ICES Journal of
Marine Science

ICES Journal of Marine Science (2017), 74(5), 1322–1333. doi:10.1093/icesjms/fsx005

Original Article

Modelling indices of abundance and size-based indicators of cod and flounder stocks in the Baltic Sea using newly standardized trawl survey data

Alessandro Orio[1,*], Ann-Britt Florin[2], Ulf Bergström[2], Ivo Šics[3], Tatjana Baranova[3], and Michele Casini[1]

[1]*Department of Aquatic Resources, Institute of Marine Research, Swedish University of Agricultural Sciences, Turistgatan 5, Lysekil 45330, Sweden*
[2]*Department of Aquatic Resources, Institute of Coastal Research, Swedish University of Agricultural Sciences, Skolgatan 6, Öregrund 74242, Sweden*
[3]*Department of Fish Resources, Institute of Food Safety, Animal Health and Environment "BIOR", Lejupes Street 3, Riga, LV 1076, Latvia*

**Corresponding author: tel: +46 725437988; e-mail: alessandro.orio@slu.se*

Orio, A., Florin, A.-B., Bergström, U., Šics, I., Baranova, T., and 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.

Received 8 July 2016; revised 6 January 2017; accepted 6 January 2017; advance access publication 7 February 2017.

Standardized indices of abundance and size-based indicators are of extreme importance for monitoring fish population status. The main objectives of the current study were to (i) combine and standardize recently performed trawl survey with historical ones, (ii) explore and discuss the trends in abundance, and (iii) the trends in maximum length (L_{max}) for cod (*Gadus morhua*) and flounder (*Platichthys flesus*) stocks in the Baltic Sea. Standardization of catch per unit of effort (CPUE) from trawl surveys from 1978 to 2014 to swept area per unit of time was conducted using information on trawling speed and horizontal opening of the trawls. CPUE data for cod and flounder stocks were modelled using generalized additive models (GAMs) in a delta modelling approach framework, while the L_{max} data were modelled using ordinary GAMs. The CPUE time series of the Eastern Baltic cod stock closely resembles the spawning stock biomass trend from analytical stock assessment. The results obtained furnish evidence of the cod spill-over from Subdivisions (SD) 25–28 to SD 24. The decline of L_{max} in recent years was evident for both species in all the stocks analysed indicating that the demersal fish community is becoming progressively dominated by small individuals. It is concluded that the standardization of long time series of fisheries-independent data constitutes a powerful tool that could help improve our knowledge on the dynamics of fished populations, thus promoting a long-term sustainable use of these marine resources.

Keywords: Baltic Sea, Gadus morhua, index of abundance, maximum length, Platichthys flesus, standardized trawl survey data.

Introduction

Indices of abundance based on fisheries-independent survey data are one of the most crucial inputs in analytical fish stock assessments (Maunder and Punt, 2004; Francis, 2011). Moreover, when analytical assessments cannot be performed, fisheries-independent data can be used to follow temporal trends in stock abundance to evaluate the state of the stock in relation to historical baselines. The lack of historical baselines, however, could lead to overly optimistic or misleading assessments of the status of fished populations that may affect management actions (Shifting baseline syndrome; Pauly, 1995; Pinnegar and Engelhard, 2008; Cardinale *et al.*, 2009). Ideally, these indices of abundance should be derived from data collected during standardized scientific surveys that have used the same gear and sampling scheme throughout the entire time series in order to avoid changes in catchability (Maunder and Punt, 2004; Cosgrove *et al.*, 2014; Thorson *et al.*, 2015). In reality, changes in gear types and sampling schemes almost always occur especially when surveys have been conducted

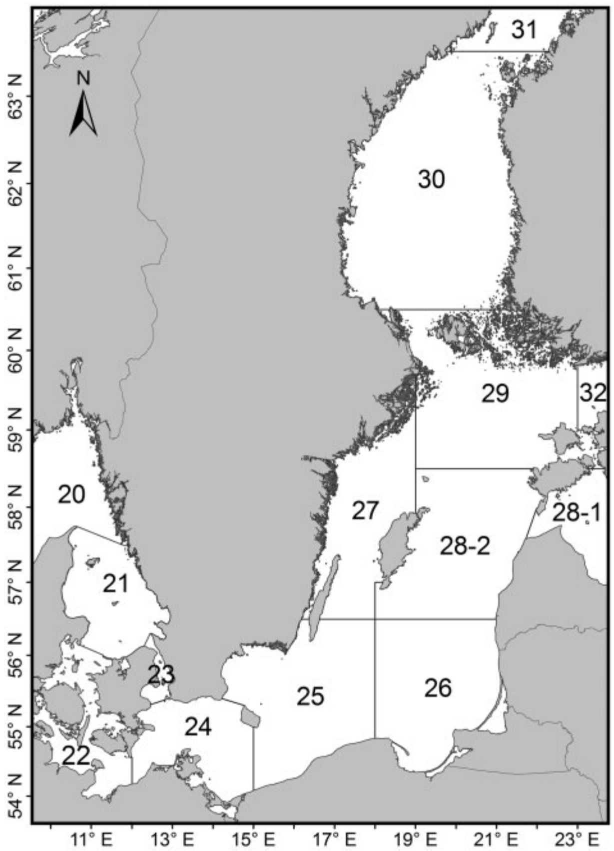

Figure 1. Map of the study area divided in ICES Subdivisions.

for a long period. Standardization is, therefore, obviously a key element in order to be able to make use of the enormous effort allocated in data collections throughout the years and thus to increase the temporal and spatial extent of the analyses.

Survey data, besides being important for stock assessment, also give information on the status of fish populations through indicators that can be derived from size frequency distribution, such as maximum length (L_{max}) or length at first maturity (Blanchard *et al.*, 2005; Shin *et al.*, 2005). Changes in size structure of a population can be caused by direct or indirect effects of fishing, changes in the environmental conditions, genetic variability as well as inter- and intraspecific interactions (Nicholson and Jennings, 2004; Shin *et al.*, 2005; Walsh *et al.*, 2006). If they remain undetected, these changes could result in the use of erroneous reference levels in stock assessments with possibly severe effects on management efficiency (Heino *et al.*, 2013). In the Marine Strategy Framework Directive (EU-COM, 2008), indicators of age and size structure are pivotal for assessing the status of exploited fish stocks, especially for stocks for which analytical assessments are not currently performed (Probst *et al.*, 2013). In particular, L_{max} is considered a good indicator of the status of a fish population because bigger individuals have higher fecundity, better egg quality, and higher reproductive success (Hixon *et al.*, 2014). Further, L_{max} is sensitive to fishing pressure since most fisheries are selectively removing the largest individuals of a population, but it can also respond to environmental factors such as, for example, changes in temperature (Piet and Jennings, 2004; Maschner *et al.*, 2008; ICES, 2012).

Cod (*Gadus morhua*, Gadidae) and flounder (*Platichthys flesus*, Pleuronectidae) are two key species of the Baltic Sea, both ecologically and commercially (Casini *et al.*, 2008; Florin and Höglund, 2008; Lindegren *et al.*, 2009). Abundance trends of cod in the Baltic Sea are known from analytical stock assessments, but long-term trends from fisheries-independent data are lacking (Eero *et al.*, 2011; ICES, 2015a). For flounder, on the other hand, information on populations' development is scarce because of the lack of analytical assessments and because the abundance trends derived from fisheries-independent data cover only the last 15 years (ICES, 2015a).

The use of fisheries-independent information collected through scientific trawl surveys is limited in the Baltic Sea by the lack of long-term standardized time series. This is due to the fact that from 2001 the Baltic International Trawl Survey (BITS; ICES, 2014a) has been carried out with a new sampling scheme and standard gear (ICES, 2015a) and that BITS data before and after 2001 have been standardized only for cod. Moreover, no data from historical surveys performed prior to BITS (i.e. before 1991) have been available to date.

Given the central importance of the indices of abundance and of size-based indicators for monitoring fish population status, the main objectives of the current study were (i) to combine and standardize recently performed trawl survey with historical ones, (ii) to explore and discuss the trends in abundance, and (iii) the trends in L_{max} for cod and flounder stocks in the Baltic Sea.

Material and methods

Available data

Catch and individual data for cod and flounder collected during the BITS (ICES, 2014a) in ICES Subdivisions (SDs) 22–29 (Figure 1) between 1991 and 2014 were downloaded from the ICES DATRAS database (datras.ices.dk; accessed on the 28 April 2015). Additionally, we compiled historical catch and individual data collected during bottom trawl surveys in the Baltic Sea carried out in the years 1978–1990 by the former Swedish Board of Fisheries (currently the Swedish University of Agricultural Sciences, Department of Aquatic Resources) and the former Baltic Fisheries Research institute (BaltNIIRH; currently the Latvian Institute of Food Safety, Animal Health and Environment). These historical data have been recently digitized. The catch data were constituted by catch in numbers per 1-cm length-class and total catch in weight for each trawl haul and were accompanied with information on haul duration, towing speed, fishing date, quarter (Q1 = January–March, Q2 = April–June, etc.), as well as setting and hauling position in latitude and longitude. Length frequency distribution (LFD) data were not available for all the trawl hauls. The individual data consisted of information on total length, total weight, age, sex, and maturity stage of individual cod and flounder caught during the trawl surveys.

For all surveys, trawl hauls classified as "Valid", "Additional" and "No Oxygen" were included in the analyses (ICES, 2014a). "Additional" hauls are valid hauls not used to calculate indices of abundance for stock assessment but mainly to collect biological parameters while "No Oxygen" hauls are hauls not performed because the bottom oxygen level is $< 1.5\ \mathrm{ml}^*\mathrm{l}^{-1}$ and the catch is assumed to be zero.

Catch per unit of efforts (CPUEs) for each length-class of cod and flounder were calculated as number of fish caught in 1 hour of trawling ($no*h^{-1}$), for the hauls in which the LFDs were available. CPUEs in weight ($kg*h^{-1}$) per length-class were estimated using the year-specific length–weight relationships ($W = a*L^b$) of the individual data. For the two Baltic cod stocks (SDs 22–24 and SDs 25–32), an analysis on the individual data showed different temporal trends in length–weight relationship (data not shown). Therefore, we used different year-specific length–weight relationships for the two stocks. For cod in SDs 22–24 individual weights were not available in 1988–1991 and an average of the parameters (a and b) estimated from 1992 to 1994 was used. For the four flounder stocks (SDs 22–23, SDs 24–25, SDs 26 & 28, SDs 27 & SDs 29–32), on the other hand, a common year-specific length-weight relationship was used since the temporal trends in the parameters a and b did not show any difference between stocks. Individual weights were not available for flounder in 1978, and thus an average of the parameters estimated from 1979 to 1981 was used. For the hauls in which the LFDs were not available, CPUEs in weight ($kg*h^{-1}$) were estimated from the total catch in weight.

Standardization of CPUE

Standardization of CPUEs from BITS and historical Swedish and Latvian surveys to swept area per unit of time was conducted using information on horizontal opening of the trawls and trawling speed, following the approach proposed by Cardinale *et al.* (2009).

The horizontal opening of each trawl is usually estimated as two-thirds of the length of the trawl fishing line (Rijnsdorp *et al.*, 1996). However, with the introduction of the sweeps (extensions of the ground rope between the wings of the net and the trawl doors) in the beginning of the 1920s, the area of seabed swept by the gear has increased considerably and substantially improved trawl efficiency at very little cost in terms of additional towing power (Galbraith and Rice, 2005). Therefore, the horizontal opening of the sweeps was summed to that of the fishing line to estimate the total horizontal opening between the trawl doors (total horizontal opening). The distance between the doors is dependent on the sweeps' length but also on the angle between the sweep and the direction of the tow. We standardized all the trawl hauls to the total horizontal opening of a TVL (standard trawl currently used in the BITS; ICES, 2014a) assuming an average angle of 15° between the sweep and the direction of the tow. We set the total horizontal opening of TVL with 75 m sweeps to 1 and the relative trawl size (RTS) of the other gears was expressed in relation to that. We gathered information about fishing line length and sweeps' length of all the gears except for seven gears that were then removed from the analysis, managing to standardize almost 90% of the hauls. The gears that have been standardized are: Grand Overture Verticale (GOV; according to the BITS gear code), Föto bottom trawl (FOT), Latvian bottom trawl (LBT), Sonderborg trawl (SON), Herring ground trawl (H20), Herring bottom trawl (P20), Cod hopper (CHP), TV3 930 meshes (TVL), and TV3 520 meshes (TVS). The gears that were removed are Russian bottom trawl (DT), Hake-4M trawl (HAK), Danish winged bottom trawl (EXP), Estonian small bottom trawl (ESB), Granton trawl (GRT), and two unspecified trawls (CAM and EGY).

We standardized all the trawl hauls to a trawling speed of three knots. We set the trawling speed of three knots to 1 and estimated the relative speed (RS) of the trawl hauls swept with a different speed. When the trawling speed was not available, the average speed of the same vessel using the same gear in the same year was used. When the vessel information was not available, the overall average speed in the same year or adjacent years were used.

All CPUEs were then multiplied by the reciprocal of the RS and of the RTS in order to make the catches of all the trawl hauls comparable. The CPUE value obtained is usually defined as an area-swept abundance estimate (Harley and Myers, 2001) and it corresponds here to the abundance of fish caught by trawling for 1 h a standard bottom swept area of 0.45 km^2 using a TVL trawl with 75 m sweeps at the standard speed of three knots.

No standardization was performed for the different mesh sizes used by the different gears during the study period because the biggest registered stretched mesh size in our data was 30 mm, which we considered to be small enough not to introduce any bias in our analyses.

Data included in the modelling of CPUE in weights and maximum length (L_{max})

We decided to include only the flounder stock in SDs 24–25 and the stock in SDs 26 & 28 in the analyses. The flounder stock in SDs 22–23 was excluded as it was impossible to standardize the gears that were used to fish in those areas; the flounder stock in SDs 27 & 29–32 was excluded because the BITS survey does not cover SDs 29–32. The merging of SD 26 and 28 in the current stock definition by ICES has been questioned since tagging show very little exchange between these SDs (ICES, 2010). We therefore also investigated the trends in these SDs separately. For cod, we performed the analysis on the Eastern Baltic cod stock (SDs 25–32) only in SDs 25–28 because the BITS survey does not cover the SDs 29–32, and because we assume that the stock temporal dynamics in SDs 25–28 (main area of distribution) are consistent with the overall stock dynamics. For the Western Baltic cod stock (SDs 22–24), we decided to perform the analysis only for SD 24 because it was not possible to standardize the gears that were used in SDs 22–23. It is known that SD 24 is an important mixing area between the Eastern and the Western Baltic cod stocks (Hüssy *et al.*, 2016) and therefore the temporal trends of CPUE and L_{max} in SD 24 were compared with those in SDs 25–28 and also with that in SD 25 separately. Hereafter, for simplicity, we will refer to cod in SDs 25–28 and cod in SD 24 as the Eastern and the Western Baltic cod stock, respectively. For both cod and flounder we excluded from the analyses the Gulf of Riga (SD 28-1) because the BITS survey does not cover this area.

For the CPUE analyses, we aimed at following the spatiotemporal changes in the spawning part of the stocks, which correspond to fish ≥ 30 cm for cod (ICES, 2015a) and ≥ 20 cm for flounder (ICES, 2014b). However, for flounder, the CPUEs per length class (i.e. the LFDs) were not available for around one third of the hauls performed before the BITS (i.e. before 1991). For the hauls in which LFDs were available, the proportion of flounder < 20 cm in the catches was relatively constant (both temporally and spatially, i.e. among SDs) and below 10% of the total catches, except for some years in SD 26. The low proportion of small flounder in the catches is explained by the fact that the surveys do not cover the shallowest areas were juvenile flounders are found (ICES, 2015a). Therefore, we assumed that the spatiotemporal changes in the total CPUEs would reliably represent the trends of the spawning part of the flounder population.

For the L_{max} analyses, the maximum length (L_{max}, [cm]) was defined as the maximum observed fish length in each haul.

Statistical analysis

The distribution of marine species is the result of the connections between the intrinsic characteristics of the populations, trophic interactions, hydrological constraints and anthropogenic factors. Because of all these interdependencies, we expect the abundance of cod and flounder to be better described by non-linear functions of space and time. In order to capture this non-linearity, we decided to use generalized additive models (GAMs) to model the trends in CPUE and L_{max}. Nonlinear approaches, like GAMs, have been found to perform better than linear models for the standardization of CPUEs (Maunder, 2001).

Because of the large amount of zero catches in our dataset (between 4.5 and 23.1% of all the hauls depending on the stock), the CPUE data for cod in SD 24, cod in SDs 25–28, flounder in SDs 24–25, and flounder in SDs 26 & 28 was modelled at first using ordinary GAMs with different error distributions that could deal with zero-inflated data (e.g. the quasi-Poisson distribution) but none of the models had acceptable residuals. We then decided to adopt GAMs in a delta modelling approach framework. This modelling approach has been found to be appropriate for the analysis of zero-inflated data (Stefánsson, 1996; Barry and Welsh, 2002; Maunder and Punt, 2004) and has been used to estimate the spatial distribution of marine organisms at large spatial scales (Loots *et al.*, 2010; Lauria *et al.*, 2011; Grüss *et al.*, 2014; Parra *et al.*, 2016), as well as to standardize CPUE data and indices of abundance (Berg *et al.*, 2014; Cosgrove *et al.*, 2014; Thorson and Ward, 2013, 2014). The delta models have become widely adopted especially in the case of survey indices standardization because they allow the separation of the model into two ecologically meaningful components (Thorson and Ward, 2013): the first estimates the probability of encountering the target species and the second estimates the population density within its range of distribution. The total abundance is then the product of the probability of encounter and the population density. The two components are essential because both the distribution range and the densities are likely changing over time.

Delta GAM for the CPUE

The delta GAM approach used in these analyses consists of two steps: the first involves modelling the presence/absence of the species using a binomial error distribution with a logit link function, and the second is modelling the abundance of only positive CPUE records, log-transformed, using a Gaussian error distribution with an identity link function (Lauria *et al.*, 2011; 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 CPUE predictions.

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

$$\begin{aligned}\text{presence/absence} = {} & \beta(\text{quarter}) + s(\text{long}, \text{lat}) + te_1(\text{depth}, \text{year}) \\ & + f_1(\text{year}) + f_2(\text{depth}) + f_3(\text{lat}) + f_4(\text{long}) \\ & + \varepsilon\end{aligned} \tag{1}$$

$$\begin{aligned}\log(\text{CPUE}) = {} & \beta(\text{quarter}) + s(\text{long}, \text{lat}) + te_1(\text{long}, \text{year}) \\ & + te_2(\text{lat}, \text{year}) + te_3(\text{depth}, \text{year}) + f_1(\text{year}) \\ & + f_2(\text{depth}) + f_3(\text{lat}) + f_4(\text{long}) + \varepsilon\end{aligned} \tag{2}$$

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 in the time period analysed.

Model selection for both models was done through a backward stepwise selection approach based on statistical significance (Wood, 2006). From the full model, the non-significant predictor with the lowest significance level was excluded at each step and the model run again. This procedure was repeated until all the predictors were significant (final model). To make the interpretation of the model results easier, we set a limit to the maximum degrees of freedom (number of knots, k) allowed to the smoothing functions of the variables latitude, longitude and depth ($k = 4$) and of the interaction between latitude and longitude ($k = 20$).

GAM for L_{max}

The L_{max} data for cod in SD 24, cod in SDs 25–28, flounder in SDs 24–25, and flounder in SDs 26 & 28 were modelled with a GAM using a Gaussian distribution since the L_{max} values were normally distributed (Hastie and Tibshirani, 1990).

The full model was formulated as follows:

$$\begin{aligned}L_{max} = {} & \beta(\text{quarter}) + s(\text{long}, \text{lat}) + te_1(\text{long}, \text{year}) + te_2(\text{lat}, \text{year}) \\ & + te_3(\text{depth}, \text{year}) + f_1(\text{year}) + f_2(\text{depth}) + f_3(\text{lat}) \\ & + f_4(\text{long}) + \epsilon\end{aligned} \tag{3}$$

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, f_i are natural cubic splines, and ϵ is an error term. The interactions were introduced to take into account the changes in the spatiotemporal distribution of the species in the time period analysed. No correlation was found between trawl duration and L_{max} of cod ($r = 0.18$) and flounder ($r = 0.04$), therefore we did not include it in the full model formulation. As for the previous models, model selection was done through a backward stepwise selection approach based on statistical significance (Wood, 2006).

To make the interpretation of the model results easier, also for L_{max} we set a limit to the maximum number of knots (k) allowed to the smoothing functions of the variables latitude, longitude and depth ($k = 4$) and of the interaction between latitude and longitude ($k = 20$).

Reconstructing the trends in CPUE and L_{max} of different stocks

The final models for each stock were used to predict the annual CPUE and L_{max} over a regular grid of $0.02° \times 0.01°$. The area in SD 27 north of 58° was removed from the predictions due to incomplete spatial coverage.

Because of poor survey coverage in shallow and deep parts of the different areas, depths shallower than 10 m were excluded from the predictions of cod in SD 24, depths shallower than 8 m and deeper than 150 m were excluded from the predictions of cod in SDs 25–28, depths shallower than 10 m and deeper than 100 m were excluded from the predictions of flounder in SDs 24–25 and depths shallower than 8 m and deeper than 150 m were excluded from the predictions of flounder in SDs 26 & 28. To produce the trends in mean CPUE and mean L_{max}, all the predicted estimates were averaged over the whole grid in the respective stock area for each year for quarter 1 (Maunder and Punt, 2004; Beare *et al.*, 2005; Cardinale *et al.*, 2011).

Reconstructing the trends in exploitation rate of different stocks

The CPUE trends produced from the final models were used to obtain trends in exploitation rate, estimated as the ratio of the commercial catches (ICES, 2015a) to the CPUEs. The commercial catches (landings and discards) of cod $\geq$ 30 cm (size range considered in the CPUEs analyses) have constituted more than $\sim$ 98% of the total catches in weights between 2000 and 2014 (ICES, 2015a) (fish $\geq$ 30 cm includes discards since the minimum landing size has varied between 35 and 38 cm in this period). In earlier years (before 1994), the minimum landing size was 33 cm, therefore still higher than the lower length boundary used in the CPUE estimations. We are therefore confident that our CPUEs for fish $\geq$ 30 cm include the component of the cod populations exploited by the fishery.

For flounder, the temporal trends in exploitation rate were estimated using the ratio of the commercial landings (official ICES landings; ICES, 2013; ICES, 2015a) to the CPUEs obtained from our final models. Flounder $\geq$ 20 cm constitute by far the largest part of the commercial catches (more than 90%), while fish $<$ 20 cm are caught (and then landed or discarded) very seldom (ICES, 2014b). We are therefore confident also for flounder that the CPUEs estimated in our study include the component of the populations exploited by the fishery. On the other hand, discards of flounder could be quite substantial in the Baltic demersal fishery, but their survival is also high, over 50% in cold seasons (ICES, 2014b). Therefore, although uncertainties exist with respect to survival rate of discarded flounder, we believe that exploitation rate as estimated in our study is a reliable proxy for fishing mortality also for this species.

All the analyses were performed using R software and the mgcv library of R (Wood, 2011; R Core Team, 2015).

Results

Trends in CPUE

Standardized CPUEs from a total of 10 198 hauls for cod and 9548 hauls for flounder, were included in the analyses (Supplementary Table S1). The equations of the final models varied between modelling approaches (Binomial and Gaussian) and stocks, but the interactions between latitude and longitude and the effect of quarters were always retained after the backward stepwise selection procedure (Table 1). Final binomial models explained between 23.3% of the deviance for cod in SDs 25–28 and 40.9% for cod in SD 24, while Gaussian models explained between 32% for flounder in SDs 24–25 and 42.9% for cod in SDs 25–28. In general, the adjusted R^2 indicated a better model fit for the Gaussian models compared to the binomial models. Analysis of the residuals in some cases revealed slight departures from the model assumptions, but we considered the overall quality of the residuals to be satisfactory (Supplementary Figures S1–S8).

Time series of the estimated CPUEs for the cod and flounder stocks are presented in Figure 2. For cod in SD 24 (Figure 2a), the highest CPUE of around 140 kg*h^{-1} was observed at the beginning of the time series (1988) and two other smaller peaks occurred around 1995 and 2007. For cod in SDs 25–28 (Figure 2b), the CPUE was at the maximum around 1981–1982 (220 kg*h^{-1}) and a smaller peak of CPUE was revealed around 2008–2010. However, the CPUE maximum in SD 25 occurred a little later (1982–1984) than in SDs 26–28. Moreover, since the early 1990s, the CPUEs in SD 25 were always higher than in SDs 26–28, while the temporal variations were coincident. The CPUE has decreased from 2009 to 2014 by around 60% in the entire area. Flounder in SDs 24–25 (Figure 2c) shows a decline in CPUEs from a maximum of 44 kg*h^{-1} at the beginning of the time series (1988) to the end of 1990s (approximately 8 kg*h^{-1}), whereas thereafter an increase of around 70% occurred up to 2014. Flounder in SDs 26 & 28 (Figure 2d) shows the highest CPUEs of 110 kg*h^{-1} at the beginning of the time series (1978–1979) and a sharp decline of around 90% up to mid-1980s. Thereafter, a general increase occurred up to early 2000s followed by a decrease of approximately 85%. However, the CPUEs in SD 28 were always higher than in SD 26, especially during the periods of highest CPUEs. In general, flounder CPUE decreased in both SDs 26 and 28 in the last 5 years but in SD 28 flounder started to decline already in the early 2000s, whereas in SD 26 the decline was evident only since 2010.

Trends in L_{max}

L_{max} values from a total of 9005 hauls for cod and 7627 hauls for flounder were included in the analyses. The formulas of the final models varied between stocks, but the interactions between latitude and longitude and between depth and year, the smoother on the year and the effect of quarters were always retained (Table 2). Final models explained between 19.6% of the deviance for cod in SD 24 and 34.6% for cod in SDs 25–28. Analysis of the residuals in some cases revealed slight departures from the model assumptions, but we considered the overall quality of the residuals to be satisfactory (Supplementary Figures S9–S12).

Time series of the estimated L_{max} for the cod and flounder stocks are presented in Figure 3. Cod in SD 24 (Figure 3a) shows a decrease in L_{max} from around 64 cm in 1988 to around 49 cm in 2014. Cod in SDs 25–28 (Figure 3b) shows the highest L_{max} of approximately 77 cm in 1983–1985, then the L_{max} decreased steadily down to around 40 cm in 2014. However, the L_{max} in SD 25 remained relatively stable between the mid-1990s and late 2000s before dropping afterwards down to 47 cm. In SDs 26–28, L_{max} declined continuously throughout the time period analysed down to 38 cm in 2014. For flounder in SDs 24–25 (Figure 3c) L_{max} fluctuated between 33.5 and 36 cm through the entire time series. In SDs 26 & 28 (Figure 3d) flounder L_{max} increased 10% from the beginning of the time series (1978) until 1994 where it reached the maximum value of approximately 37.5 cm, and then has decreased steadily down to around 33 cm in 2014. However, L_{max} was lower in SD 26 than in SD 28 before the mid-1990s, whereas afterwards the spatial difference was reversed with L_{max} lower in SD 28 than in SD 26. In particular, L_{max} of flounder in SD 26 was lower than 30 cm at the beginning of the time series, then increased until reaching a maximum of around 37.5 cm in 1994 and in the last part of the time series decreased down to around 33 cm. In SD 28, on the other hand, L_{max} of flounder increased from around 37.5 cm in 1978 to around 39.5 cm in 1985 and then decreased to around 28 cm in 2014.

Table 1. Summary statistics of the Delta GAMs used to estimate the CPUE trends for each stock analysed.

Stocks	Years	Quarters	Models	n	df	Variables retained	Dev%	Adj-R^2
Cod 24	1988–2014	1,4	Binomial	2036	19.3	Lat:Long, Depth (as linear effect), Year, Quarter	40.9	0.277
			Gaussian	1944	48.6	Lat:Long, Depth:Year, Lat, Long, Year, Quarter	40.9	0.394
Cod 25–28	1978–2014	1,2,3,4	Binomial	8162	47.4	Lat:Long, Depth:Year, Lat, Long, Quarter	23.3	0.250
			Gaussian	6784	78.0	Lat:Long, Lat:Year, Long:Year, Depth:Year, Lat, Year, Quarter	42.9	0.423
Flounder 24–25	1988–2014	1,3,4	Binomial	5230	33.5	Lat:Long, Depth:Year, Lat, Year, Quarter	31.1	0.310
			Gaussian	4709	73.2	Lat:Long, Lat:Year, Long:Year, Depth:Year, Lat, Year, Quarter	32.0	0.309
Flounder 26 & 28	1978–2014	1,2,3,4	Binomial	4318	41.0	Lat:Long, Depth:Year, Year, Quarter	26.8	0.276
			Gaussian	3320	70.7	Lat:Long, Lat:Year, Long:Year, Depth:Year, Depth, Quarter	34.9	0.335

The variables retained in the final models are indicated; n = numbers of hauls used in the models; df = degrees of freedom; Dev% = explained deviance; Adj-R^2 = adjusted R^2.

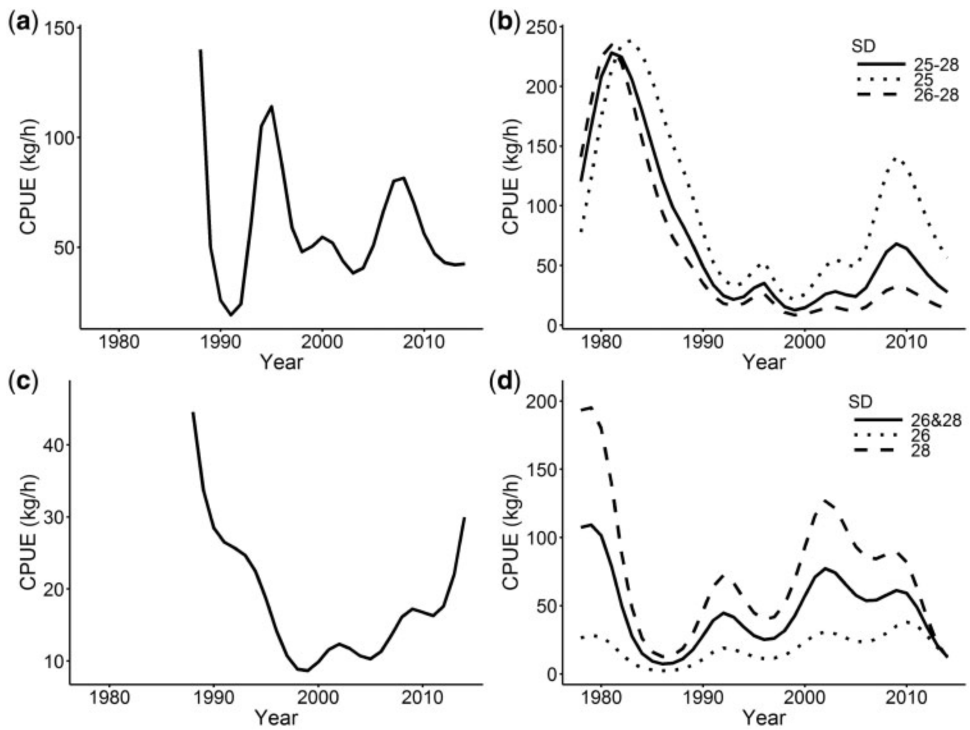

Figure 2. Estimated average yearly CPUE (kg*h^{-1}) predicted by the models for (a) cod in SD 24, (b) cod in SDs 25–28, (c) flounder in SDs 24–25 and (d) flounder in SDs 26 & 28.

Table 2. Summary statistics of GAMs used to estimate the L_{max} trends for each stock analysed.

Stocks	Years	Quarters	n	df	Variables retained	Dev%	Adj-R^2
Cod 24	1988–2014	1,4	1979	40.4	Lat:Long, Depth:Year, Year, Quarter	19.6	0.180
Cod 25–28	1978–2014	1,2,3,4	7026	79.2	Lat:Long, Lat:Year, Long:Year, Depth:Year, Depth, Year, Quarter	34.6	0.339
Flounder 24–25	1988–2014	1,3,4	4706	57.4	Lat:Long, Lat:Year, Long:Year, Depth:Year, Depth, Year, Quarter	22.8	0.218
Flounder 26&28	1978–2014	1,2,3,4	2921	65.7	Lat:Long, Lat:Year, Long:Year, Depth:Year, Year, Quarter	31.7	0.301

The variables retained in the final models are indicated; n = numbers of hauls used in the models; df = degrees of freedom; Dev% = explained deviance; Adj-R^2 = adjusted R^2.

Trends in exploitation rate

Cod in SD 24 was subject to a fairly constant exploitation rate throughout the time series (Figure 4a). For cod in SDs 25–28, the exploitation rate continuously increased from the beginning of the time series until reaching a maximum in the year 2000 and then decreased reaching a minimum value in 2008. In the last 6 years, the exploitation rate slightly increased (Figure 4b). For flounder in SDs 24–25, the exploitation rate strongly increased from the late 1980s up to late 1990s, then fluctuated around the same level and then decreased from 2005 onwards (Figure 4c). In SDs 26 & 28 (Figure 4d), the exploitation rate was less dynamic than in SDs 24–25 with the exception of one peak in the late

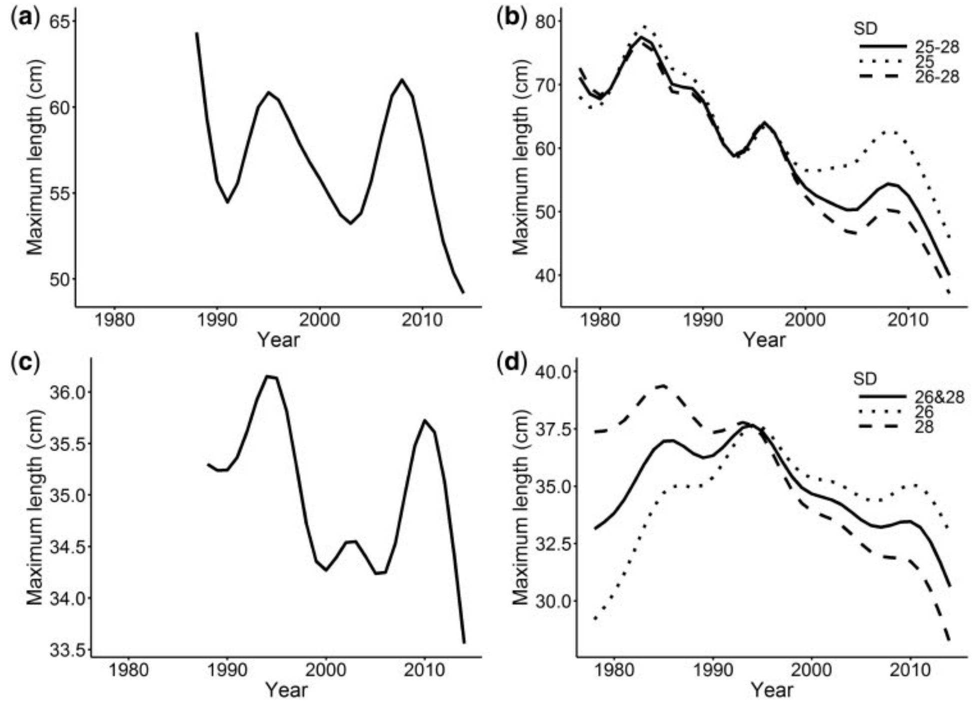

Figure 3. Estimated average yearly L_{max} (cm) predicted by the model for (a) cod in SD 24, (b) cod in SDs 25–28, (c) flounder in SDs 24–25 and (d) flounder in SDs 26 & 28.

1980s and one in the last 2 years of the time series. However, the exploitation rate in SD 28 was almost constant compared to SD 26 that presented an important peak in the late 80s.

Discussion

In this study, we reconstructed the trends in CPUE and L_{max} of two cod and two flounder stocks in the Baltic Sea by analysing an extensive and unique dataset from scientific trawl surveys. The primary and most relevant steps that allowed us to perform these analyses were the collection of modern and historical trawl survey data complete with gear geometries and the subsequent standardization of the data. The standardized time series of CPUE and L_{max} provide unprecedented opportunities for utilizing an impressive amount of data collected during the past 40 years in the Baltic Sea.

Cod

The CPUE time series of the Eastern Baltic cod stock we have produced, closely resembles the spawning stock biomass (trend of the latest accepted analytical stock assessment (ICES, 2013). The biomass of this cod stock had a major increase in the late 1970s and beginning of the 1980s and the spatial distribution of the stock was the widest ever recorded, with spill-over in areas where cod normally do not occur, such as the Gulf of Riga (SD 28-1) and the Bothnian Sea (SD 30; Casini *et al.*, 2012; Casini, 2013). When the cod stock crashed during the mid-1980s, it started to contract to the southern areas and especially to SD 25 (Eero *et al.*, 2012). The results of our model also revealed this spatiotemporal change, showing that in the early 1980s, the CPUEs in SD 25 and SDs 26–28 were similar, whereas after the cod crash in the early 1990s, the CPUE in SD 25 has been twice than in SDs 26-28. Since the mid-2000s, the CPUE has generally increased but mainly in SD 25 (~60% of the CPUE maximum in 1981), while the persisting low CPUE in SDs 26–28 indicates that cod has not yet succeeded in re-expanding its distribution into more northern areas. After the late 2000s, a drop in CPUE has occurred picturing a current situation with very low spawning population size. The temporal dynamics in cod abundance have been historically attributed to the concomitant effects of changes in fishing pressure, seal predation and hydrological conditions acting on recruitment (Eero *et al.*, 2011). Notably, the lack of cod recovery and re-expansion of its distribution since the early 1990s can be attributable to persisting high fishing pressure, low body condition, decrease in suitable spawning and feeding areas due to oxygen deficiency in the northern areas and loss of subpopulations (Möllmann *et al.*, 2011; Eero *et al.*, 2012, 2015; ICES, 2015b).

The L_{max} of Eastern Baltic cod showed a constant decline from the mid-1980s onwards, which is in line with the findings by Svedäng and Hornborg (2014) who evidenced a decrease in the asymptotic length for this stock between 1991 and 2014. Our analysis however, extending back to the late 1970s, was able to reveal that the decrease in L_{max} started already in the mid-1980s, concomitant with the stock collapse. The drop in L_{max} during the past 30 years was probably caused by a mix of excessive fishing pressure and changes in growth. Fishing mortality has been high, far above safe reference points, since the late 1980s (ICES, 2013). This could have caused the drop in L_{max} due to the selective nature of the fishery, targeting and therefore selectively removing the largest and most valuable fish (Vainikka *et al.*, 2009). However, the decrease in L_{max} could also be due to a reduction in individual growth rates that could be linked to food shortage, physiological responses to increased hypoxic areas and/or density-dependence (Eero *et al.*, 2012; Svedäng and Hornborg, 2014; ICES, 2015c; Casini *et al.*, 2016). The trends in L_{max} of SD

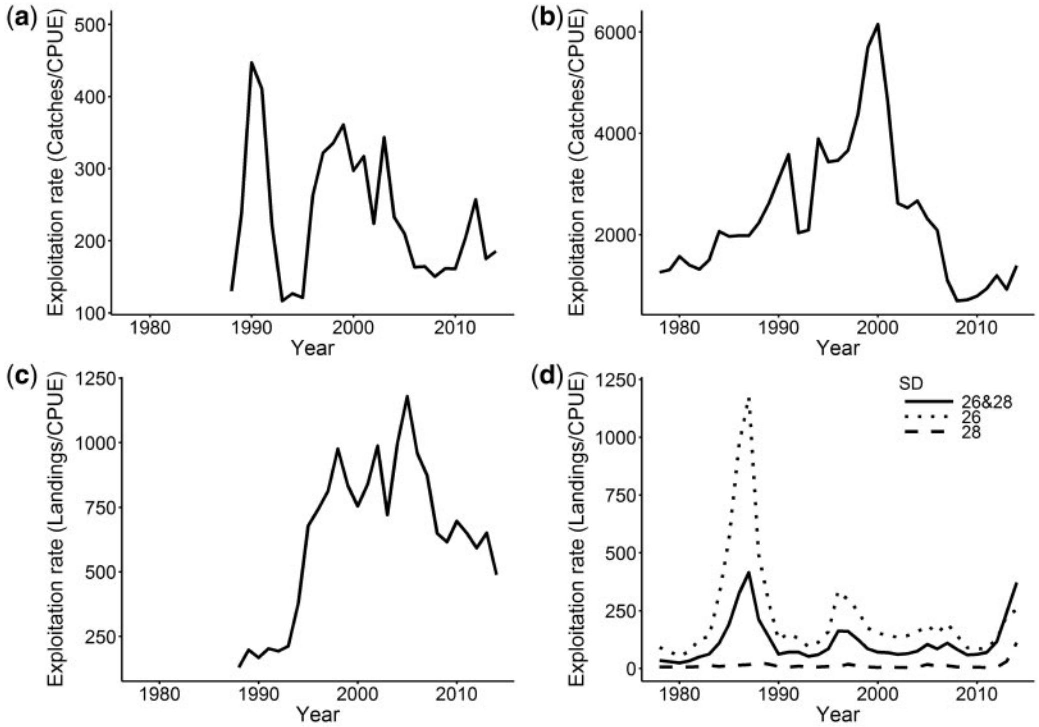

Figure 4. Estimated average yearly exploitation rate (catches/CPUE) for (a) cod in SD 24 and (b) cod in SDs 25–28, (c) (landings/CPUE) flounder in SDs 24–25 and (d) flounder in SDs 26 & 28 (for the whole stock and separately for SD 26 and SD 28).

25 and SDs 26–28 were almost identical until the late 90s, when they diverged: SDs 26–28 showed a continuous decline while in SD 25 L_{max} showed a relatively stable pattern until 2008 followed by a steep decline. Beside spatial heterogeneity in the fishery (ICES, 2015a), food availability (Gårdmark *et al.*, 2015) and hydrological conditions (Casini *et al.*, 2012), we speculate that the spatial differences in L_{max} during the past 15 years were also related to the absence of suitable spawning areas in SDs 26–28 causing a higher concentration of mature and larger fish in SD 25. Considering its ecological and economic relevance, explaining the continuous decrease in cod L_{max} during the past 30 years should be a priority for future investigations.

The dynamics of CPUE and L_{max} in SD 24 (eastern part of the Western Baltic stock) resemble those of the Eastern Baltic stock. In fact, the peaks of CPUEs in SD 24 occurred in the same years of high CPUE values in SD 25 with the exception of the last peak in mid 2000s that seems to occur a couple of years earlier in SD 24. The slight asynchrony of the last high CPUE value could be explained by the use of different models to predict the trends in the two different areas that could have slightly different smoothing parameters. Also L_{max} showed a striking synchrony between SD 24 and SD 25. In SD 24 and SD 25, the hydrological conditions, management, and biology of the two stocks are different (Hüssy, 2011; ICES, 2015a) and we hypothesize that the synchrony in the dynamics of the two stocks is not caused by common drivers. We therefore conclude that these results furnish evidence of the cod spill-over from SD 25 to SD 24 and of the occurrence of mixing between the Eastern and Western Baltic cod stocks in SD 24, especially in periods of high abundances in SD 25 (ICES, 2015a; Hüssy *et al.*, 2016).

Flounder

The reconstructed time series of flounder CPUE in SDs 24–25 shows that the population in this area was more abundant in the late 1980s compared to the current situation, while the stock index of abundance that have been used so far in stock assessment and advice shows only an increase of abundance due to the shorter time series used (ICES, 2015a). The limited amount of years in the assessment time series could therefore lead to an overoptimistic view of the stock status. The flounder in this area suffered a drastic decrease in abundance between 1920s and 1940s presumably caused by intense fishery (Molander, 1955). During the same time period, the mean size at age and size at maturity increased and Molander (1938) suggested that this was due to the relaxation of the earlier density dependent limitation in growth. L_{max} in our study, however, showed no apparent correlation with the fluctuations in abundance suggesting that other mechanisms were also involved in the variations of L_{max} in SDs 24–25.

The results of the model of the CPUE of flounder in SDs 26 & 28 show that the stock abundance was high at the end of the 1970s and then crashed, reaching its minimum around the mid-1980s. This high abundance and consequent collapse of this flounder stock has never been shown before in the literature but it is known that in the 1980s the flounder in SD 28 reached an extremely low level of abundance and a fishing ban on the specialized flounder fishery was enforced by the Soviet Union (D. Ustups, pers. comm.). If we take into account the two areas separately, the difference between the dynamics in SD 26 and SD 28 is striking; while the part of the stock in SD 26 shows a less variable CPUE time series, the flounder in SD 28 reveals strong fluctuations driving the trend of the whole stock. One reason for the fluctuation in stock size in SD 28 might be the variations in available reproductive volume. Ustups *et al.* (2013) found a strong relationship between reproductive volume (determined by salinity and oxygen) in the Gotland deep and the subsequent larval production in the area. The decline of flounder in the northernmost Baltic (SDs 29 and 32) is speculated to depend on environmental change such as pollution and eutrophication but also changes in salinity might be important (Jokinen *et al.*, 2015). Salinity is a limiting factor for reproduction of marine teleosts like flounder and cod, and salinity has earlier been shown to be related to flounder abundance in the central Baltic (SD 27; Olsson *et al.*, 2012) and Gulf of Finland (SD 32; Ojaveer *et al.*, 1985; Ojaveer and Kalejs, 2005). SD 28 might be more sensitive to saltwater inflow as it is on the margin for successful reproduction of flounder (10 PSU for offshore pelagic eggs and 7 PSU for coastal demersal eggs; Nissling *et al.*, 2002) potentially explaining the more dynamic CPUE time series in this SD. Moreover, it is possible that the dissimilar trends between the areas are driven by different causes; SD 28 could potentially be mostly driven by environmental factors such as salinity, while SD 26 by higher fishing pressure compared to SD 28 as indicated by higher landings in SD 26 compared to SD 28 in the analysed timeframe (ICES, 2013; ICES, 2015a). Finally, the different CPUE trends of flounder in SDs 24–25 and in SDs 26 & 28 suggest that the degree of mixing between the two stocks is low.

The L_{max} for the flounder stock in SDs 26 & 28 overall decreased in the last 20 years. The results obtained for SD 26 and SD 28 separately are interesting, showing a steep decline in L_{max} in SD 28 throughout the whole time series and a relatively dome-shaped trend in SD 26. The interpretation of these results is quite complicated especially in SD 28 since this area is occupied also by another stock of flounder, the coastal spawning flounder with demersal eggs (Nissling *et al.*, 2002; Florin and Höglund, 2008). This spawning type mainly resides in SDs 27 & 29–32, but it is known to occur also in SD 28, although at low densities (ICES, 2014b). The demersal spawning flounder is known to have smaller body size (Nissling and Dahlman, 2010), and thus we cannot exclude that the decrease in L_{max} in SD 28 is partly due to a change of the proportion of the two flounder ecotypes in this area.

Potential interactions between cod and flounder

The flounder stock started to decline during the rapid increase of the cod stock in the late 1970s–early 1980s and after the cod stock collapsed the flounder in SDs 26 & 28 began to recover. This potential negative link between cod and flounder dynamics has not been studied before, even though large cod can feed on flounder (Almqvist *et al.*, 2010; ICES, 2016) and the two species potentially compete for benthic prey (Arntz and Finger, 1981; Gjøsæter, 1988). Only Persson (1981) speculated on the fact that the low abundances of cod in the southern part of the Baltic at the beginning of the 20th century could have been caused by the effects of high competition for benthic preys between young cod and flatfishes, especially the dab (*Limanda limanda*, Pleuronectidae). Studies performed in some areas of the North Atlantic, in the Bering Sea and on the Scottish coast have shown that gadoid predation on juvenile flatfishes are quite widespread (Bailey, 1994 and references therein; Ellis and Gibson, 1995). In the Bering Sea predation of arrowtooth flounder (*Atheresthes stomias*, Pleuronectidae) on juvenile pollock (*Theragra chalcogramma*, Gadidae) has been proposed to affect recruitment success of the gadoid population (Hunsicker *et al.*, 2013). At Georges Bank studies have shown competition between haddock (*Melanogrammus aeglefinus*, Gadidae) and yellowtail flounder (*Limanda ferruginea*, Pleuronectidae) (Link *et al.*, 2005 and reference therein). Similar ecological links between cod and flounder may play a role in their population dynamics in the Baltic Sea.

Changes in the demersal fish community

The decline of L_{max} evidenced in all the stocks considered in this study raise concern about the ecosystem state of the Baltic Sea. On a population level, the presence of large and old individuals plays a role in population resilience: e.g. large and old fishes usually are characterized by high fecundity and fitness, large eggs, a prolonged spawning period and are considered as reservoirs of desirable genes (Vallin and Nissling, 2000; Froese, 2004; Nissling and Dahlman, 2010; Hixon *et al.*, 2014). On a community level, our results show that the fish demersal component is becoming progressively dominated by small individuals. Similar results have been shown for the Baltic pelagic community (Oesterwind *et al.*, 2013). These structural changes in the Baltic fish communities may reflect changes in the trophic interactions within the community and could be caused by disproportionate high fishing mortality on larger individuals and/or by changes in the environmental conditions affecting growth.

Concluding remarks

The delta modelling framework used to produce the CPUE time series for cod and flounder captured the known dynamics of cod in SD 25–28. Still, our models suffer from a number of limitations and could be improved. The most important issue is related to the assumed independence between the presence/absence and the abundance model (Thorson and Ward, 2013). The inclusion of environmental variables such as salinity, oxygen and temperature in the presence/absence models could potentially increase the model fit and the predictive power of the binomial model.

The collection and standardization of historical survey data are important in the Baltic, with its changes in salinity, temperature, oxygen conditions as well as eutrophication, and fishing effort (Niiranen *et al.*, 2013). An extraordinary amount of data has been collected through time by the states bordering the Baltic Sea during nationally and internationally trawl surveys. Our standardization of these survey data and the subsequent modelling of the time series constitute a powerful tool that improves our knowledge on fished populations in the Baltic Sea, thus promoting long-term sustainable use of these marine resources.

The long time series of CPUE and L_{max} presented here are a step forward in the knowledge of the dynamics of the four stocks considered. In future analyses, the standardization of CPUE might be considered to be integrated in stock assessments as suggested by Maunder (2001). For the cod stocks, these stock assessments already exists, although the assessment for Eastern Baltic cod stock has been rejected in the last years and the fisheries-independent time series used before have been shorter. For flounder, which is equally important for fisheries and has a central role in the ecosystem (Florin *et al.*, 2013; Östman *et al.*, 2013; ICES, 2016) analytical stock assessments are not available. The CPUE time series and size-based indicators we developed hopefully help the conservation and management of these stocks in the Baltic Sea.

Supplementary data

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

Acknowledgements

We thank Valerio Bartolino for his valuable comments on the modelling. We are also grateful to all the colleagues and experts that helped us gathering the gear geometries for the standardization. Two anonymous reviewers provided constructive comments on a previous version of the manuscript. This work was financed by the BONUS INSPIRE project supported by the Joint Baltic Sea Research and Development Programme BONUS (Art 185), funded jointly by the EU and the Swedish Research Council Formas (Sweden) and the State Education Development Agency (Latvia).

References

Almqvist, G., Strandmark, A. K., and Appelberg, M. 2010. Has the invasive round goby caused new links in Baltic food webs? Environmental Biology of Fishes, 89: 79–93.

Arntz, W. E., and Finger, I. 1981. Demersal fish in the western Baltic: their feeding relations, food coincidence and food selection. ICES CM/J, 6: 1–28.

Bailey, K. M. 1994. Predation on juvenile flatfish and recruitment variability. Netherlands Journal of Sea Research, 32: 175–189.

Barry, S. C., and Welsh, A. H. 2002. Generalized additive modelling and zero inflated count data. Ecological Modelling, 157: 179–188.

Beare, D. J., Needle, C. L., Burns, F., and Reid, D. G. 2005. Using survey data independently from commercial data in stock assessment: an example using haddock in ICES division VIa. ICES Journal of Marine Science, 62: 996–1005.

Berg, C. W., Nielsen, A., and Kristensen, K. 2014. Evaluation of alternative age-based method for estimating relative abundance from survey data in relation to assessment models. Fisheries Research, 151: 91–99.

Blanchard, J. L., Dulvy, N. K., Jennings, S., Ellis, J. R., Pinnegar, J. K., Tidd, A., and Kell, L. T. 2005. Do climate and fishing influence size-based indicators of Celtic Sea fish community structure? ICES Journal of Marine Science, 62: 405–411.

Cardinale, M., Bartolino, V., Llope, M., Maiorano, L., Sköld, M., and Hagberg, J. 2011. Historical spatial baselines in conservation and management of marine resources. Fish and Fisheries, 12: 289–298.

Cardinale, M., Linder, L., Bartolino, V., Maiorano, L., and Casini, M. 2009. Conservation value of historical data: reconstructing stock dynamics of turbot during the last century in the Kattegat-Skagerrak. Marine Ecology Progress Series, 386: 197–206.

Casini, M. 2013. Spatio-temporal ecosystem shifts in the Baltic Sea: top-down control and reversibility potential. Advances in Environmental Research, 28: 149–167.

Casini, M., Blenckner, T., Möllmann, C., Gårdmark, A., Lindegren, M., Llope, M., Kornilovs, G., *et al.* 2012. Predator transitory spillover induces trophic cascades in ecological sinks. Proceedings of the National Academy of Sciences, 109: 8185–8189.

Casini, M., Käll, F., Hansson, M., Plikshs, M., Baranova, T., Karlsson, O., Lundstrom, K., *et al.* 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.

Casini, M., Lövgren, J., Hjelm, J., Cardinale, M., Molinero, J. C., and Kornilovs, G. 2008. Multi-level trophic cascades in a heavily exploited open marine ecosystem. Proceedings of the Royal Society B, 275: 1793–1801.

Cosgrove, R., Sheridan, M., Minto, C., and Officer, R. 2014. Application of finite mixture models to catch rate standardization better represents data distribution and fleet behavior. Fisheries Research, 153: 83–88.

Eero, M., Hjelm, J., Behrens, J., Buchmann, K., Cardinale, M., Casini, M., Gasyukov, P., *et al.* 2015. Eastern Baltic cod in distress: biological changes and challenges for stock assessment. ICES Journal of Marine Science, 72: 2180–2186.

Eero, M., MacKenzie, B. R., Köster, F. W., and 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.

Eero, M., Vinther, M., Haslob, H., Huwer, B., Casini, M., Storr-Poulsen, M., and 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.

Ellis, T., and Gibson, R. N. 1995. Size-selective predation of 0-group flatfishes in a Scottish coastal nursery ground. Marine Ecology Progress Series, 127: 27–37.

EU-COM. 2008. Directive 2008/56/EC of the European parliament and of the council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=OJ:L:2008:164:0019:0040:EN:PDF.

Francis, R. I. C. C. 2011. Data weighting in statistical fisheries stock assessment models. Canadian Journal of Fisheries and Aquatic Sciences, 68: 1124–1138.

Florin, A. B., Bergström, U., Ustups, D., Lundström, K., and Jonsson, P. R. 2013. Effects of a large northern European no-take zone on flatfish populations. Journal of Fish Biology, 83: 939–962.

Florin, A. B., and Höglund, J. 2008. Population structure of flounder (*Platichthys flesus*) in the Baltic Sea: differences among demersal and pelagic spawners. Heredity, 101: 27–38.

Froese, R. 2004. Keep it simple: three indicators to deal with overfishing. Fish and Fisheries, 5: 86–91.

Galbraith, R. D., and Rice, A. 2005. An introduction to commercial fishing gear and methods used in Scotland. Scottish Fisheries Information Pamphlet, 25: 44pp.

Gårdmark, A., Casini, M., Huss, M., van Leeuwen, A., Hjelm, J., Persson, L., and de Roos, A. M. 2015. Regime shifts in exploited marine food webs: detecting mechanisms underlying alternative stable states using size-structured community dynamics theory. Philosophical Transactions of the Royal Society B, 370: 20130262.

Gjøsæter, J. 1988. Competition for food and predator-prey relationships among young cod (*Gadus Morhua*) and some other fish from shallow waters. Flødevigen Rapportserie, 1: 1–15.

Grüss, A., Drexler, M., and Ainsworth, C. H. 2014. Using delta generalized additive models to produce distribution maps for spatially explicit ecosystem models. Fisheries Research, 159: 11–24.

Harley, S. J., and Myers, R. A. 2001. Hierarchical Bayesian models of length-specific catchability of research trawl survey. Canadian Journal of Fisheries and Aquatic Sciences, 58: 1569–1584.

Hastie, T., and Tibshirani, R. 1990. Generalized Additive Models. Chapman and Hall, London.

Heino, M., Baulier, L., Boukal, D. S., Ernande, B., Johnston, F. D., Mollet, F. M., Pardoe, H., *et al.* 2013. Can fisheries-induced evolution shift reference points for fisheries management? ICES Journal of Marine Science, 70: 707–721.

Hixon, M. A., Johnson, D. W., and Sogard, S. M. 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. ICES Journal of Marine Science, 71: 2171–2185.

Hunsicker, M. E., Ciannelli, L., Bailey, K. M., Zador, S., and Stige, L. C. 2013. Climate and Demography Dictate the Strength of Predator-Prey Overlap in a Subarctic Marine Ecosystem. PLoS ONE, 8: e66025.

Hüssy, K. 2011. Review of western Baltic cod (*Gadus morhua*) recruitment dynamics. ICES Journal of Marine Science, 68: 1459–1471.

Hüssy, K., Hinrichsen, H. H., Eero, M., Mosegaard, H., Hemmer-Hansen, J., Lehmann, A., and Lundgaard, L. S. 2016. Spatio-temporal trends in stock mixing of eastern and western Baltic cod in the Arkona Basin and the implications for recruitment. ICES Journal of Marine Science, 73: 293–303.

ICES. 2010. Report of the ICES/HELCOM Workshop on Flatfish in the Baltic Sea (WKFLABA), 8 - 11 November 2010, Öregrund, Sweden. ICES CM 2010/ACOM:68. 85 pp.

ICES. 2012. Marine Strategy Framework Directive - Descriptor 3+, ICES CM 2012/ACOM:62. 173 pp.

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

ICES. 2014a. Report of the Baltic International Fish Survey Working Group (WGBIFS), 24–28 March 2014, Gdynia, Poland. ICES CM 2014/SSGESST:13. 527 pp.

ICES. 2014b. Report of the Benchmark Workshop on Baltic Flatfish Stocks (WKBALFLAT), 27–31 January 2014, Copenhagen, Denmark. ICES CM 2014/ACOM:39. 320 pp.

ICES. 2015a. Report of the Baltic Fisheries Assessment Working Group (WGBFAS), 14–21 April 2015, ICES HQ, Copenhagen, Denmark. ICES CM 2015/ACOM:10. 806 pp.

ICES. 2015b. Report of the Benchmark Workshop on Baltic Cod Stocks (WKBALTCOD), 2–6 March 2015, Rostock, Germany. ICES CM 2015/ACOM:35. 172 pp.

ICES. 2015c. Cod (*Gadus morhua*) eastern Baltic stock in Subdivisions 25–32 (Eastern Baltic Sea) and Subdivision 24. In: Report of the ICES Advisory Committee 2015. ICES Advice, 2015. Book 8.

ICES. 2016. Report of the Workshop on Spatial Analyses for the Baltic Sea (WKSPATIAL), 3-6 November 2015, Rome, Italy. ICES CM 2015/SSGIEA:13. 37 pp.

Jokinen, H., Wennhage, H., Lappalainen, A., Ådjers, K., Rask, M., and Norkko, A. 2015. Decline of flounder (*Platichthys flesus* (L.)) at the margin of the species' distribution range. Journal of Sea Research, 105: 1–9.

Lauria, V., Vaz, S., Martin, C. S., Mackinson, S., and 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.

Lindegren, M., Möllmann, C., Nielsen, A., and 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, 106: 14722–14727.

Link, J. S., Fogarty, M. J., and Langton, R. W. 2005. The trophic ecology of flatfishes. *In* Flatfishes: Biology and Exploitation. Ed. by R. N. Gibson. Blackwell Publishing, Oxford, pp. 185–204.

Loots, C., Vaz, S., Planque, B., and 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.

Maschner, H. D. G., Betts, M. W., Reedy-Maschner, K., and Trites, A. W. 2008. A 4500 year time series of Pacific Cod (*Gadus macrocephalus*): archaeology, regime shifts, and sustainable fisheries. Fishery Bulletin, 106: 386–394.

Maunder, M. N. 2001. A general framework for integrating the standardization of catch per unit of effort into stock assessment models. Canadian Journal of Fisheries and Aquatic Sciences, 58: 795–803.

Maunder, M. N., and Punt, A. E. 2004. Standardizing catch and effort data: a review of recent approaches. Fisheries Research, 70: 141–159.

Molander, A. R. 1938. Investigations into the growth-rates of the common dab and the flounder in the southern Baltic. Rapports Et Procès-Verbaux Des Réunions, Conseil International Pour L'Exploration De La Mer, 108: 90–101.

Molander, A. R. 1955. Swedish investigations on plaice and flounder in the southern Baltic. Journal Du Conseil, Conseil International Pour L'Exploration De La Mer, 21: 25–43.

Möllmann, C., Blenckner, T., Casini, M., Gårdmark, A., and Lindegren, M. 2011. Beauty is in the eye of the beholder: management of Baltic cod stock requires an ecosystem approach. Marine Ecology Progress Series, 431: 293–297.

Nicholson, M. D., and Jennings, S. 2004. Testing candidate indicators to support ecosystem-based management: the power of monitoring surveys to detect temporal trends in fish community metrics. ICES Journal of Marine Science, 61: 35–42.

Niiranen, S., Yletyinen, J., Tomczak, M. T., Blenckner, T., Hjerne, O., MacKenzie, B. R., Müller-Karulis, B., *et al.* 2013. Combined effects of global climate change and regional ecosystem drivers on an exploited marine food web. Global Change Biology, 19: 3327–3342.

Nissling, A., and Dahlman, G. 2010. Fecundity of flounder, *Pleuronectes flesus*, in the Baltic Sea – reproductive strategies in two sympatric populations. Journal of Sea Research, 64: 190–198.

Nissling, A., Westin, L., and 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.

Ojaveer, E., and Kalejs, M. 2005. The impact of climate change on the adaptation of marine fish in the Baltic Sea. ICES Journal of Marine Science, 62: 1492–1500.

Ojaveer, E., Kalejs, M., Aps, R., Labaika, I., and Vitins, M. 1985. The impact of recent environmental change on the main commercial fish stocks in the Gulf of Finland. Finnish Fisheries Research, 6: 1–14.

Oesterwind, D., Psuty, I., Pachur, M., Von Dorrien, C., Lejk, A., Casini, M., and Larson, N. 2013. Proportion of large fish in the community. HELCOM Core Indicator Report.

Olsson, J., Bergström, L., and Gårdmark, A. 2012. Abiotic drivers of coastal fish community change during four decades in the Baltic Sea. ICES Journal of Marine Science, 69: 961–970.

Parra, H. E., Pham, C. K., Menezes, G. M., Rosa, A., Tempera, F., and Morato, T. 2016. Predictive modelling of deep-sea fish distribution in the Azores. Deep-Sea Research II. http://dx.doi.org/10.1016/j.dsr2.2016.01.004i.

Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends in Ecology & Evolution, 10: 430.

Persson, L. E. 1981. Were macrobenthic changes induced by thinning out of flatfish stocks in the Baltic proper? Ophelia, 20: 137–152.

Piet, G. J., and Jennings, S. 2004. Response of potential fish community indicators to fishing. ICES Journal of Marine Science, 62: 214–225.

Pinnegar, J. K., and Engelhard, G. H. 2008. The "shifting baseline" phenomenon: a global perspective. Reviews in Fish Biology and Fisheries, 18: 1–16.

Probst, W. N., Kloppmann, M., and Kraus, G. 2013. Indicator-based status assessment of commercial fish species in the North Sea according to the EU Marine Strategy Framework Directive (MSFD). ICES Journal of Marine Science, 70: 694–706.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rijnsdorp, A. D., Van Leeuwen, P. I., Daan, N., and Heessen, H. J. L. 1996. Changes in abundance of demersal fish in the North Sea between 1906–1909 and 1990–1995. ICES Journal of Marine Science, 53: 1054–1062.

Shin, Y. J., Rochet, M. J., Jennings, S., Field, J. G., and Gislason, H. 2005. Using size-based indicators to evaluate the ecosystem effects of fishing. ICES Journal of Marine Science, 62: 384–396.

Stefánsson, G. 1996. Analysis of groundfish survey abundance data: combining the GLM and delta approaches. ICES Journal of Marine Science, 53: 577–588.

Svedäng, H., and Hornborg, S. 2014. Selective fishing induces density-dependent growth. Nature Communications, 5: 4152.

Thorson, J. T., Shelton, A. O., Ward, E. J., and Skaug, H. J. 2015. Geostatistical delta-generalized linear mixed models improve precision for estimated abundance indices for West Coast groundfishes. ICES Journal of Marine Science, 72: 1297–1310.

Thorson, J. T., and Ward, E. J. 2013. Accounting for space–time interactions in index standardization models. Fisheries Research, 147: 426–433.

Thorson, J. T., and Ward, E. J. 2014. Accounting for vessel effects when standardizing catch rates from cooperative surveys. Fisheries Research, 155: 168–176.

Ustups, D., Müller-Karulis, B., Bergström, U., Makarchouk, A., and Sics, 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.

Vainikka, A., Gårdmark, A., Bland, B., and Hjelm, J. 2009. Two- and three-dimensional maturation reaction norms for the eastern Baltic cod, *Gadus morhua*. ICES Journal of Marine Science, 66: 248–257.

Vallin, L., and Nissling, A. 2000. Maternal effects on egg size and egg buoyancy of Baltic cod, *Gadus morhua*: implications for stock structure effects on recruitment. Fisheries Research, 49: 21–37.

Walsh, M. R., Munch, S. B., Chiba, S., and Conover, D. O. 2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. Ecology Letters, 9: 142.

Wood, S. N. 2003. Thin-plate regression splines. Journal of the Royal Statistical Society (B), 65: 95–114.

Wood, S. N. 2006. Generalized Additive Models: An introduction with R. Chapman and Hall/CRC, Boca Raton, Florida.

Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society (B), 73: 3–36.

Östman, Ö., Boström, M. K., Bergström, U., Andersson, J., and Lunneryd, S. G. 2013. Estimating competition between wildlife and humans – a case of cormorants and coastal fisheries in the Baltic Sea. PLoS One, 8: e83763. doi:10.1371/journal.pone.0083763

Handling editor: Jan Jaap Poos