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Original Article

Implications of stock recovery for a neighbouring management unit: experience from the Baltic cod

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Cod in the Baltic Sea is assessed and managed as two separate stocks, i.e. eastern and western Baltic cod. The eastern Baltic cod has recently started to recover after several decades of severe depletion. In the present study, we suggest that the recovery of the eastern Baltic cod population has also substantially increased cod abundance in a specific area of the adjacent western Baltic management unit. This is investigated through long time-series of spatially resolved stock assessment data supplemented by genetic analyses of origin of the cod currently found in the transition area between the two populations. Due to immigrating cod from the east, there are currently large spatial differences in cod abundance and mean weight in the western Baltic management unit that raise new management concerns. First, the high abundance of cod of eastern origin found in the western Baltic management unit can mask the relatively poor state of the western Baltic cod population. Second, the current fishing mortality estimates for the entire western Baltic management unit, used as basis for fisheries management, are difficult to interpret as these are highly influenced by mixing of biological populations and the spatial distribution of fisheries.

Keywords: Baltic sea, cod recovery, fisheries management, local depletion, stock mixing.

Introduction

Management of marine fisheries is generally conducted in certain geographical areas often called management units. Boundaries for management units should be defined using stock identification studies, to ensure that the management units correspond to meaningful biological entities (e.g. Palsbøll *et al.*, 2007; Cope and Punt, 2009; Machado-Schiaffino *et al.*, 2011; Ulrich *et al.*, 2013). The concept of a fish stock is basic for fisheries management, as it forms the basic unit on which assessments are performed to evaluate the status of these stocks and propose appropriate management measures (Begg *et al.*, 1999). In practice, it is recognized that the boundaries of fish stocks defined for management purposes are confounded by migration, mixing, political and administrative considerations, and do not always match biological populations (Campana *et al.*, 1999; Stephenson, 1999; Martien and Taylor, 2003). Consequently, a fisheries management unit may or may not be equivalent to a single biological unit (Reiss *et al.*, 2009), and failure to recognize biological units could result in unsustainable management (Heath *et al.*, 2014).

Cod in the Baltic Sea is assessed and managed as two separate stocks, i.e. eastern and western Baltic cod, located in ICES Subdivisions (SD) 25–32 and 22–24, respectively (see Figure 1 for location of SDs). This boundary between the two cod stocks was set in the 1970s (ICES, 1974) and has been applied throughout the entire stock assessment history of the Baltic cod. The boundary between the eastern and western cod reflects their geographical distributions based on historical studies of migration patterns derived from taggings studies (Berner, 1967, 1971a, b; Berner and Borrmann, 1985; Otterlind, 1985; Aro, 1989) and phenotypic differences (Kändler, 1949; Birjukov, 1969; Berner and Vaske, 1985; Müller, 2002). In recent years, the existence of two different populations has been confirmed by genetic analyses (Nielsen *et al.*, 2003, 2005), with some mixing taking place in the Arkona Basin (SD 24).

The stock size of cod in the western Baltic Sea has been relatively stable at an intermediate level since the 1990s. In contrast, the eastern Baltic cod has been severely depleted for two decades until the mid-2000s when it started to recover rapidly (ICES, 2013a).

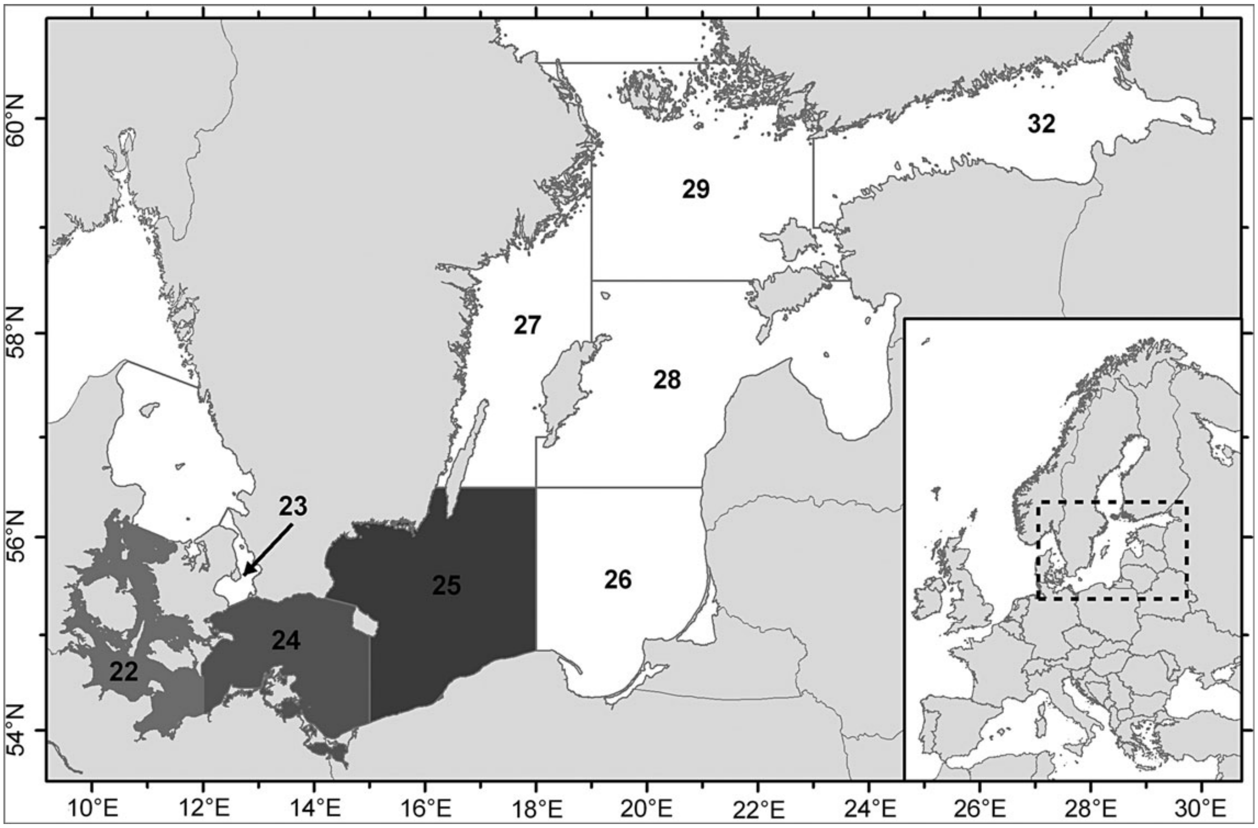

Figure 1. ICES Subdivisions (SD) in the Baltic Sea. SD 22 – 24 correspond to the western and SD 25 – 32 to the eastern Baltic cod management unit (SDs 30 and 31, located north of SD 29, where cod is hardly present are not shown on the map). The highlighted SDs (22, 24, 25) illustrate the focus areas for this study.

This was achieved by a combination of improved compliance to management measures coinciding with increased recruitment production (Cardinale and Svedäng, 2011; Eero *et al.*, 2012a). However, the recovering eastern Baltic cod has not re-occupied its former northeasterly distribution range, but remains concentrated in a limited area in the south (mainly in SD 25; Figure 1), close to the border to the neighbouring stock, i.e. the western Baltic cod (Eero *et al.*, 2012b). The cod in this densely populated area (SD 25) shows signs of density dependence, apparent in the form of drastically reduced mean weight and condition, at least partly due to limited food availability (Eero *et al.*, 2012b).These circumstances are believed to have resulted in spill-over of the eastern Baltic cod to the western Baltic management area, and a large part of the fishery is currently operating at the borders between SDs 24 and 25, presumably catching a mixture of the eastern and western Baltic cod (ICES, 2013a).

In this paper, we investigate links between the adult cod dynamics across the borders of the eastern and western management units. This is done by (i) developing time series of adult cod abundance and biomass by subareas within the western Baltic Sea and comparing these with the dynamics in the bordering area to the eastern Baltic Sea, (ii) investigating differences in body weight and nutritional condition of cod by subareas; and (iii) genetic analyses. We then use these results to highlight new challenges for fisheries management associated with recent stock recovery in one management unit affecting a neighbouring stock. This work is intended to contribute to a potential revision of the long-term management plan for cod in the Baltic Sea, robust to inter-linkages between adjacent management units.

Material and methods

Stock dynamics by subarea

To investigate cod dynamics by subareas within the western Baltic management unit (SD 22–24), separate stock assessments were conducted for SDs 22 and 24. The Sound (SD 23) that also belongs to the western Baltic cod management unit but is considered as a separate sub-population (Lindegren *et al.*, 2014) was not included in this study. To compare the area specific cod dynamics in the western Baltic Sea (SDs 22 and 24) with that in the neighbouring area belonging to the eastern Baltic management unit (SD 25), a separate stock assessment for SD 25 was performed as well. These assessments represent cod dynamics in respective geographical areas, regardless of the population of origin of the cod found in these areas.

Input data on catches and mean weights at age of cod in the catches by SDs were obtained from the Baltic multispecies assessment database (ICES, 1997) for years 1977–1995 and from the annual reports of the ICES Baltic Fisheries Stock Assessment Working Group for years 1996–2012. The biological information on mean weight in the stock was obtained from the Baltic International Trawl Surveys (BITS), calculated separately for SDs 22, 24, and 25 following the same procedures as in official ICES assessments. Maturity ogive and natural mortality by SD were assumed the same as used for the combined stocks in a given management unit. For tuning, indices from BITS in the first and fourth quarter were used, calculated separately for SDs 22, 24 and 25, following the same procedures as in ICES assessments. Differently from ICES assessments, commercial tuning indices that are not available for all SDs were not used, to base all the SD-specific assessments on comparable data sources. The assessments by SD were conducted using state-space assessment model formally used to assess both the eastern and western Baltic cod stocks in ICES, applying the same model configurations as used in ICES assessment for these stocks (ICES, 2013a).

Body weight and nutritional condition of cod

The growth of cod in the Baltic Sea is known to vary by subregions. The cod inhabiting northeasterly areas are generally characterized by slower growth and consequently lower mean weight at age compared with the cod from southwest (Bagge *et al.*, 1994). In light of the recent drastic decline in mean weight of adult cod observed both in the eastern and western Baltic Sea (ICES, 2013a), SD-specific analyses of mean weight were conducted to elucidate potential area-specific patterns in this development. Data on mean weight at age of cod by SD were compiled as part of the input data to the area-specific stock assessments described above. The weight-at-age measurements of individual fish are from size stratified sampling (ICES, 2011a), but these were subsequently raised with total length frequencies in survey catch, to obtain mean weight at age estimates in the stock.

The analyses of mean body weight were supplemented by SD-specific estimates of nutritional condition factor (Fulton K) of individual cod as a measure of energy status. The Fulton K condition factor presented in this paper is an average value for the fish sampled on BITS surveys in the first quarter of year using data on total length (L) and whole weight (W) of individual cod.

$$K = 100 \times \frac{W}{L^3} \qquad (1)$$

The analyses included cod between 40 and 60 cm in length and covered the period from 1991 to 2012. To identify the proportion of cod in critically low condition, a threshold of Fulton K below 0.8 was applied (Marteinsdottir and Begg, 2002).

Genetic analyses

Earlier studies have shown that spawning groups in SD 25 and SD 22 represent clearly differentiated genetic populations (Nielsen *et al.*, 2003). Consequently, the population of origin of fish captured within SD 24 was determined by genetic analyses using samples from spawning populations collected from SD 25 and SD 22 in 2007 as baseline. Genetic assignment of the fish captured within SD 24 used a panel of 39 single-nucleotide polymorphisms (SNPs) (see Nielsen *et al.*, 2012 for concept and methodology). Individual fish were assigned to populations of origin based on their multi-locus genotypes, using the baseline samples from SDs 22 and 25. We applied a Bayesian approach (Rannala and Mountain, 1997) implemented in the program GeneClass (Piry *et al.*, 2004), and used a threshold score of 95% for assignment. Consequently, individuals with scores below this threshold were excluded. In total, 539 fish were analysed, collected from SD 24 in June 2011 (see Figure 2 for spatial distribution of sampling sites). In addition, 50 fish from SD 22 (collected in February 2012) and 50 specimens from SD 25 (collected in June 2011) were assigned for comparison.

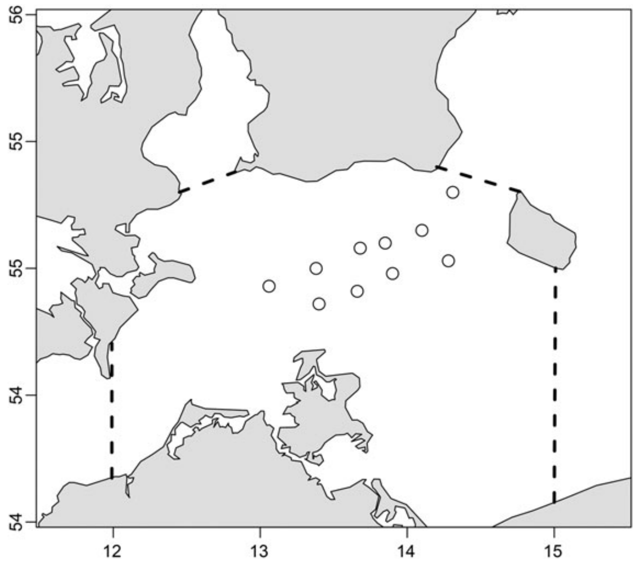

Figure 2. Geographic location of samples for genetic analyses from ICES Subdivision (SD) 24. Broken lines show SD borders.

Analyses of fishing mortality

In cases of differential mean body weight of fish within a single management unit, spatial distribution of catches can affect the overall fishing mortality. At the same level of total yield (in weight), the overall fishing mortality (traditionally calculated based on numbers of fish) will be lower when the yield consists of fewer individuals with higher individual weight, compared with the opposite case where more individuals with lower body weight are needed to obtain the same yield.

The impact of distribution of fisheries yield between SDs 22 and 24 on overall fishing mortality of cod in the western Baltic management unit was analysed. This was done using stock numbers at age ($N_{a+1,\ t+1}$) from the latest ICES assessment and a total yield of 20 000 t (Y_t). The purpose of this exercise is only to demonstrate the magnitude of impact on estimated fishing mortality caused by spatial distribution of total yield, due to differences in mean body weight of cod by SDs. Thus, the values for stock numbers and total yield used for this calculation are arbitrary, but were taken from ICES assessment to base the analysis on realistic values.

In the scenarios explored, the yield of 20 000 t was distributed between SDs 22 and 24 in different proportions, at steps of 10%. Altogether 11 scenarios were explored, allocating from 0 to 100% of the yield to SDs 22 and 24, respectively. The age structure of the catch and mean weight at age in SDs 22 and 24 were set to the average SD-specific values observed in 2010–2012. The sum of catch numbers taken from SDs 22 and 24, corresponding to a total yield of 20 000 t, gave the total catch numbers at age for a particular scenario ($C_{a,t}$).

In each scenario, stock numbers at age ($N_{a,t}$) and fishing mortalities ($F_{a,t}$) corresponding to given catch numbers ($C_{a,t}$) were calculated using Pope's approximation (Haddon, 2001).

$$N_{a,t} = \left(N_{a+1,t+1} \times \exp\left(\frac{M_{a,t}}{2}\right) + C_{a,t} \right) \times \exp\left(\frac{M_{a,t}}{2}\right) \qquad (2)$$

Natural mortality at age (M_a) was assumed the same both in SD 22 and 24, and was set equal to the values used in ICES (2013a).

Fishing mortality at age ($F_{a,t}$) in each scenario was calculated as:

$$F_{a,t} = \ln\left(\frac{N_{a,t}}{N_{a+1,t+1}}\right) - M_{a,t} \quad (3)$$

Results

Stock development

Trends in adult cod abundance in the two subareas (SDs 22 and 24) of the western Baltic management unit are similar from the late 1970s until the early 1990s (Figure 3). Since then, the cod abundance in SD 22 has generally declined up to the present relatively low level, while the abundance of cod in SD 24 has substantially increased in later years and is currently at the highest level on record. The abundance of adult cod in SD 24 through the whole time series has followed the population trends of cod in eastern adjacent area, i.e. in SD 25. Both in SD 24 and SD 25, peaks in cod abundance have occurred in the early 1980s and in the mid-1990s, and the stock size has substantially increased since the mid-2000s (Figure 3).

The recent increase in stock size in SD 24 is less pronounced when looking at the spawner biomass instead of the abundance of adult cod, which is due to a reduction in mean body weight of cod in later years (see below). Nevertheless, the majority of the spawner biomass of cod within the western Baltic management unit is currently distributed in SD 24, while the spawner biomass in SD 22 is close to the historically lowest level (Figure 4). Despite the record high stock size in SD 24, recruitment to the entire western Baltic Sea (SD 22–24) has been low since the mid-2000s. Periods of frequent stronger year-classes have generally coincided with periods of relatively high cod stock in SD 22, except for a few years (e.g. 1991) when a relatively strong year-class was recorded at a low stock size in SD 22 (Figure 4).

Body weight and nutritional condition

Among the three subareas investigated, the mean weight of adult cod has historically been lowest in the eastern Baltic Sea (SD 25), highest in the western part of the western Baltic Sea (SD 22) with intermediate values in the eastern part of the western Baltic Sea (SD 24) (Figure 5a). Since the mid-2000s, differences in mean weight between SDs 24 and 25 have diminished and the mean weight has substantially declined in both areas. Currently, the mean weights of adult cod (age 4–6) in SDs 24 and 25 are relatively similar and about threefold lower compared with the mean weight in SD 22. Consequently, pronounced spatial differences in the mean

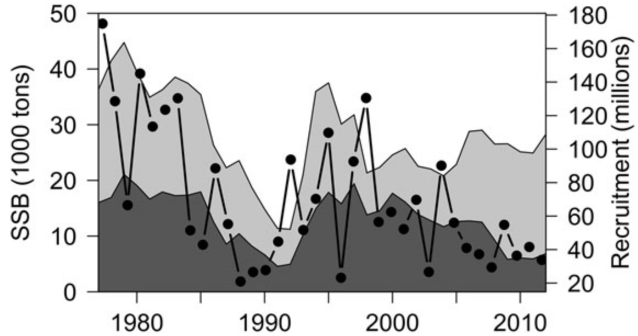

Figure 4. Spawning-stock biomass of cod in SD 22 (dark grey area) and 24 (light grey area) and recruitment in the entire western Baltic Sea (SD 22–24; line).

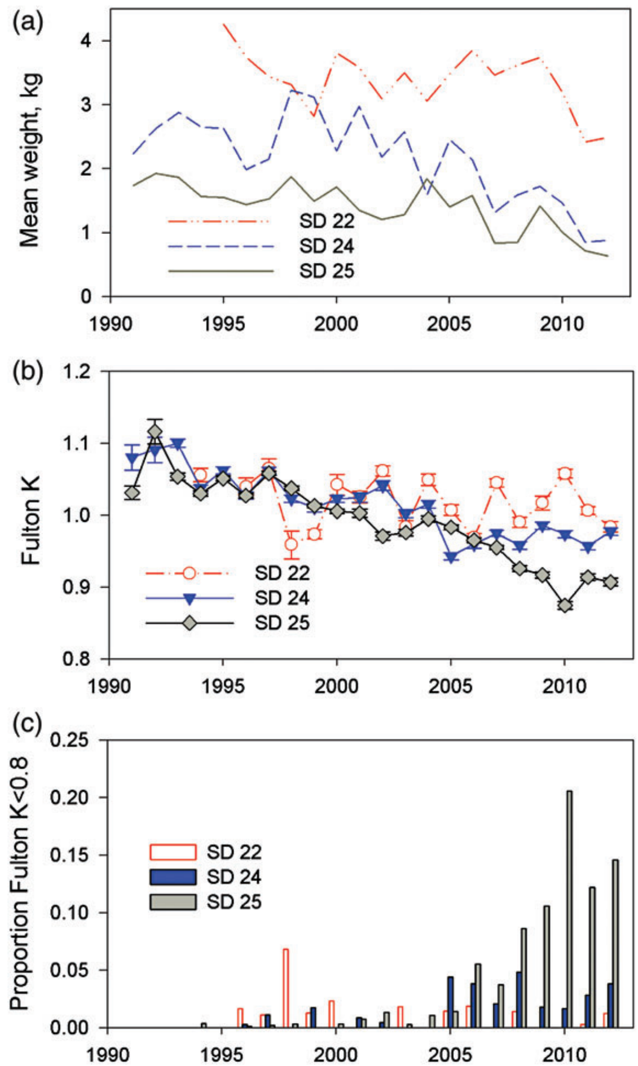

Figure 5. (a) Mean weight of adult cod (ages 4–6); (b) mean Fulton K condition factor for cod at 40–60 cm in length (the error bars represent SE of the mean) and (c) the proportion of cod in low condition (Fulton $K < 0.8$), by SDs.

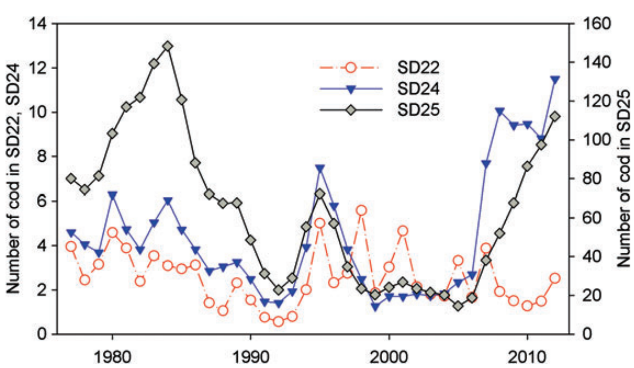

Figure 3. Numbers of adult cod (age 4+) in SDs 22 and 24 (western Baltic management area) compared to the numbers of adult cod in SD 25 (eastern Baltic management area).

weight of cod within the management unit of the western Baltic Sea are evident (Figure 5a).

The decline in mean weight of cod in SD 25 in recent years is accompanied by a reduction in nutritional condition (Figure 5b). In 2010–2012, approximately 15% of cod sampled in this area were in a low condition (Fulton $K < 0.8$) (Figure 5c). The average condition of cod in SD 24 has declined during the 1990s, but has been stable in recent years and generally better compared with SD 25. In SD 24, <5% of cod were found in low condition (Fulton $K < 0.8$). This is despite the even more pronounced reduction in mean weight in SD 24 in recent years compared with that in SD 25. In SD 22, no clear trend in average condition was detected during the analysed period, and only a few cod were found in a low condition in this area in recent years (Figure 5b and c).

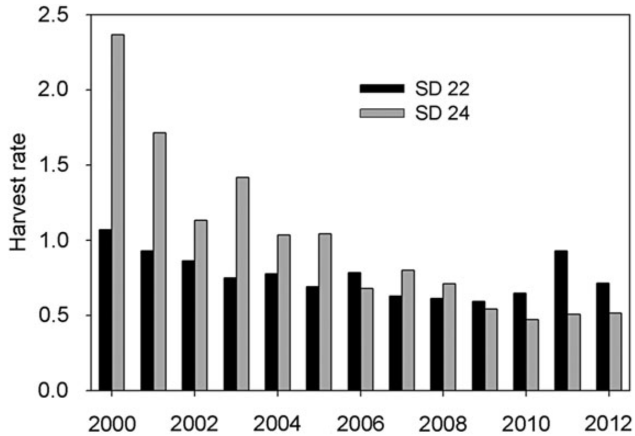

Figure 6. Harvest rate (yield/spawner biomass) of cod in SDs 22 and 24.

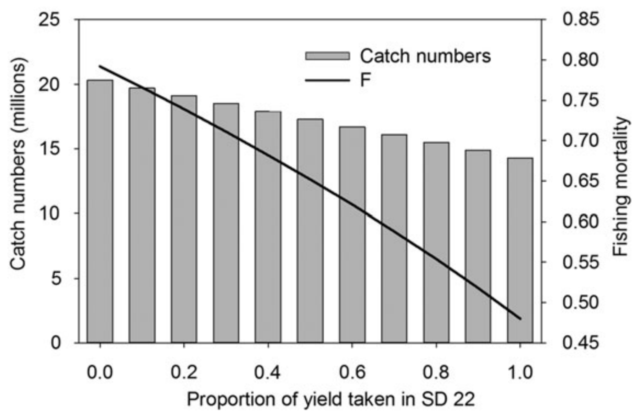

Figure 7. Total fishing mortality and catch numbers corresponding to different scenarios of proportion of total yield taken in SD 22.

Genetics

Genetic analyses showed that all fish sampled in SDs 25 and 22 (50 individuals in each) assigned to their expected baseline populations. In contrast, genetic assignment of fish sampled from SD 24 (539 individuals) indicated a mixture of fish from different populations with the majority (88%) of the cod assigning to the eastern Baltic cod population and 10% to the western population. Only 2% of the fish caught in SD 24 could not be assigned to any of the two baseline samples.

Fishing mortality

Recent developments in fishing pressure in the western Baltic Sea by subareas were expressed as harvest rate (yield/spawner biomass) instead of instantaneous fishing mortality by age that is traditionally used in ICES assessments. This is because harvest rate is considered relatively more robust to potential age-specific movement of fish between areas (see the discussion for further explanation). In SD 24, the harvest rate has declined fourfold since 2000, while it has been relatively stable in SD 22. Until the late 2000s, the stock component in SD 24 has been harvested more intensively, compared with that in SD 22. This has changed in later years, and currently the harvest rate in SD 22 is exceeding that in SD 24, which is a matter for concern given the poorer stock status in SD 22 (Figure 6).

Simulations of overall instantaneous fishing mortality under different relative proportions of total yield taken from SDs 22 and 24 revealed an increasing overall fishing mortality with increasing proportion of yield taken from SD 24 (Figure 7). This is because more individuals are needed to obtain the same total yield from SD 24 compared with SD 22. The extreme scenarios with 0 and 100% of total yield allocated to SDs 22 and 24, respectively, showed an approximately 30% difference in total numbers of fish removed corresponding to the same yield. This corresponds to about 40% difference in overall fishing mortality (for age range 3–5) (Figure 7). Thus, due to the pronounced differences in mean weight between the two areas, allocating a larger proportion of yield to SD 24, where the stock is more abundant, will result in an overall increase in estimated fishing mortality in the western Baltic management unit.

Discussion

Connection between the eastern and western Baltic cod management units

Phenotypic differences with respect to number of fin rays, body height, otolith size, head characteristics, and length–weight ratios (Kändler, 1949; Birjukov, 1969; Berner and Vaske, 1985; Müller, 2002) as well as genetic differences (Nielsen *et al.*, 2003, 2005) have long been known to exist between the eastern and western cod in the Baltic Sea. Cod in the Baltic Sea seem to exhibit natal homing for spawning (Berner, 1967; Nielsen *et al.*, 2013), and a difference of ~4 months in the timing of the peak spawning season between the two stocks may add to the separation between the eastern and western populations (Bleil *et al.*, 2009). Further, recent genetic analyses have shown that the eastern Baltic population is most likely adapted to the unique environmental conditions (Nielsen *et al.*, 2009; Hemmer-Hansen *et al.*, 2013).

Even through genotyping has confirmed a genetic differentiation between the two populations (Mork *et al.*, 1985; Nielsen *et al.*, 2003, 2005; Johannesson and André, 2006 and references therein), historical tagging experiments suggest mixing across the boundary between the management units. For example, although most of the cod tagged in the eastern Arkona Basin (SD 24) were recaptured in the western Baltic Sea, some were also recaptured east of Bornholm (SD 25) (Berner, 1967, 1971b; Otterlind, 1985). On the other hand, cod tagged in SD 25 showed some migration to west of Bornholm (i.e. to SD 24), though primarily staying in the eastern Baltic Sea (Berner, 1967, 1971b; Otterlind, 1985). Superimposed on these spatial patterns is a temporal aspect, in that the migration destinations seem to depend on the tagging season, with fish tagged early in the year migrating towards the west and those tagged later migrating towards the east (Berner and Borrmann, 1985). The direction and timing of these migrations may thus reflect different stock affiliations of individual fish and their respective spawning migrations. The extent of migrations between the two management units, their temporal patterns and impact on stock reproduction have not yet been resolved.

Our aim in this paper is not to resolve the unknown issues related to stock mixing in the past or question the historical separation between the eastern and western Baltic cod management units. Instead, we focus on the new issues emerged since the mid-2000s, related to the onset of spatially diverse stock developments within the western Baltic management unit, evidently related to stock recovery of the eastern Baltic cod. The analyses conducted in this paper demonstrate that the main stock trends in the three analysed subareas, i.e. SD 22, 24, and 25, have been similar from the late 1970s until the second half of the 2000s, when the dynamics in SD 24 started to diverge from that in SD 22, following the dynamics in SD 25. Also biological parameters, such as mean weight at age, have become similar between SDs 24 and 25, where historically differences have been observed. In SD 25, the recent drastic reduction in mean weight has been related to food limitation (Eero *et al.*, 2012b) supported by poor nutritional condition of adult cod in this area since 2007. In contrast, a similar deterioration of condition is not apparent in SD 24. Thus, the observed drastic reduction in mean weight at age in SD 24 is unlikely due to poor feeding conditions in this area. This is expected as the absolute cod abundance in SD 24 is nearly tenfold lower than that in SD 25 (Figure 3), whereas the abundance of sprat, one of the main food items for adult cod, has in recent years been higher in SD 24 than in SD 25, at least during parts of a year (ICES, 2011b).

The strong reduction in mean weight at age of cod caught in SD 24 could possibly be due to immigrating cod from the east (SD 25), carrying along a generally lower body weight at a given age, due to slower growth of cod in eastern areas compared with the west (Bagge *et al.*, 1994). The migration would likely be undertaken by those individuals of eastern cod still being in a relatively good condition. This could explain the stable and relatively good condition of cod found in SD 24, while weight has substantially declined. Prolonged starvation or even reduced feeding degrades body reserves of proteins and lipids, and actively swimming fish use up these reserves much faster than sedentary fish (Simpkins *et al.*, 2003). Also, reduced somatic condition increases the cost of swimming (Martínez *et al.*, 2004). It is therefore not likely that already starving fish are physiologically capable of undertaking energetically demanding migrations. Moreover, after periods of restricted feeding, fish are known to show "compensatory growth response" following re-feeding. They are able to gain the weight lost during a protracted period of starvation within only a few weeks (Jobling *et al.*, 1994). Thus, their nutritional condition would improve quickly after moving to areas with better feeding opportunities.

The potential immigration from the east is supported by genetic assignment of the cod caught in SD 24, where a clear majority of the analysed fish belonged to the eastern population. Thus, our results suggest that the currently similar developments in SDs 24 and 25 are largely due to physical mixing of populations across the borders of the two management units. It should however be noted that the genetic results reflect a snapshot from a specific month and year (June, 2011), and it is so far not known if these patterns are temporally and spatially stable. Also, the degree of physical mixing between SD 24 and 25 in the past is unknown. The historically similar stock trends in SDs 24 and 25 could partly be a response to common environmental or ecological drivers in independent populations.

From a management perspective, even if SD 24 always has contained significant proportions of immigrants from the eastern stock, new concerns have emerged in recent years that have not been similarly relevant in the past. This is because until the mid-2000s cod dynamics has been relatively homogenous between the subareas of the western Baltic management unit, and differences in biological parameters of cod found in these areas have been less pronounced. In light of recent developments, when the cod abundance in the eastern part of the western Baltic management unit (SD 24) is substantially higher and contains individuals with substantially lower mean weight than in the west (SD 22), evidently influenced by a stock recovery in the adjacent management unit (SD 25), we focus the management-related discussion in the present paper on the new challenges emerging from such situation. Below we discuss the implications of strong spatial heterogeneity within the management unit for fisheries management and identify what is needed to develop appropriate solutions.

Challenges for fisheries management

One of the current concerns related to cod in the western Baltic Sea is that the relatively high stock size in the transition area between the eastern and western populations (in SD 24) can overshadow the relatively poor status of the "true" western cod in SD 22. Several studies have emphasized the importance of taking into account spatial sub-population structure in management, since failure to do so can increase the risk of local depletions (e.g. Shackell *et al.*, 2005; Sterner, 2007; Ying *et al.*, 2011; Heath *et al.*, 2014). A severe consequence of depleted sub-populations could be a potential weakening of the productivity of the entire stock (Frank and Brickman, 2000; Berkeley *et al.*, 2004; Svedäng *et al.*, 2010).

For cod in the western Baltic Sea, the relative contribution of sub-populations to overall recruitment is not well understood. From a visual inspection it is apparent that a high stock size in SD 24 is generally not associated with strong recruitment to the western Baltic Sea. This is particularly evident in recent years, where recruitment has been among the lowest in the time series despite the historically high cod biomass in SD 24 (Figure 4). Historically, the large-scale fluctuations in cod recruitment in the entire western Baltic Sea have often followed trends in stock size in SD 22. Besides the potential effect of stock size, the recruitment of the western Baltic cod is strongly influenced by survival of early life stages (Hüssy, 2011). Interaction between temperature and salinity limit the spawning areas suitability for successful egg development (Hüssy *et al.*, 2012). Lower temperatures also prolong egg development time (Wieland *et al.*, 1994), which leads to longer drift duration and consequently a higher probability of being advected out of the spawning areas. However, the temporal trends in spawning habitat suitability (Hüssy *et al.*, 2012) and drift dynamics (Hinrichsen *et al.*, 2012) cannot explain the recently observed low levels of recruitment in western Baltic cod. Therefore, maintaining a viable stock component in SD 22 may be important to ensure future recruitment in the western Baltic Sea.

The concerns related to a risk of depletion of the SD 22 cod are supported by the current distribution of fishing pressure. The cod in the western Baltic Sea (SD 22–24) has historically been exploited at mortality rates far above the level corresponding to maximum sustainable yield. In recent years, the overall fishing mortality has started to decline (ICES, 2013a). However, our analyses show that a substantial decline in fishing pressure has taken place mainly in SD 24 that currently is suggested to contain significant amounts of the eastern Baltic cod. The fishing pressure on "true" western cod in SD 22 has remained stable in the last decade and is currently exceeding that in SD 24. In this analysis, we have used harvest rate instead of instantaneous fishing mortality that is formally used to measure the status of fishing pressure. This is because ICES assessments have revealed high uncertainties in ages-specific fishing mortality estimates for cod in western Baltic management unit in later years, particularly for older ages (ICES, 2013a). This is due to large interannual variability in stock indices measuring a given cohort in later years (ICES, 2013a), probably at least partly related to varying age-specific proportions of movement of cod across the borders of the two management units. Harvest rate, i.e. a ratio between yield and biomass, can be considered relatively more robust to variability in individual age groups. Instantaneous fishing mortality is one of the key measures formally used in ICES to assess the status of a stock in relation to management targets, and evaluate the efficiency of management measures. Thus, increased uncertainty in fishing mortality estimates in later years due to stock mixing complicates such evaluations.

Another issue related to fishing mortality is that the large spatial differences in mean weight of cod within the western Baltic management unit can lead to invalid interpretation of the overall estimates of fishing mortality. Our analyses demonstrate that at present SD-specific mean weights of cod, spatial distribution of the yield can result in up to 40% difference in overall fishing mortality estimates for the western Baltic management unit. Controversially, reallocating fishing effort from SD 22 to SD 24 to protect the weaker stock component in SD 22 would result in an increase in the estimated overall fishing mortality when measured in numbers. Therefore, currently the two management goals, to protect the cod in SD 22, as suggested by ICES (ICES, 2013a), and at the same time reduce the overall fishing mortality estimate in the entire western Baltic Sea management unit seemingly counteract each other. This apparent contradiction arises from the fact that the stock assessment relates to a certain geographical area, i.e. western Baltic management unit, while not taking the biological populations within this area into account. From a biological perspective, reallocating fishing effort from SD 22 to SD 24 would likely increase the fishing mortality on the eastern population, given that the proportion of the eastern cod found in SD 24 is relatively high as indicated in this study.

The temporal development in the extent of mixing of the two populations in the eastern part of the Western Baltic Sea (SD 24) is unknown. However, even if the proportion of eastern cod found in SD 24 is currently similar to the past, the much lower stock size in SD 22 (inhabited by "true" western Baltic cod) relative to that in SD 24 (mixing area) suggests that the overall proportion of eastern cod found in the western Baltic management unit is currently higher than in earlier years. In such case when the eastern cod occurs in the western Baltic Sea in varying proportions between years, this would also invalidate the biological reference points for the western Baltic management unit, as the two populations possibly differ in terms of their potential to contribute to the recruitment in this area.

Conclusions and future perspectives

In the present study, we have demonstrated a remarkable impact from the eastern Baltic cod population on the western Baltic management unit in later years. Developing and implementing appropriate long-term solutions to the new management challenges rising from this situation largely remain a future challenge, including further validation of the current perception of the extent of stock mixing within the western Baltic Sea.

A possible solution may be to adjust the boundaries separating the two management units. However, given the temporal variability in stock abundances and distribution patterns, simply adjusting the management units to the present, perhaps temporary, situation may not be appropriate. Approaches to derive management units that fluctuate over time depending on underlying population dynamics have been suggested in literature (Cope and Punt, 2009). Short-term changes in management units may however not be desired from a practical management point of view, due to administrative issues such as those related to historical regulation systems and quota distribution keys between countries, where temporal stability in management units is preferred.

As an alternative, a quantitative separation of the cod of eastern and western origin in the mixing area in routine stock assessments may be possible, as done for other stocks, e.g. for herring in the western Baltic Sea, to overcome the problem of stock mixing (ICES, 2013b). This could be done with genetic assignment or other population identification methods, such as otolith shape analyses (Paul *et al.*, 2013). Regardless of the approach chosen, continuous monitoring would be required to determine the temporal and spatial variation in mixing proportions within SD 24.

Developing an appropriate management approach to stock mixing requires better understanding of the connectivity of cod within and between the two management units. For example, it is currently unclear whether the cod of eastern origin found in the western Baltic Sea are new permanent residents contributing to the recruitment in the western Baltic area, or whether a return migration, e.g. related to spawning, takes place. Knowledge on the contribution of different stock components to the recruitment is essential to setting biomass reference points that currently assume even contribution of the individuals of eastern and western origin to the recruitment in the western Baltic management unit.

An immediate short-term solution to reduce risk of local depletion of the western Baltic cod population would be to reduce the relative proportion of landings taken in SD 22. Further, the current stock structure and spatial heterogeneity are important to bear in mind when interpreting fishing mortality estimates for the entire western Baltic management unit. Using a harvest rate that is measured in the same units as TACs (in weight) instead of fishing mortality (based on numbers) could provide a more robust measure of fishing pressure, being less sensitive to spatial differences in mean weight. However, the issues associated with targeting different biological populations when fishing either in SD 22 or in SD 24 would remain. Therefore, continued research activities towards an appropriate long-term solution and developing management frameworks that are able to account for extensive mixing of fish across the borders of management units are needed.

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