Conservation value of historical data: reconstructing stock dynamics of turbot during the last century in the Kattegat-Skagerrak

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ABSTRACT: A quasi-complete time series of biomass, maximum body size and spatial distribution was reconstructed for turbot *Psetta maxima* L. in the Kattegat-Skagerrak based on standardized research surveys extending back to 1925. Here we show that biomass has declined by about 86% over the time series, maximum body size has decreased by 20 cm and the northern component of the population has virtually vanished. These trends are likely to be underestimated due to the conservative approach we used by assuming a low level of 'technological creep' during the survey period, suggesting that the actual reduction in biomass might have been between 92 and 95%. Absence of trend in former analyses of data collected in the last 2 or 3 decades is dangerously misleading. This substantial difference in stock status, based on historical data, highlights the general importance of the historical perspective for managing natural resources.

KEY WORDS: Historical population dynamics · Shifting baselines · Research data · Sustainability

INTRODUCTION

Ecologically sound management approaches and sustainable use of natural resources require a thorough understanding of the current status of those resources. Considering biological resources, such as fish stocks, many important aspects at the population level should be considered while framing management and/or conservation plans; these usually include stock productivity and resilience to exploitation in a fluctuating environment as well as consequences related to the socioeconomic impact of management measures (e.g. Fowler et al. 2005). Marine fish populations have been heavily exploited in most areas since at least the 1950s (Lotze & Milewski 2004, Myers & Worm 2005) and the current biodiversity crisis occurring in oceans worldwide is the obvious result of overexploitation and habitat degradation and destruction (Jackson et al. 2001, Ardizzone et al. 2006).

Most fishery management systems and almost all marine stock analyses are based on changes in population parameters as measured against an established baseline. Classical examples of these measures are trends in biomass, variations in the demographic structure of the population and changes in its spatial distribution (i.e. ICES 2007). To avoid an overly optimistic assessment of the conservation status of fish populations, a problem often referred to as the shifting baseline syndrome, these measures should be referred to a baseline of a relatively unfished (or unexploited) population, or at least a population only marginally exploited (Pauly 1995, Roberts 2007). The use of erroneous baselines can lead to erroneous assessments of stock status (Rose 2004) and ill-advised management strategies that could lead to stock depletion, collapse or even extirpation of entire populations (Hutchinson et al. 2003).

Even for biological systems for which long time series of data have been collected (e.g. many fish

stocks in the North Atlantic; Rijnsdorp & Millner, 1996, Rijnsdorp et al. 1996), conservation assessments are usually based on data and analyses covering the last few decades only (ICES 2007), and thus include populations that are far from pristine (Mackinson 2002, Engelhard 2008, Perdikaris & McGovern 2008). A number of complex population models have been developed with the aim of improving population estimates and coping with the many sources of uncertainty (Sumaila 2001, Harwood & Stokes 2003), but to really provide a better assessment of the conservation status of exploited species the available estimates should be re-evaluated using historical data, referring to populations before the onset of the industrial fishery exploitation (Lotze & Milewski 2004, Myers & Worm 2005).

We used the turbot *Psetta maxima* L. in the Kattegat-Skagerrak area as a case study to demonstrate the usefulness of historical data for assessing the conservation status of marine fish populations. The Kattegat-Skagerrak area connects the North Sea to the Baltic Sea and has not received as much research attention as other regions of the North Sea (Daan et al. 1996, Casini et al. 2005), especially considering the abundance, structure and distribution of the demersal fish populations distributed along the Swedish west coast (Støttrup et al. 2002, Svedäng 2003, Casini et al. 2005). In the North Sea, the turbot has been considered a highly prized fish (prime) since the middle of the 1800s and historically has been exploited within a multi-species fishery targeting turbot, brill *Scophthalmus rhombus* and sole *Sole solea* (Mackinson 2002). In the Kattegat-Skagerrak, a semi-industrialized longline fishery targeting halibut, ling, cod, haddock and skate developed in the 1800s (Hasslöf 1949). During the late 1800s and early 1900s, trawling was introduced on a broad scale; this sector of the fleet was already larger than the longliners before the First World War (Andersson 1954). Unfortunately, no quantitative data exists on the development of the effective fishing effort in the area. Fish stocks at that time were considered lightly exploited compared to what has been observed in the last 3 decades (Roberts 2007, Sparholt et al. 2007). However, considering that a semi-industrialized fishery started at least a century before, the beginning of 1900s likely represents only a waypoint rather than a baseline from which it is possible to estimate the decline of fish populations in the North Sea (Garstang 1900, Roberts 2007).

Turbot is a species potentially vulnerable to fisheries due to its ecological (distributed mostly in coastal shallow areas; Curry-Lindahl 1985) and morphological (high gear vulnerability due to the particular body shape) characteristics. However, and despite its high commercial value and wide distribution (from the eastern Mediterranean to the North Sea), the stock status of turbot has not been assessed and it is not managed in the Kattegat-Skagerrak or in any other part of the North Sea. The Swedish Species Information Centre (www.artdata.slu.se/rodlista) classifies the turbot as near threatened, although no information is currently available in the literature about historical abundance or distribution trends of the species in the North Sea. Even though the species has been targeted since the beginning of the development of fisheries in the North Sea (mid-19th century; Robinson 1996), all previous analyses have considered at most the last 15 to 30 yr; Casini et al. (2005) analyzed the abundance of flatfish species in the Kattegat-Skagerrak during the period 1981–2003 and found no clear trend in the biomass of turbot, which was characterized by wide yearly fluctuations. Støttrup et al. (2002) also argued that turbot is not severely declining (since the 1990s) in the Kattegat-Skagerrak and, considering the last 2 decades of data, claimed that the species is not in need of any particular conservation measure.

Here we present standardized time series of population biomass, individual maximum size and spatial distribution of turbot based on research trawl survey data from the Swedish Institute of Marine Research. We provide the first historical time series analysis of turbot population dynamics in the North Sea dating back to the early part of the last century (1925 to 2007). Our results outline the potential risks associated to any assessment of marine fish stocks status based on short time series, especially in ecosystems historically affected by high anthropogenic pressures.

MATERIALS AND METHODS

Data. We compiled all known archived data from otter trawl surveys carried out in the Kattegat-Skaggerak (Fig. 1) from 1925 to 2007 by the Swedish Institute of Marine Research (Lysekil, Sweden) and its predecessors. These data are the result of a large project that started in Sweden in 2001 and aimed to collate all archived historical information concerning experimental trawls conducted by the Swedish authorities. This database incorporates a considerable number of different types of bottom trawls and 9 different research vessels, reflecting the numerous technological advances that occurred in the fishing industry since the early part of the last century. Since 1974, most surveys were conducted by the Swedish international RV 'Argos' within the International Bottom Trawl Survey (IBTS; ICES 1992), although national trawl surveys were also carried out (since 2000). For each trawl station the following information was available: date, haul duration, towing speed, setting and hauling position (latitude and longitude; prior to the use of a GPS those were reconstructed from detailed fishing area information
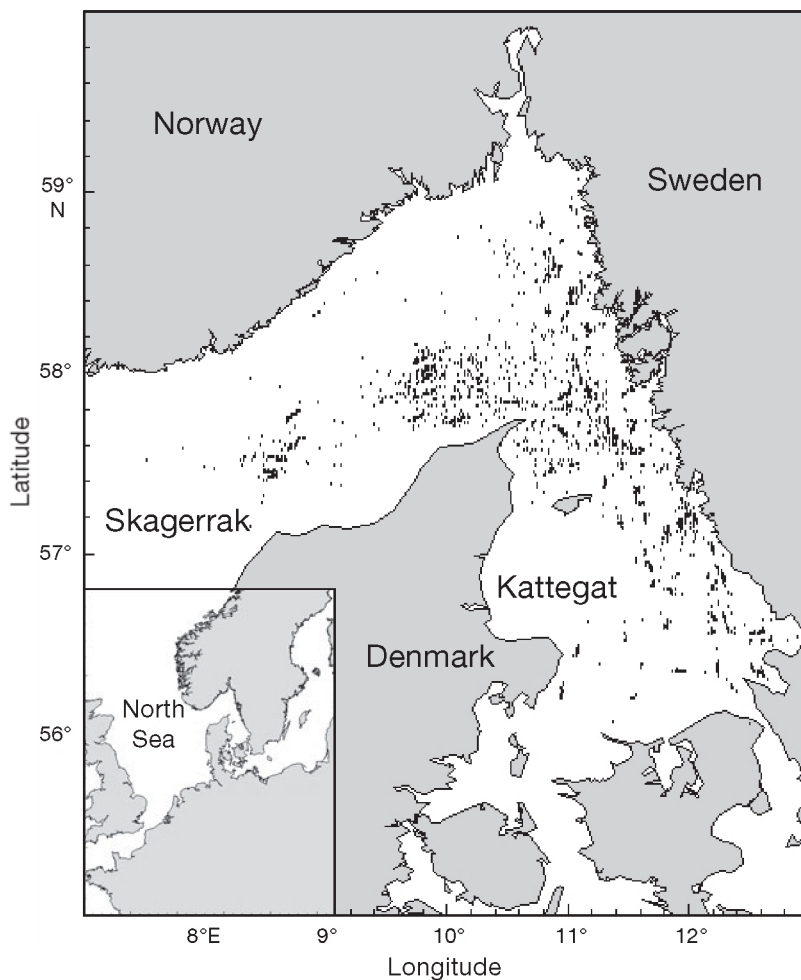
Fig. 1. Study area with location of the hauls (dots) conducted during the surveys and used in the analysis

While standardization of the catches to swept areas largely improves CPUE comparability, it does not address gear-specific differences in selectivity (Knijn et al. 1993). CPUE information derived from different vessels, trawls and mesh sizes may be biased due to differences in the size at full selectivity, even if a single species is considered (Gunderson 1993, Knijn et al. 1993, Rijnsdorp et al. 1996, Harley & Myers 2001). By restricting the analysis to length classes that can be considered fully selected by the largest mesh size included in the dataset (in our case length classes >25 cm), inconsistencies related to the gear selectivity are substantially reduced. We assume that above this size all individuals are equally vulnerable to the different gears used in the survey. Our standardization procedure minimizes the effect of different trawls and provides an acceptable compromise between the need for a robust comparison between years and the lack of complete information on trawl-specific catchability and selectivity. This procedure can also be used to reduce errors related to the different sampling strategies used from 1925 to 2007, with a bias against small fish that, especially in early surveys, might have been measured and reported less frequently than larger ones. Further details on the standardization procedure are available in Supplement 1.

included in the archived haul information) and depth. We included in the analyses only hauls carried out during daylight, and for each haul the total number of turbot caught and the total length of each individual were recorded. Further details of the survey database as well as standardization procedures and data analysis described below are available as supplementary material in 'Supplement 1' at www.int-res.com/articles/suppl/m386p197_app.pdf.

Standardization of catch per unit effort (CPUE). The first step in standardizing CPUE values was to produce a bottom swept area abundance estimate for each haul (Rijnsdorp et al. 1996, Daan et al. 2005). Due to the different gear widths, tow times and tow speeds, we standardized each haul to a swept area of 0.89 km². Such a procedure is usually defined as an area-swept abundance estimation (Harley & Myers 2001) and in the present study it corresponds to the abundance of fish caught in 1 h trawling a swept area of 0.89 km² (see 'Supplement 1' for details).

Data analysis. *Estimation of spawning stock biomass and average maximum length:* In fish populations, trends in stock spawning biomass are representative of the reproductive potential of the stock as stock biomass is directly linked to the fecundity of the population (Hilborn & Walters 1992). However, given that individual weights were not available in our database, to obtain haul-specific CPUE in biomass (kg h^{-1}) and calculate an index of stock biomass for the turbot stock, we estimated individual fish weight (W) from length (L) measurements. Individual fish weights were estimated fitting a length–weight power relationship ($W = aL^b$) on individual data collected between 1991 and 2007 in the Kattegat-Skagerrak (a = 0.00001, b = 3.1319, n = 89).

Yearly average maximum length (L_{max}, in cm) was defined as the mean of the observed maximum length between hauls and was consequently not affected by haul standardization procedures. L_{max} is usually considered as a robust proxy for evaluating the conservation status of a fish population as it assumes that size

reduction is due to intensified exploitation that removes the older and larger individuals (Piet & Jennings 2005, Bailey et al. 2008).

Generalized additive model. To account for the unbalanced design in the sampling between year, month, latitude, longitude and depth, we used generalized additive models (GAMs; Hastie & Tibshirani 1990) to model the haul-specific CPUE in biomass. In particular, to account for the large number of zero values in our data set (like most data sets in ecology and conservation; Martin et al. 2005), we used a quasi-Poisson distribution (Minami et al. 2007) to model CPUE with variance proportional to the mean and a log-link function to constrain the estimates to be positive. The quasi-likelihood approach assumes that the scale parameter of the distribution is unknown so that it could account for more over-dispersion than the classical Poisson distribution (Wood 2006).

Inspection of the distribution of L_{max} revealed that it was normally distributed. Accordingly, a second GAM was used to model L_{max} using the normal distribution with a log-link function. Thus, the following full additive models were formulated respectively for CPUE and L_{max}:

$$\text{CPUE} \sim \beta_1 + f_1(\text{lat} \times \text{long}) + f_2(\text{lat} \times \text{year}) + f_3(\text{long} \times \text{year}) + f_4(\text{year}) + f_5(\text{month}) + f_6(\text{depth}) + \varepsilon$$

$$L_{max} \sim \beta_1 + f_1(\text{lat} \times \text{long}) + f_2(\text{year}) + f_3(\text{month}) + f_4(\text{depth}) + \varepsilon$$

where β_1 is the intercept, f_i are smoothing functions and ε is a normally distributed error. We used isotropic smoothing (thin plate regression spline) to model the interaction between latitude and longitude as suggested by Wood (2006) and a cyclic cubic regression spline to smooth the month predictor because it forces the smoothing to have the same value and first few derivatives at its initial and final points. The interactions between year and latitude and year and longitude were modelled using a tensor product smoothing function as suggested by Wood (2006). This approach has been considered a good choice when product covariates have different unit scales and a different amount of smoothness is appropriate along the 2 axes (Wood 2006). All other predictors were modelled using the thin plate smoothing spline function (Wood 2004). The spatial temporal interactions for the CPUE model were included to allow for investigating changes in the spatial distribution of turbot during the long time-period analyzed. However, such a level of model complexity was not required in the L_{max} model as it was only used for a temporal analysis and no mapping of L_{max} was expected.

Several reduced models were tested excluding one or more covariates. Smoothing parameter estimation and model comparison was based on generalized cross validation (GCV; Wood 2001, 2003). GCV is a proxy for the model's out-of-sample predictive mean squared error. Therefore, a model with lower GCV has more explanatory power, and hence is preferred, compared to a model with higher GCV. Final models were selected based on the GCV criteria and the significance of the predictors fulfilled at the same time. A backward stepwise selection procedure was used by excluding the variable explaining the lowest amount of variance at each step. To simplify the interpretation of the results, the maximum number of knots was limited for the smooth term month and depth (k = 4) and for the interaction between latitude and longitude (k = 20). Residuals were analysed to inspect for homogeneity of variance and violation from normality assumptions and other anomalies in the data or in the model fit using graphical methods (Cleveland 1993). Considering the large data set used to fit the GAM (>4000 points), a sensitivity analysis was done to test the CPUE model stability with respect to the amount of information provided (see 'Supplement 1' for details).

Estimating yearly average SSB and L_{max} values: The yearly average values of CPUE and L_{max} (with 1st and 3th quartiles; Q1, Q3) were predicted from the respective final models. To estimate the year effect for CPUE, we calculated CPUE over the grid used for spatial mapping and converted kg h^{-1} into kg km^{-2} considering that 1 h of standard bottom swept area corresponded to 0.89 km^2 (see 'Supplement 1' for how differences in net characteristics and towing speeds were accounted for). The estimates were then summed over the whole grid to get yearly biomass estimates over the entire area. It is important to consider that, as catchability is unknown and assumed constant for the entire time series, the calculated biomass is not representative of the total population biomass in the area but only of the relative trend during the time series. Estimation of the annual turbot biomass over the entire grid area represents an effective way to appropriately weight different areas, reconstruct trend biomass for the entire study period and extract the year effect from the model (Beare et al. 2005), also under spatial–temporal interactions (Maunder & Punt 2004). The analysis was performed using the mgcv library of R (Wood 2001; www.r-project.org)

Mapping CPUE and reconstructing long-term trends in biomass and L_{max}: The spatial distribution of CPUE was reconstructed, averaging over 10 yr time intervals using the estimates calculated during January to March for each point of the grid. We used the final model to obtain CPUE estimates over a regular grid of 0.5×0.5 km (160 402 cells) that covered the Kattegat-Skagerrak area including the main fjords along the Swedish coast. Waters shallower than 5 m depth were

excluded because no hauls were conducted below this depth (depth was measured with the data available through the Baltic GIS website, http://gis.ekoi.lt/gis/index.php). A time series analysis was performed to describe the historical trends of L_{max}. We estimated the values corresponding to missing years, interpolating the values from adjacent observations using a simple exponential smoothing function (Gardner 1985).

Accounting for changes in catchability: Like other indicators of stock abundance, CPUE relies on the assumption that catchability is constant over time. Unquestionably, this assumption does not hold if technological creeping and changes in fleet characteristics affect the catching efficiency of the fleet. Increasing catching efficiency (known also as technological creep or, simply, creep) of the fleet is usually positively related to the increase in skipper skills, investments in auxiliary equipment and more efficient gear and materials, replacement of old vessels by new ones and, to a lesser extent, upgraded engines (Rijnsdorp et al. 2006). Creep has been estimated to be around 1.6 to 2.8 % per year for the beam trawl fishery targeting sole and plaice in the North Sea (Rijnsdorp et al. 2006), 0.6 to 3.1 % for the prawn fisheries in Australia (O'Neill & Leigh 2007) and up to 10 % for Australian northern prawn fisheries (Ellis & Wang 2006). Creep has been seldom estimated for surveys, although it is also known to occur in this case (Engelhard 2008). Marchal et al. (2003) estimated up to a 10 % annual increase in catching efficiency for a survey in the North Sea. Creep in surveys is generally due to several factors, including improved efficiency of the gear due to enhanced materials, improved hydrodynamic performance of the trawl and better trawl contact with the bottom. These factors were not obviously accounted for in the swept area and GAM standardization; thus we corrected the long-term trend in CPUE estimates using a power function with an increase in catching efficiency of 1, 2 and 3 % per year. Creep was applied until 1974, when modern, fully standardized IBTS surveys began. From 1974 onwards, creep was considered null (but see Marchal et al. 2003).

RESULTS

Changes in turbot abundance

We considered a total of 4485 hauls covering 66 yr during the period 1925–2007 (Fig. 1, Table S1, Supplement 1. All the predictors included in the final CPUE model were statistically significant with the predictors year, interaction between latitude and longitude and depth explaining the largest part of the deviance (Table 1). The final biomass model explained almost 38 % of the total deviance (Table 2).

Relative biomass estimates assuming a technological creeping of 1 % were used as a baseline scenario for describing historical trends. The effects of the significant univariate predictors included in the final models (month and depth) were plotted for a straightfor-

Table 1. Summary of all generalized additive models tested to select the final model to estimate catch per unit effort (CPUE) of stock biomass and average maximum body length (L_{max}) of turbot in the Kattegat-Skagerrak. Year, Month, Depth, Latitude, Longitude and the interaction between Latitude and Longitude (Lat:Long), Latitude and Year (Lat:Year) and Longitude and Year (Long:Year) are predictive factors included in the initial models. DEV: total deviance explained by the reduced models; GCV: proxy for the models out-of-sample predictive mean squared error; LED: predictors that explained the largest part of the model deviance

n	Predictive factors	DEV	GCV	LED
CPUE (>25 cm)				
1	Long:Lat, Lat:Year, Long:Year, Lat, Long, Year, Month, Depth	38.0	3.03	Long: Lat,Year
2	Long:Lat, Lat:Year, Long:Year, Lat, Long, Year, Month	36.5	3.10	
3	Long:Lat, Lat:Year, Lat, Long, Year, Month	32.3	3.29	
4	Long:Lat, Lat:Year, Lat, Year, Month	31.1	3.33	
5	Long:Lat, Lat, Year, Month	25.3	3.58	
L_{max}				
1	Long:Lat, Lat, Long, Year, Month, Depth	38.1	58.4	
2	Long:Lat, Lat, Year, Month, Depth	38.1	57.4	
3	Long:Lat, Year, Month, Depth	35.7	59.3	
4	Long:Lat, Year, Depth	35.6	59.2	Year, Depth
5	Year, Depth	28.4	61.6	

Table 2. Summary of final generalized additive models used to estimate catch per unit effort (CPUE) of stock biomass and average maximum body length (L_{max}) of turbot in the Kattegat-Skagerrak. n: no. of hauls used in the analysis; DEV: total deviance explained by the final models

df	Variable	F	p
CPUE (>25 cm) (n = 4486, DEV = 38.0 %)			
8.9	Year	10.2	<0.0001
8.8	Latitude	25.3	<0.0001
8.9	Longitude	6.7	<0.0001
1.9	Month	38.3	<0.0001
1.8	Depth	6.8	<0.0005
16.5	Lat:Year	7.7	<0.0001
19.9	Long:Year	11.5	<0.0001
15.9	Lat:Long	12.1	<0.0001
L_{max} (n = 427, DEV = 35.6 %)			
8.6	Year	10.1	<0.0001
2.1	Depth	4.3	<0.006
13.6	Lat:Long	2.1	<0.007

ward interpretation (Fig. S1, Supplement 1). Turbot was mainly caught during the winter in shallow areas (Fig. S1, Supplement 1). Fig. 2a represents the yearly average CPUE predicted by the final GAM model using only the observed data. Fig. 2b shows the estimated biomass, relative to the value estimated in 1925, calculated by summing the model predictions over the entire area. The largest biomass level was observed at the beginning of the time series and it declined thereafter (Fig. 2a). After a small recovery at the end of the 1980s, turbot stock has fluctuated slightly during the 1990s and 2000s, remaining relatively stable since the mid-1990s. The decline in CPUE was about 86% of the maximum biomass of turbot observed at the beginning of the time series based on the first and last year of the time series. The decline is obviously more accentuated (between 90 and 95%) if considering larger values of creep during the century (Fig. 2b).
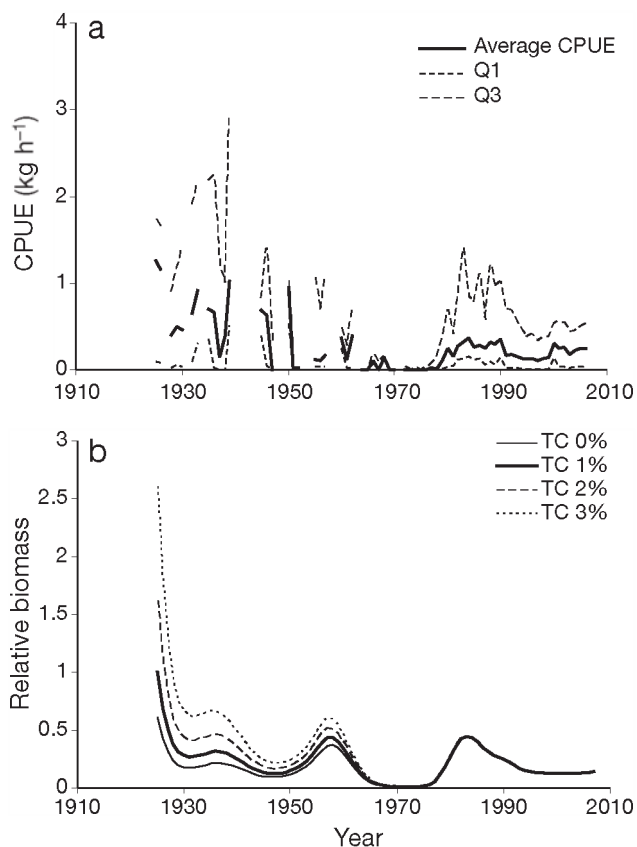
Changes in maximum average length

Year, depth and the geographical coordinates were significant in the final maximum length model (L_{max}), with year accounting for the largest part of the deviance. The final model explained more than 35% of the total deviance (Table 1). A similar pattern as for CPUE was observed for L_{max} along the whole time period investigated. The largest value was observed at the beginning of the time series. From the mid-1950s, L_{max} declined rapidly until the late 1970s and fluctuated afterwards around a constant value that was almost 20 cm less than the maximum observed length (Fig. 3a,b). The effects of the significant predictors included in the final models are plotted in Fig. S2, Supplement 1. The largest fishes were caught at depths >~35 m (Fig. S2, Supplement 1).
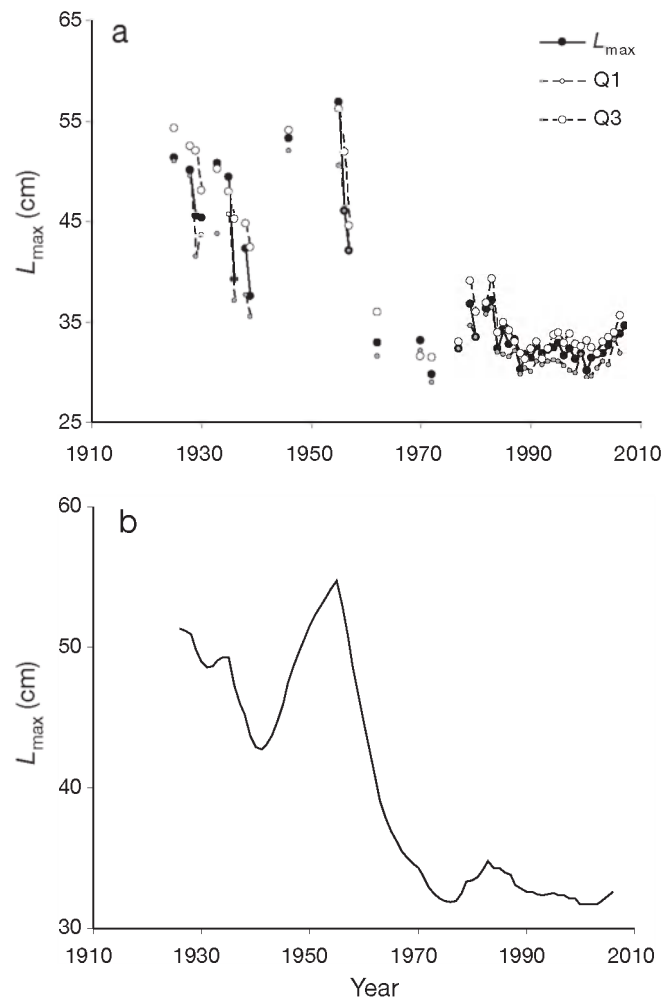

Fig. 2. (a) Estimated yearly CPUE (kg h^{-1}; average, 1st [Q1] and 3rd quartiles [Q3]) predicted by the model using only the observed data. (b) Historical trend of the stock in terms of relative biomass compared to the value estimated in 1925 and assuming different levels of technological creep (TC). Stock biomass is calculated summing up CPUE predicted over the grid used for spatial mapping and converting kg h^{-1} into kg km^{-2} (see 'Mapping CPUE and reconstructing long-term tends in biomass and L_{max}' for details)

Fig. 3. (a) Historical trends in average maximum length (L_{max} in cm) of turbot (average, 1st [Q1] and 3th quartiles [Q3]). (b) Long-term trends in L_{max} after exponential smoothing (see 'Mapping CPUE and reconstructing long-term tends in biomass and L_{max}' for details)

Changes in geographical distribution

The effects of the variables that occurred in the models as multidimensional spatiotemporal smoothing (geographical position and year) were evaluated through time series maps (Fig. 4). Variations in geographical distribution and stock biomass characterize the time series maps with subsequent contraction and expansion of both distribution area and biomass, for example, during its historical minimum in the 1970s (Fig. 4). In the 1920s, at the beginning of the time series, high densities of turbot were observed in many parts of the Kattegat-Skagerrak. These large aggregations declined from the 1930s to the 1950s when only a few hotspots were located offshore of the southeastern coasts of Denmark, the central and west coast of Sweden and in the fjord system (e.g. Gullmar and Hake fjords). Further decreases in the stock occurred from the 1950s to 1970s, when turbot densities were very low throughout almost the entire Kattegat-Skagerrak, with the exception of a small hotspot offshore of Denmark. Since the end of 20th century, the status of the turbot stock has slightly improved, especially in the southern part of the Kattegat-Skagerrat, where the highest concentrations can currently be located. However, the reductions to near-zero values of CPUE for the northern component of the stock suggests severe stock depletion in that area.
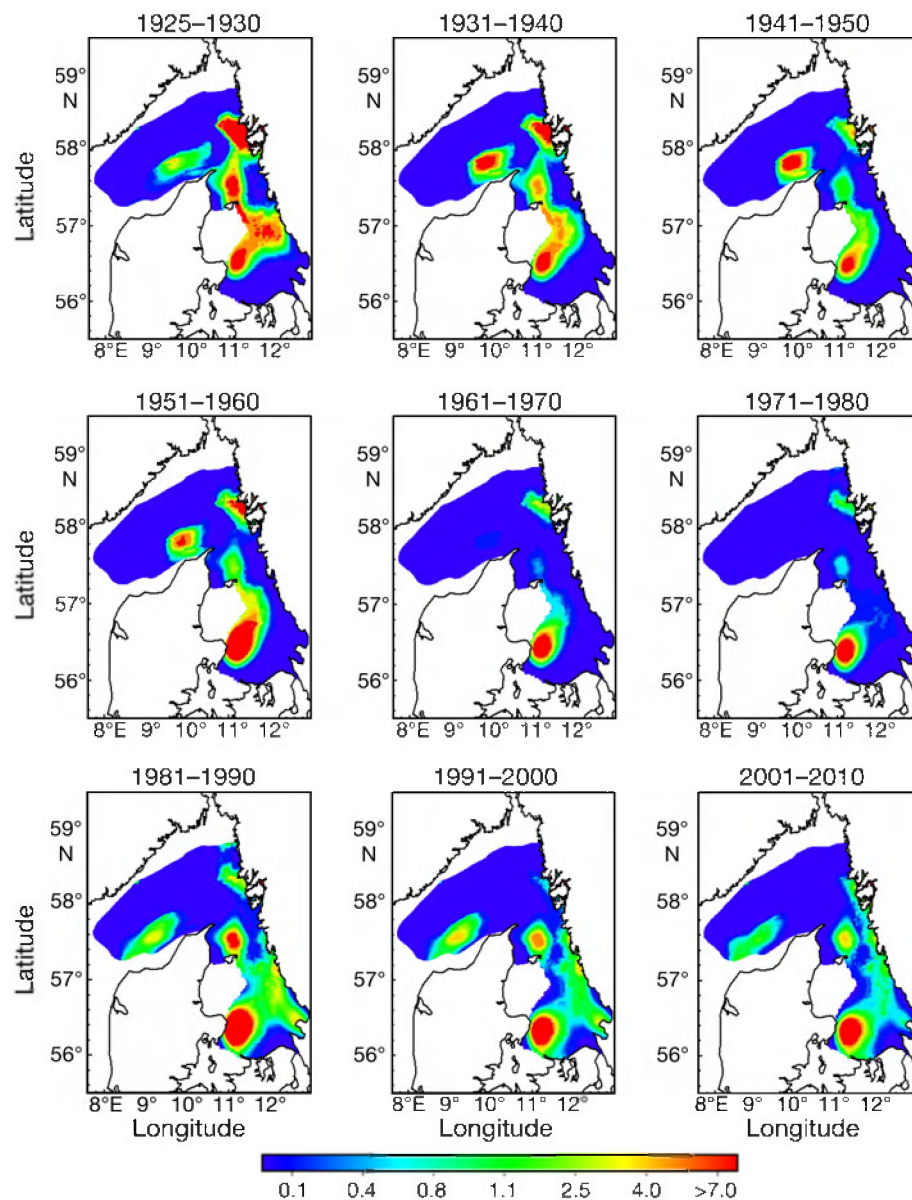

Fig. 4. Historical trends in spatial distribution of CPUE (kg h^{-1}) and aggregation pattern of turbot in the Kattegat-Skagerrak (decadal average) estimated between January and March

DISCUSSION

Our analyses are based on the assumption that the 83 yr database used here can be analyzed without introducing serious biases into results. We based our analyses on the explicit inclusion of technological creeping, which provided a practical way of taking into account the paradigm shift in fisheries technology (Engelhard 2008). The effect of alternative technological creep values was tested, showing increasing reduction in the stock size in the second part of the time series (from 86 to 95% reduction in the estimated biomass) for increasing creep levels and clearly demonstrating that our conclusion would not have been influenced. We also performed a sensitivity analysis demonstrating that our results are fairly consistent and stable over increasingly smaller sample sizes, even with a 50% reduction in size of the data set considered, yielding confidence in its predictions. We were not able to completely solve all selectivity issues, such as the role of the catchability of different size classes that may vary with vessel speed or trawl type. Nevertheless, we consider our approach to provide estimates that are fairly robust with respect to amount of information, standardization procedures and underlying model assumptions, and therefore we are confident that our formulation is able to model an authentic signal from the data.

In the North Sea, turbot has been historically caught within a multispecies fishery targeting turbot, brill and sole (Mackinson 2002). These species were already considered as highly prized fish in the middle of the 1800s (Roberts 2007); despite this, little effort has been devoted to assess the conservation status of turbot in European waters. Blanchard et al. (2007) suggested that more than 30 yr of survey data are necessary for detecting trends with high power (i.e. >0.95) for stocks which exhibit moderate patchiness and occur in periods of climate changes. Even though stock assessments based on 30 to 40 yr of data are not uncommon (ICES 2007), only a very limited number of studies have considered a time span that goes back to or precedes the beginning of the industrial fisheries (e.g. Rijnsdorp & Millner 1996, Rijnsdorp et al. 1996, Eero et al. 2008). Here we present such an analysis and also the first attempt at assessing trends of turbot for the North Sea using a reconstructed time series of biomass, maximum body size and spatial distribution based on standardized research surveys beginning in 1925. We also show that a time series beginning only 30 yr ago would have given erroneous values for estimating baseline levels of the turbot stock status in the Kattegat-Skagerrak. These results imply that having a historical perspective is fundamental for estimating management reference points to be used in restoration and long-term management of exploited fish populations. Our analysis thus provides a data-driven demonstration of the shifting baseline syndrome (Pauly 1995, Roberts 2007). Sáenz-Arroyo et al. (2005) showed that this situation can potentially affect the stock assessment of vulnerable species by masking real population trends. The reduction of turbot in the study area before the massive fishery that occurred after the 1950s (Lotze & Milewski 2004), which is usually considered the main cause of the decline of several stocks of demersal species, suggests instead that the pre-industrial fishery (Blegvad 1943) had already had a significant impact on the stock. An alternative interpretation is that the quality of the turbot nursery grounds has deteriorated due to pollution (in particular eutrophication) and increased frequency of hypoxia events occurring in the shallow sandy coastal waters of Denmark and Sweden (Pihl et al. 2005), affecting the productivity of the stock. As flatfish abundance appears to be determined during the nursery phase (Van der Veer et al. 2000), a decrease in the nursery habitat quality may reduce overall population abundance. However, the decline in biomass was also accompanied by a large decrease in average maximum length, with large individuals more abundant at the onset of the last century. One might argue that a decrease in maximum body size could also be an effect of environmental changes, such as a decrease in sea temperature or food availability that might affect growth rates (Maschner et al. 2008). However, we observed a decrease in mean size of the population during a period of general increasing temperature in the area (Rayner et al. 2003). Another explanation might be the expected changes in size selectivity due to changes in mesh size of the trawl. Nonetheless, the largest decline in L_{max} occurred much before (1950 to 1970) the use of the smallest mesh size (since 1973) and thus it is unlikely that this was the cause of the observed trend. Thus, the above considerations again corroborate the hypothesis that observed trends in length and stock size are a result of overexploitation.

This result provides important complementary information for a correct interpretation of the observed decreasing trend in the turbot stock biomass although no estimates of fishing mortality for turbot in the Kattegat-Skagerrak have been explicitly considered. Also, trends in both SSB and L_{max} seem to indicate that turbot declined strongly in the inter-war years, from high post-World War I levels, while the stock recovered just after World War II, a phenomenon that was caused by the quasi-cessation of trawling activity during the wars (Wimpenny 1953). The decline then accelerated after the 1950s as also observed for other stocks in the North Sea (Holden 1978). Within this perspective, our findings strongly agree with the results from Christensen et al. (2003), who showed that the biomass of high-trophic

level fish species in the North Atlantic declined by two-thirds during the second half of the 20th century, and by a factor of around 9 for the century as a whole.

Our analyses clearly demonstrate that the lack of information from the pre-industrialized exploitation phase can potentially lead to misleading results with respect to the status of the stock being assessed and, consequently, to the possible implementation of ill-suited fishery management strategies. In particular, the lack of clear trends in turbot population estimates in the last 30 yr does not imply that the stock is safely exploited and with no need of conservation measures. As reported by Casini et al. (2005), the turbot biomass dynamics over the last 25 yr are mostly characterized by yearly fluctuations that are essentially uninformative about the real status of the stock. Prolonged exploitation significantly increases the probability for the stock to experience a roughly stable state at low quantities (Rose 2004) and, in some cases, a complete extinction (Hutchinson et al. 2003).

When viewed in a historical perspective it is clear that the turbot stock is likely to be largely overexploited and mainly constituted by relatively small individuals within a reduced geographical distribution area, a classical effect of overexploitation and a clear sign of a highly threatened status (Gaston et al. 2000). The substantial variation presented here in stock status over time indicates the importance of enforcing conservation measures to assure that the stock is not endangered (Waples et al. 2007) and can support a sustainable fishery in the future. Historical estimates therefore are important components of understanding the response of biological systems to exploitation and correctly evaluating the status of resources in human-dominated ecosystems (Jackson et al. 2001, Rick & Erlandson 2008). The limited information available from the pre-industrialized fishery exploitation phase is extremely informative and should be taken under much higher consideration within a framework of conservation and sustainable long-term exploitation of natural resources and ecosystems.

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