance = mean + μ * mean^2), with a log-link function. Variogram was used to test for potential occurrence of spatial autocorrelation in the residuals (Wood, 2006). The partial effects of the GAM were used to qualitatively analyse behavioural and ecological traits of the cod, as the response to low oxygen conditions, the depth preference and the variation in CPUEs with time of the day.

The GAM analysis was limited to the area covering SDs 25–29 (hereafter referred to as the central Baltic Sea), due to the scarcity of data in SD 30 (Figure 2). Based on the fitted model, we predicted cod CPUE in each ICES statistical rectangle for which we had a sufficient spatio-temporal coverage (Supplementary Figure S4), after having accounted for the effect of Ttime, Tdepth, and Odepth. Cod CPUE in each SD was estimated by averaging the predicted CPUEs of all ICES rectangles included in the respective SD. Cod CPUE in the whole central Baltic Sea was estimated by averaging the predicted CPUEs of all ICES rectangles. One thousand simulations from the posterior distribution of model coefficients were used to calculate the 95% confidence interval of the predicted CPUEs.

In addition, the pelagic CPUE time-series for the central Baltic Sea, as estimated by our model, was compared to the time-series of cod CPUEs from the bottom trawl surveys in the fourth quarter (BITS and historical national surveys) recently standardized by Orio *et al.* (2017). For the comparison between the pelagic and bottom trawl surveys, we excluded data from SD 29 because the BITS does not cover representatively this area (ICES, 2017a).

Results

The model results are shown in Figure 3. All terms included in the model were significant, explaining together 64.6% of the total deviance. The partial effects of the model showed that cod CPUE was higher during night-time and lower at day-time (Figure 3a). Moreover, with increasing Odepth (or increasing bottom depth), the highest CPUEs were also predicted to be progressively deeper in the water column, as shown by the generally bottom-left to top-right diagonal pattern of the isolines in Figure 3b, and the highest CPUEs were generally predicted to be just above the hypoxic layer (red dots) or the sea floor (black dots). At bottom depth shallower than around 50 m this pattern appears to change with the highest CPUEs predicted to be progressively more distant from the sea floor with increasing bottom depth. For each value of Odepth (or bottom depth), however, CPUE decreased progressively towards the surface. The highest CPUEs overall were predicted to be in the depth interval between 50 and 80 m just above Odepth (or bottom depth) (Figure 3b). The relationship between fitted values and residual variance showed a clear quadratic pattern (curvature of the relationship $\mu = 1.5$), which provides support to our assumption of residuals following a negative-binomial distribution (Figure 3c). The variogram of model residuals showed no obvious spatial autocorrelation as indicated by the flat relationship between the variogram values and the spatial distance between observations (Figure 3d).

The predicted CPUE by ICES rectangle (Figure 4) revealed that cod was distributed in the whole central Baltic Sea in the late 1970s and early 1980s, with the highest peaks occurring in SD 27. From the late 1980s a contraction in the distribution started to occur and cod disappeared gradually from the northern SDs. In the latest 20 years the cod has been mainly present in the western part of SD 25 (Figure 4).

The predicted CPUE time-series revealed that in the southernmost area (SD 25), CPUE declined sharply up to 1990s (Figure 5a). Thereafter CPUE reached peaks in the mid-1990s and second half of 2000s, and declined thereafter. In all the others SDs of the central Baltic Sea (SDs 26–29) CPUE peaked in the early 1980s and thereafter dropped stabilizing at very low levels since the beginning of the 1990s (Figure 5b–d). A minor CPUE peak around the mid-1990s was observed in SD 27. For the Bothnian Sea (SD 30), only few years of observations were available and therefore no GAM was attempted. However, in SD 30 cod was recorded in the early 1980s whereas thereafter no cod was caught by the survey (Figure 2). Overall, in the whole central Baltic Sea, cod CPUE in the pelagic waters has drastically decreased from the mid-1980s and remained very low, although slightly oscillating, since the early 1990s (Figure 5f). The confidence intervals of the predictions were higher at the beginning of the time-series mirroring the lower number of hauls performed in those years (Supplementary Table S1).

The general long-term trends in cod CPUE modelled from our pelagic trawl data were similar to the CPUEs from the bottom trawl survey (Figure 6a). However, there were differences in the most recent period. Especially, the peak in CPUEs observed in the bottom trawl survey between 2007 and 2012 was not evident in the pelagic data. Overall, the relative CPUE of cod in the pelagic water declined during the study period (Figure 6b), with low values observed also in the early 1990s.

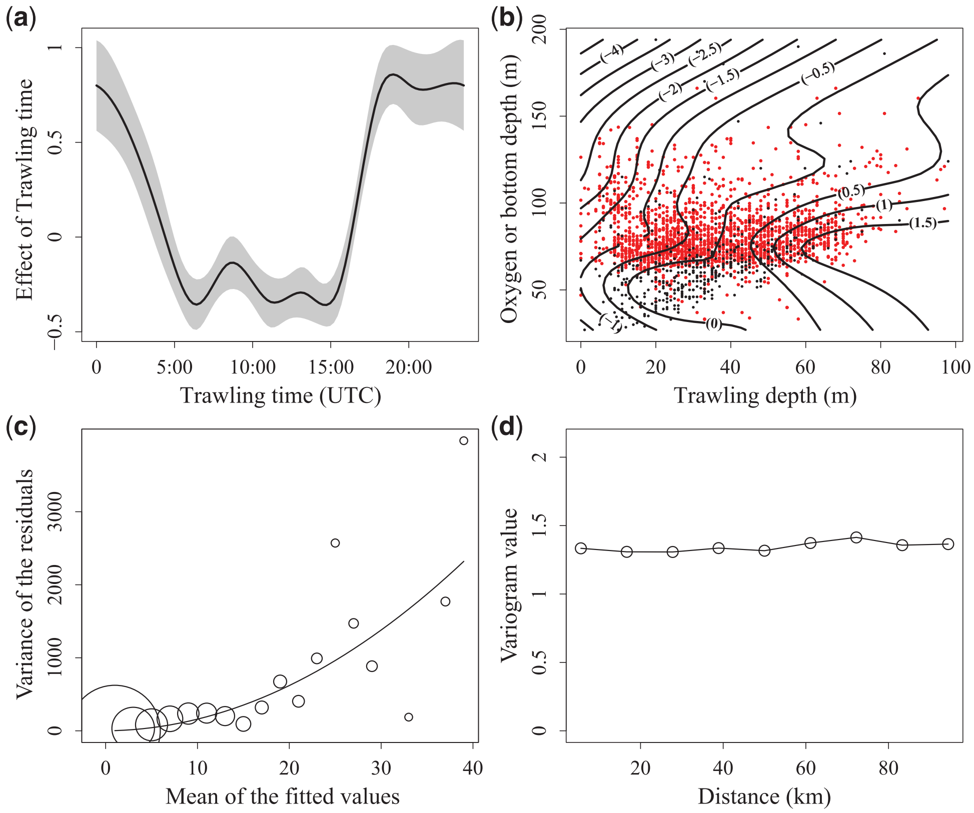

Figure 3. Model results and model validation. (a) and (b) Partial effects of each term on normalized cod CPUE (kg h^{-1}, cod length $\geq$30 cm); the partial effects are centred so that the values sum to 0 over the predictors' values: (a) effect of trawling time and (b) interactive effect of trawling depth and depth with oxygen concentration 1 ml l^{-1} (trawl hauls as red dots) or of trawling depth and bottom depth in the case the whole water column had an oxygen concentration >1 ml l^{-1} (trawl hauls as black dots); isolines depict surfaces in the water column with equal predicted CPUEs and go from negative values in the upper left corner to positive values in the lower right corner. (c) and (d) Model validation: (c) relationship between the fitted values and the variance of the residuals. This plot is used to check if the negative binomial distribution used in the model is correct. The negative binomial distribution assumes a quadratic relationship between fitted values and residual variance, as in our case, supporting our choice. For illustration, CPUE = 2 kg h^{-1} was here used as interval to aggregate the fitted values and corresponding residuals into groups (the size of the bubbles corresponds to the number of observations within each group; only the groups that had more than 10 observations were used); the line is the relationship between fitted values and residual variance. (d) Variogram of the model residuals. In case of spatial autocorrelation, the variogram values would increase sharply with distance before eventually forming a plateau. In our case, the flat variogram suggests no spatial autocorrelation between observations.

Discussion

This study explores the spatio-temporal trends in the Eastern Baltic cod population using for the first time pelagic trawl catches from an acoustic survey designed to monitor herring and sprat. The predicted CPUEs from our study, covering the whole central Baltic Sea up to the entrance to the Bothnian Sea, constitute the most comprehensive fishery-independent standardized time-series currently existing for the Eastern Baltic cod.

Our analyses showed a change in the spatial distribution of this cod population from being distributed over the whole Baltic Sea to being almost exclusively concentrated in the southern part. Interesting is the fact that in the late 1970s and early 1980s cod had high densities also in the northernmost central Baltic Sea (northern SD 29). The raw, non-standardized, data from the Bothnian Sea also showed the occurrence and subsequent disappearance of cod in this area in the first years of the time-series, which previously were only revealed by commercial catches (Bartolino *et al.*, 2017).

The temporal and spatial patterns in cod CPUE from our study follow well those from the bottom trawl survey which is ordinarily used to monitor cod (Orio *et al.*, 2017). Both surveys, in fact, show a dramatic decreased in CPUE since the early 1980s, which has stabilized at very low level since the beginning of the 1990s. However, some differences appeared, especially in the most recent period, where the bottom trawl survey evidences a slight increase in CPUEs, while the pelagic survey a further decline. Specifically, the peak in CPUEs observed in the 2007–2012 in the bottom trawl survey was not evident in the acoustic survey. We speculate that one potential explanation of the relatively lower CPUE in the pelagic waters in recent years could be due the decreased body condition of cod (Casini *et al.*, 2016). Under these circumstances cod could adopt a more stationary and energy-saving strategy reducing the excursions into the pelagic habitat (Mehner and Kasprzak, 2011). Other explanations could be linked to the relative density of pelagic and benthic prey in the area and to minimize the predation risk from the increased seal population (see Mehner and Kasprzak, 2011 and references therein). Moreover, hypoxic areas have increased fourfold after the mid-1990s (Casini *et al.*, 2016) and since 2010 have kept at the highest level ever observed in the past five decades. It could be

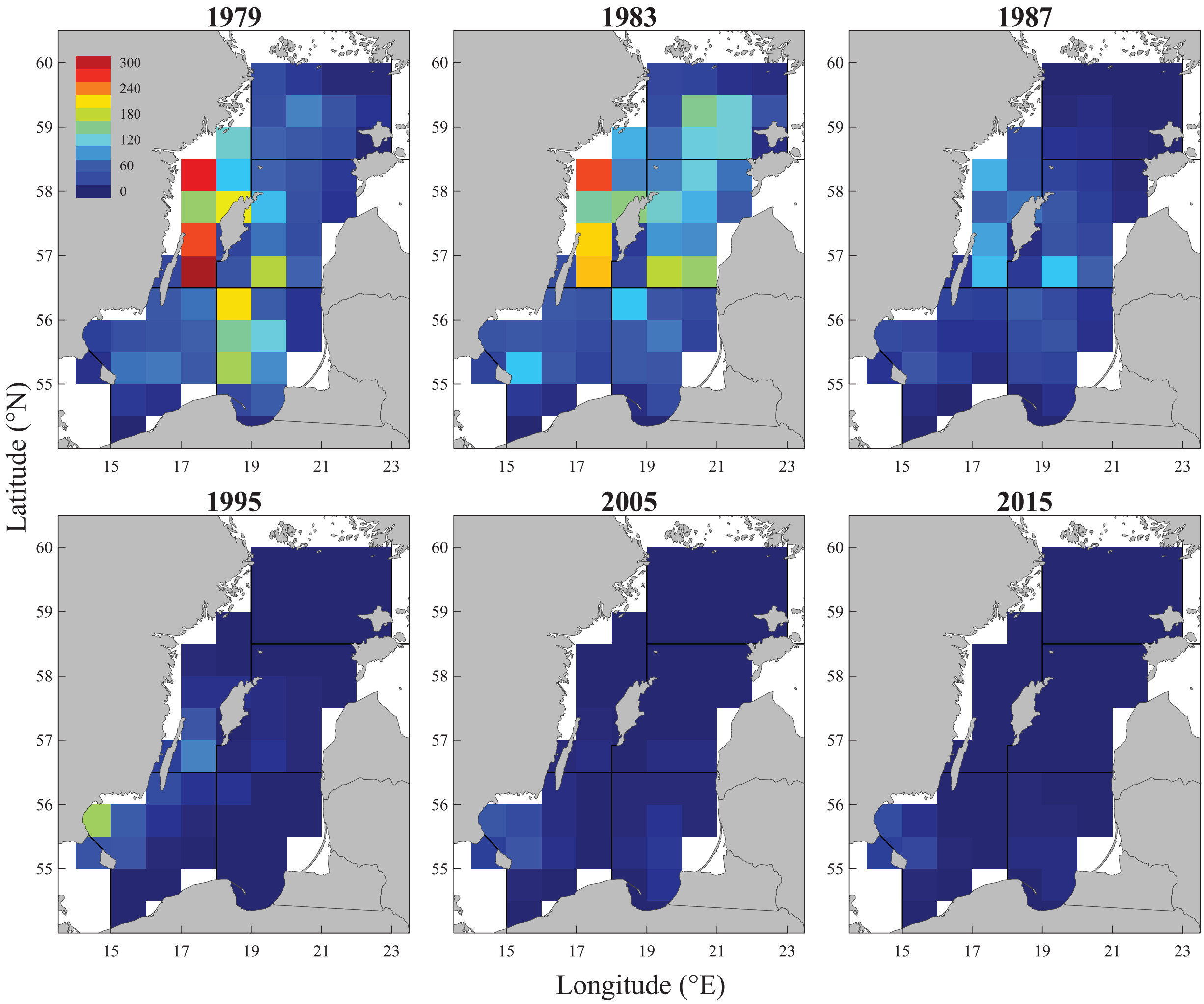

Figure 4. Predicted CPUE (kg h^{-1}, cod length ≥30 cm) by ICES rectangle in six selected years representing the temporal changes in spatial distribution of cod during the period 1979–2015.

therefore that, under these chronic adverse conditions in the deep waters, cod has moved to more coastal and oxygenated waters instead of using the pelagic habitat as a short-term refuge.

Our model was also able to capture characteristic ecological features of cod. Cod rarely occur in waters with oxygen concentrations below 1–1.5 ml l^{-1} (Tomkiewicz *et al.*, 1998; Schaber *et al.*, 2009, 2012; ICES 2017a). In these circumstances cod has been observed dwelling in more pelagic waters where the oxygen concentration is above this threshold (Schaber *et al.*, 2012). Our model was able to depict this behaviour, showing the highest cod CPUEs at depths just above the depth with 1 ml l^{-1} in oxygen concentration (red dots in Figure 3b). Moreover, in areas where oxygen conditions were favourable for cod (oxygen concentration >1 ml l^{-1} in the whole water column, black dots in Figure 3b), the highest CPUEs were found close to the sea floor, and decreased progressively towards the surface, this remarking the association of this species with the demersal habitat. The highest CPUEs were however found at depths between 50 and 80 m (i.e. corresponding to the average depth of the halocline in the study area) confirming the findings of previous studies performed using bottom trawl data (Oeberst, 2008).

Interestingly, we found a higher CPUE at night-time than day-time. We interpret this pattern as the result of cod DVM at the population level. In other areas it has been shown that cod is generally occurring close to the bottom at day-time and distributed over a wider range of depths (and therefore more catchable during the pelagic trawling) at night-time (McQuinn *et al.*, 2005; Strand and Huse, 2007 and references therein) in relation for instance to buoyancy regulation, stomach fullness, or pelagic prey availability (Strand and Huse, 2007). The existence of DVM for Baltic Sea cod has been suggested before in small-scale field investigations using a combination of pelagic and bottom trawling (ICES, 2008, 2009), but in our knowledge our study is the first to provide evidence of this pattern using monitoring data spanning several years and covering a large area of the cod distribution. It is worth stressing that, in the GAM, the effect of trawling time on cod CPUE (which provides indication of DVM, Figure 3a) furnishes an overall view of cod behaviour, after having accounted for the effect of the other terms used in the model (i.e. location, year, depth at oxygen concentration = 1 ml l^{-1}, and trawling depth), and does not obviously depict single fish behaviour that can be irregular (Godø and Michalsen, 2000; Neuenfeldt *et al.*, 2009). Further indications for the occurrence of DVM behaviour in Baltic Sea cod

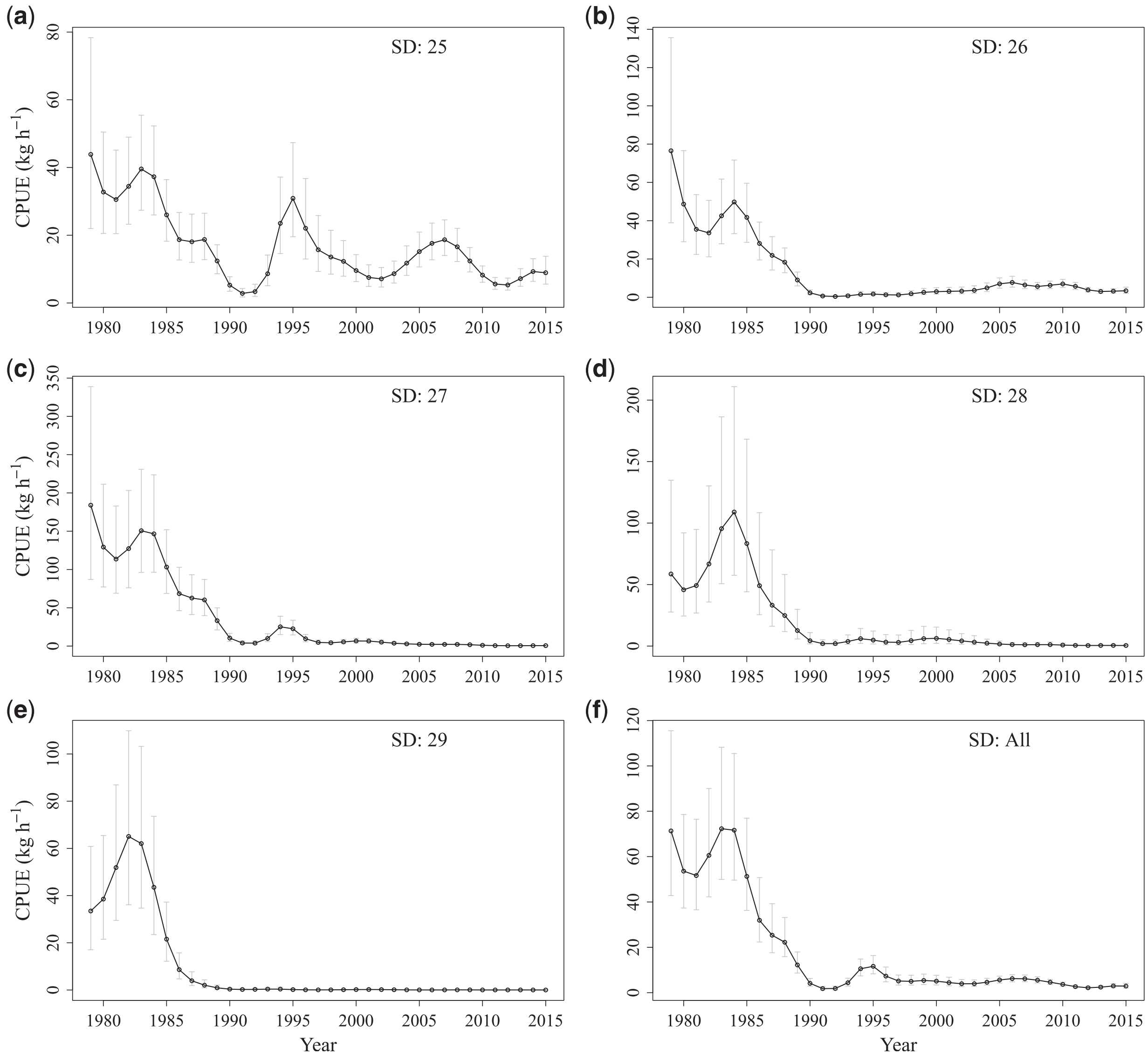

Figure 5. Predicted trends in mean CPUE (kg h^{-1}, cod length $\geq$30 cm) for the different ICES SDs (a-e) and the whole central Baltic Sea, SDs 25–29 (f). Bars represent 95% confidence intervals. Note the different scale on the *y*-axis.

come from the fishery. Commercial bottom trawling on cod in the southern Baltic Sea is concentrated during day-time in autumn and winter. The fishers claim that this is because cod rise off the bottom during dark hours, decreasing the catchability for the commercial vessels fishing demersally (Michele Casini personal communication with several Swedish fishers). The extent of these DVM would not need to be major, even in the range of just few metres, to affect the catchability to the pelagic trawling and thus be detectable in our CPUEs. However, we cannot rule out that the daily patterns in CPUEs found in our study could also be partially the result of other factors, such as visual avoidance to the trawl during day-time (Walsh, 1996 and references therein) or varying vertical herding during day and night (Glass and Wardle, 1989). Further analyses on cod vertical distribution at the population level, using a combination of pelagic and bottom trawl data, and also acoustics and tagging, are necessary to fully understand the mechanisms behind the general daily patterns in CPUE observed in our analysis.

The analyses of cod CPUEs as presented in our study rely on catch data that are normally stored during an already existing survey targeting pelagic fish (i.e. the BIAS). The high spatial extension of the BIAS, covering nearly the whole Baltic Sea from the Danish Belts to the Bothnian Sea and the Gulf of Finland, provides a remarkable and underutilized opportunity to monitor the large-scale dynamics of the Baltic cod over its entire potential area of distribution. Currently, the cod stock is mainly distributed in the southern Baltic Sea (this study; Bartolino *et al.*, 2017), but in the case the stock would recover it could re-expand into the northern historically occupied areas. Under these circumstances, the catches from acoustic surveys in the northern Baltic Sea could provide information on cod abundance, distribution, and biology in these areas which are not covered by the Baltic International Trawl Survey (BITS). The main limitations of the use of these pelagic catches to monitor cod are represented by the relatively low spatial sampling frequency (usually two trawl hauls for each ICES statistic rectangle, ICES, 2017a) and the presence of trawl hauls at depths where cod

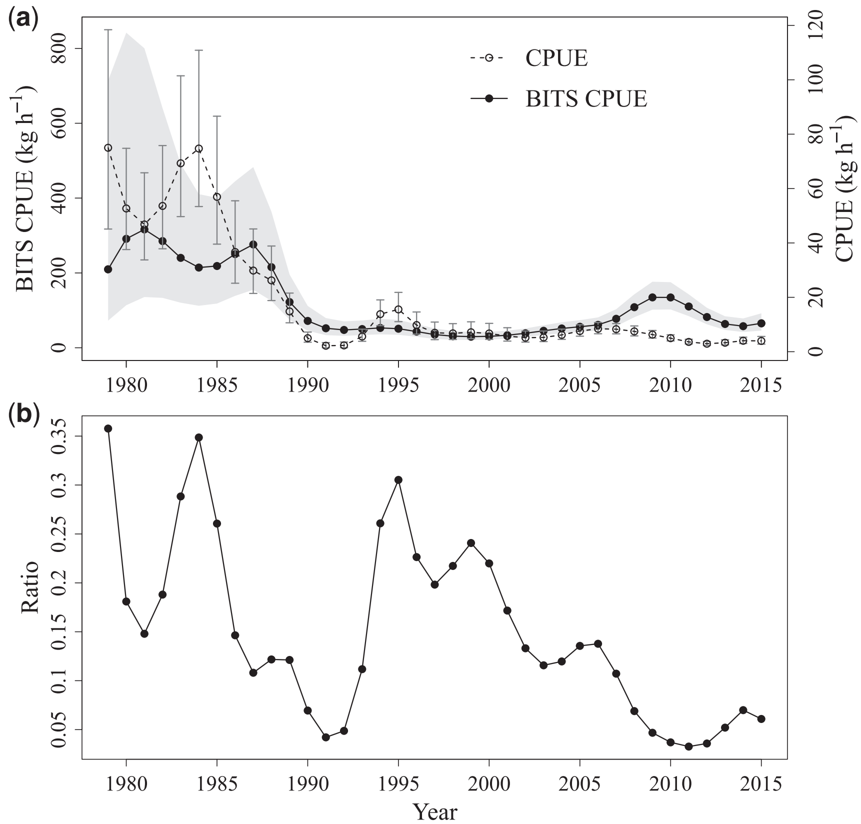

Figure 6. Comparison between acoustic survey (this study) and bottom trawl survey BITS in the fourth quarter: (a) mean CPUE (kg h^{-1}, cod length ≥30 cm) with 95% confidence intervals. (b) Ratio between the pelagic and bottom trawl CPUEs. In this comparison only the SDs 25–28 were used because the BITS covers mainly this area.

seldom occur, further reducing the actual number of observations. The use of acoustic methods (either acoustic backscattering values split among species or single fish echotracking; Simmonds and MacLennan, 2005; Schaber *et al.*, 2012) would obviously provide higher-quality and fine-scale information about the abundance and vertical distribution of cod, at both the individual and population level. The use of pelagic catch data as shown in our study could constitute, however, a reliable and simple approach to follow the large-scale spatio-temporal patterns in the cod population.

The fluctuating proportion of cod in the pelagic vs. demersal habitat (as indexed by our CPUEs, Figure 6) suggests that both habitats need to be sampled and accounted for to study the temporal changes in the population dynamics of this population. Specifically, information on pelagic cod catches, intertwined with the relevant information from hydro-acoustic measurements, would furnish data on the relative density and age-(size) composition of the pelagic component of the population that could improve cod stock analytical assessment that currently is based solely on the bottom trawl survey (ICES, 2008, 2009). Our analysis is a first step in this direction and can lay the first basis for a future combination of bottom trawl and acoustic surveys data (Kotwicki *et al.*, 2018) in the evaluation of the Eastern Baltic cod population. Sampling in the pelagic habitat could furnish important information on cod above hypoxic/anoxic water layers, which bottom trawl surveys evidently cannot provide. This is especially relevant in late summer and autumn, when the extent of hypoxic areas is the highest and therefore information from BITS and BIAS autumn surveys could be integrated to have a more comprehensive view of the cod population. The information collected from both surveys could also cast more light on the behavioural ecology of cod and the factors affecting its vertical and horizontal distribution in the Baltic seascape. Besides being related to hypoxia, the pelagic occurrence of Baltic cod is also related to the onset of predation on sprat and herring (at around 30 cm, Huwer *et al.*, 2014), and therefore the data can be used to analyse size-specific responses of cod behaviour (such as DVM) to temporal and spatial environmental variations, such as hydrological conditions and pelagic vs. benthic prey availability. This would allow to investigate the effect of cod population size structure on its habitat occupation. On the other hand, the changes in the relative proportion of cod occurring in the demersal and pelagic habitat may have strong implications for the predation on its pelagic prey (as sprat and herring) and benthic preys, and thus for the whole ecosystem structure and functioning (as benthic vs. pelagic energy flows, Tomczak *et al.*, 2012).

Supplementary data

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

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