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New perspectives on Eastern Baltic cod movement patterns from historical and contemporary tagging data

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Eastern Baltic cod movement patterns

Abstract

Knowledge of the movement patterns and area utilisation of commercially important fish stocks is critical to management. The Eastern Baltic cod (*Gadus morhua*) has been one of the most commercially and ecologically important stocks in the Baltic Sea but is currently one of the most severely impacted fish stocks in Europe. During the last two decades, this stock has experienced drastic decreases in population size, distributional range, individual growth, and body condition, all of which could have affected the stock's movements between different areas of the Baltic Sea.

In this study, we investigated the seasonal movement patterns of Eastern Baltic cod by re-analysing historical tagging data collected by the countries surrounding the Baltic Sea (1955-1988), and compared historical patterns with contemporary data from a recent international tagging experiment (2016-2019). Our re-analyses of historical data showed the presence of different movement behaviours, resident and seasonally migratory, with larger distances moved by cod released in the northern and central Baltic areas compared to cod released in the southern Baltic areas. Furthermore, trends from the recent tagging experiment indicate a persistent resident strategy in the southern Baltic area.

These findings present additional information on general movement patterns and area utilisation of Eastern Baltic cod that could inform future management actions and aid stock recovery.

Keywords: Baltic Sea, *Gadus morhua*, fish movement, mark-recapture, historical data, home range, kernel density estimation, generalized additive model

1. Introduction

Fish often undertake regular migrations between areas of feeding and spawning in order to maximize the benefits available from certain habitats for a particular activity or life-stage (Metcalfe, 2006). As a consequence, knowledge of migration and dispersal behaviour, termed "movement patterns", is fundamental for managing commercially fished populations, especially in areas where population mixing takes place (Rose & Rowe 2015, Neat et al. 2014, Zemeckis et al. 2014), where environmental conditions are subject to change (Drinkwater 2005, 2015, Engelhard et al. 2014) or where ontogenetic movements generate marked differences in the spatial distribution of different age groups.

One of the most widely applied methods to study the movements of wild animals is to use individual markers. Particularly, conventional tagging experiments, which provide information on release and recapture positions, and are used for investigating broad-scale patterns such as area of utilisation and movement patterns of individuals (e.g., Righton & Metcalfe 2019).

The movements of Atlantic cod (*Gadus morhua*) have been studied extensively with tagging experiments (Robichaud & Rose 2004). Cod migratory behaviour has been shown to vary markedly with respect to area, season, and major environmental factors (Pálsson & Thorsteinsson 2003). Cod of the same population may adopt different migration routes between areas and their speed of travel can vary considerably during and between journeys (Righton & Metcalfe 2019). Differences in migratory strategies have also been identified, with some cod remaining relatively stationary, while others redistribute over vast spatial distances that exceed 1000 km (Robichaud & Rose 2004). Cod migratory patterns therefore appear to be complex and there are cases where populations of predominantly migratory and predominantly sedentary cod overlap in certain areas and at certain times of the year (e.g., cod at the Lofoten Islands, Nordeide 1998).

Baltic Sea cod inhabit an area that differs from most of the other areas where the species is found. The Baltic Sea is, in fact, one of the largest brackish areas in the world, where severe changes in biotic and environmental conditions have occurred in the past hundred years (Reusch et al. 2018). Two genetically distinct cod populations are present in this area: the western Baltic cod (WBC) stock in ICES subdivisions (SD) 22-24, and the Eastern Baltic cod (EBC) stock in SD 24-32 (Fig.1) with mixing of the two stocks occurring in SD 24 (Hüssy et al. 2016, ICES 2021).

In this extreme environment, the EBC have uniquely adapted to survive and successfully reproduce in the low salinity and low oxygen conditions of the eastern Baltic Sea (Andersen et al. 2009, Nissling et al. 1994), experiencing temperatures and salinities at the upper and lower tolerance limits of Atlantic cod, respectively (Köster et al. 2005, Mackenzie et al. 2007). Historically, cod have been one of the most important commercial species in the Baltic Sea (Bagge et al. 1994; ICES 2014) and, as a major piscivorous fish, play an important structuring role in the ecosystem (Casini et al. 2009). However, the EBC stock is currently one of the most severely threatened fish stocks in Europe (ICES 2020) and since 2019 the scientific advice has recommended a complete closure of the EBC fishery (ICES 2021).

The EBC stock size has changed considerably, with a peak in the early 1980s (ca. 200,000 tonnes) and a subsequent decline (Eero et al. 2015). Concurrent with the decline in stock size, a number of changes have been observed in the EBC stock, which include reduced body condition, maturation at a smaller size, shift in the timing of peak spawning, reduced growth, increased parasite infestation and thiamine deficiency (Eero et al. 2015, Mion et al. 2021, Engelhardt et al. 2020, Horbowy et al. 2016). After the late 1980s, the decline in cod abundance was also accompanied by a spatial contraction of the stock, primarily to the southern Baltic Sea (SD 25) (Eero et al. 2012, Bartolino et al. 2017, Orio et al. 2019, Wieland et al. 2000). This contraction has been linked to different biotic and abiotic conditions, which caused some areas to become "cod hostile" (Möllmann et al. 2009, Casini et al. 2009). In fact, in the last 40 years, the extent of hypoxic areas in the Baltic Sea has increased 5-fold (Carstensen et al. 2014, Meier et al. 2018). In addition, since the mid-1980s, the hydrographic conditions in the eastern spawning areas (in SDs 26 and 28) were thought to be no longer suitable for survival of cod eggs, and SD 25 is now considered the only area supporting successful reproduction of EBC (Köster et al. 2017, Fig.1). All of these dramatic changes in the marine environment, biology and distribution of the EBC stock may have resulted in changes in the movement patterns of the stock.

Extensive conventional tagging experiments were conducted from the 1950s to the 1980s to study the movement patterns of cod in the Baltic Sea and adjacent areas. The results of these historical tagging experiments have been summarised by a number of authors (Aro 1989, 2002, Bagge & Steffensen 1989, Robichaud & Rose 2004). Briefly, these studies showed that both sedentary and migratory behaviours were present in the EBC stock and that generally EBC exhibited strong migratory tendencies towards the southern Baltic. However, these studies only presented a description of the general movements, rather than a quantitative analysis, and a comparison with contemporary data in light of the deteriorated situation of the EBC stock is lacking.

In the studies of Mion et al. 2020, 2021, data from most of these historical tagging experiments, together with recent tagging experiments carried out in the southern Baltic Sea in 2016-2019, were digitised and collated for the first time in a unique database. This database provides a perfect opportunity to reanalyse historical data and investigate how the movement patterns of EBC may have changed through time. To achieve this quantitatively, kernel density estimation and generalized additive models were used to explore seasonal movement patterns and area utilisation of EBC in different areas of the Baltic Sea. Based on previous research (Aro 1989, 2002, Bagge & Steffensen 1989, Robichaud & Rose 2004), we hypothesise that during the historic period EBC will exhibit both migratory and sedentary movement strategies, with distance travelled and area utilisation varying based on release area. Conversely, in the contemporary data, we might expect that changing biotic and abiotic conditions in the northern and central Baltic, as well as contractions in the spatial distribution of EBC towards the south, may have impacted movement rates and area utilisation. Consequently, we hypothesise that recently tagged EBC will show a greater utilisation of southern areas, as northern and central areas are no longer suitable for spawning and are now considered "cod hostile". Any changes in movement patterns or area utilisation of EBC could impact the level of mixing with the WBC stock in the southern Baltic, with potential implications for management and future stock recovery.

2. Materials & Methods

Data from historical cod tagging experiments performed between the 1950s and 1980s covering the main historical distribution area of the EBC stock (SDs 24-32), and the more recent TABACOD dataset (2016-2019) covering the main current distribution area of the EBC stock (SDs 24-26), were extracted from the database compiled in Mion et al. (2020, 2021). All records were quality checked for movement analyses, selecting only the records where release and recapture dates and geographical positions as well as total body length measurements at release ($Length_{rl}$, cm) were present. Any recaptures of cod that occurred within 30 days of release were excluded. This was to ensure that all cod in this study had sufficient time to recover from the tagging procedure and move to different areas following release. A summary of the different tagging procedures and detailed information on releases and recaptures for these datasets can be found in Mion et al. (2020, 2021) and Hüssy et al. (2020).

2.1 Historical data

In total, there were 6,798 records suitable for movement analyses. Each record consisted of release and recapture dates and geographical positions (Fig. 2, S1a) as well as measurements of $Length_{rl}$ (Fig. S1c). Tagging efforts were focused in SDs 24-32 (Fig. 2. S2) and the recaptures were mainly reported by commercial fishers from their catches. The precision of the reported recapture locations varied largely between fishers. When only a location name was given (e.g., 4 nm south-east of Dueodde lighthouse), a geographical position was assigned as precisely as possible. In some cases, historical maps of the tagging experiments were used to confirm the position of a particular location name (an example is provided in Fig. 3).

Records for tagged cod spanned the mid-1950s to the 1980s, with 65% of cod recaptured during the 1970s (Fig. S1a). Cod were released year-round, but with reduced effort in quarter 3 (July-September). Tagging effort was likely reduced in the warmer months of quarter 3 as the thermocline is more pronounced and less tolerated by cod during the tag and release process (Otterlind 1984, Table S1a). Tagging effort varied in space and time. In the southern Baltic areas, in particular the Bornholm basin (SD 25), tagging occurred throughout the historical period, whereas in the central and northern Baltic areas, tagging effort was more concentrated in certain time periods (Fig. S2).

The time between release and recapture (days at liberty, *DAL*) ranged between 30 and 3,928 days (median: 174 days; Fig S1b). The historical dataset consisted of a mix of adults and juveniles with a $Length_{rl}$ range from 17 to 98 cm (median: 40 cm; Fig. S1c; size at sexual maturation in the historical period was

45 to 50 cm for females and 37 to 41 cm for males; Cardinale & Modin, 1999). The return rate (i.e., the % of tagged cod that were recaptured and returned to the research institutes) was on average 11.8% (Mion et al. 2021).

2.2 Contemporary data

The contemporary dataset consists of 301 records suitable for movement analyses from the TABACOD project (Hüssy et al. 2020), spanning the years 2016 to 2019. Again, each record consisted of release and recapture dates and geographical positions (Fig. 2, S1a) as well as measurements of $Length_{rl}$. Cod were released year-round, but with limited numbers in quarter 3 (Table S1b). Tagging efforts were concentrated in SDs 24-26 (Fig. 2), covering the main current distribution area of the stock (Orio et al. 2019). The contemporary dataset consisted mainly of adults with a $Length_{rl}$ range from 18 to 55 cm (median: 39 cm; current size at sexual maturation is 19 cm; Köster et al. 2017; Fig. S1c). *DAL* ranged between 30 and 927 days (median: 220 days) (Fig. S1b). The return rate of tagged cod from the TABA-COD project was 1.5% (Mion et al. 2021).

2.3 Analyses of fish movement

Due to changes in the main distribution of the Baltic Sea cod stock (Orio et al. 2019 and references therein), the spatial coverage differed by dataset (Fig. 1). The historical data contained records spanning almost the entire Baltic Sea (SDs 24-32), whereas the contemporary dataset contained records restricted to the southern Baltic Sea (SDs 24-26) where cod concentrate nowadays.

To assess seasonal differences in movement patterns, records were divided into two recapture seasons: spawning and feeding. For the historical dataset, the spawning season was defined as January to June, which includes the main spawning season and a period of migration to and from the spawning grounds (Aro 1989, Wieland et al. 2000), whereas the feeding season was defined as July to December (Aro 1989). Since the 1990s, a shift in the timing of peak spawning towards the summer has occurred (Wieland et al. 2000, Bleil & Oeberst 2004); therefore, the spawning season for the contemporary dataset was defined as April to September, while the feeding season was defined as October to March.

Average values and coefficient of variation (CV; calculated as standard deviation divided by mean) for distance travelled by cod in km (d) were estimated for each SD of release (SD_{rl}) and for each season. d was calculated as the great-circle distance (i.e., geodesic distance) between release and recapture locations using the function distm() in the package "geosphere" in R (Fig. 4). All analyses were conducted in R using the R version 4.0.2 (R Core Team 2020).

2.3.1 Kernel Density Estimation

Kernel Density Estimation (KDE) was used to describe the main distributional areas of EBC tagged in different SD_{rl}. Assuming a homogenous fishing effort, this analysis provides a visualisation of the probability of recapturing a tagged individual in a given location (Worton, 1987), conditional on the grouping factors applied (SD_{rl}, season of recapture and time period) and the constraints of the data (DAL > 30 days). All KDEs were calculated assuming a bivariate normal kernel using the kernel probability density function from the adehabitatHR package (Calenge 2015) in R. A detailed description of this approach can be found in Calenge (2015) and Griffiths (2019) and has been previous used to describe the area utilisation of Atlantic cod in the Gulf of Maine (Dean et al. 2014) and in the waters surrounding the United Kingdom (Righton et al. 2007; Neat et al. 2014). For clarity, the default 'reference bandwidth' approach was used to estimate the smoothing parameter h for each KDE. Moreover, as is common in the movement ecology literature, the 95% and 50% probability contours were extracted from each KDE and assumed to represent the population's 2-dimensional "home range" and "core area", respectively (Worton 1989, Seaman & Powell 1996, Sólmundsson et al. 2015). Home range identifies the area occupied by the majority of cod in their normal activities of spawning and feeding, and the core area identifies the most intensively used areas within an animal's home range (Burt 1943, Powell 2000).

For each SD_{rl}, KDEs were estimated separately for the EBC spawning and feeding recapture seasons. Due to possible mixing of stocks (EBC and WBC) in SD 24 and the fact that some cod released in SD 24 might belong to the WBC stock, a sensitivity analysis was conducted to estimate KDEs for the WBC spawning (i.e. December to April which includes the main spawning season and a period of migration to and from the spawning ground; Hüssy 2011) and feeding seasons (defined as May to November). This analysis showed that the estimated KDEs from the WBC feeding and spawning seasons were similar to the estimated KDEs from the EBC feeding and spawning seasons, both for historical and contemporary datasets (Fig. S3). In addition, for the contemporary data, genetic and otolith shape analyses revealed that ~ 80 % of the recaptured cod released in SD 24 belonged to the EBC stock, highlighting a higher presence of EBC in the recaptures (Hüssy et al. 2020).

The size (km^2) of the home ranges and core areas for each SD_{rl} and season were calculated in ArcMAP (v.10.4.1). In addition, in the southern Baltic Sea, the area of home range overlap (%) and core area overlap (%) between historical and contemporary datasets were also calculated for each SD_{rl}.

2.3.2 Generalized additive models (GAMs)

For the KDE analyses, records were grouped into seasons without taking into account the effects of DAL on d (e.g., cod that were at liberty for two months were considered alongside cod that were at liberty for two years). Previous studies on North Atlantic cod stocks described a linear relationship between d and DAL for some groups, while for other groups a non-linear relationship linked to seasonality was found (Rogers et al. 2014, Espeland et al. 2008). Therefore, to further explore the seasonal movement patterns of EBC, generalized additive models (GAMs), with a restricted maximum likelihood approach (Wood 2006), were applied to the relationship between *d* and *DAL*. Our prior expectation was that the relationship between *d* and *DAL* would be affected by cod release location. Thus, *d* would change according to the proximity of SD_{rl} to spawning and feeding areas (e.g., with shorter *d* for cod recaptured during the spawning period and released in an area closer to the spawning ground). $Length_{rl}$ was included as an additional explanatory variable to assess possible effects of fish size and ontogeny on *d*.

The GAM model was formulated as follows:

$$d = \alpha + s(DAL{:}SD_{rl}) + Length_{rl} + \varepsilon \qquad (2)$$

where α is the intercept, *s* is the thin plate smoothing spline function (Wood, 2003) and ε an error term. An interaction was used between the continuous variable *DAL* and the factor SD_{rl} to assess possible seasonal differences in *d* between SD_{rl}.

Due to the low number of recaptures for the contemporary dataset, the GAM was performed only with the historical dataset. To analyse the shape of the relationship between *d* and *DAL*, two separate models were fitted to data with release dates from quarter 2 (April – June; spawning period) and from quarter 4 (October – December; feeding period). Preselection of the quarter of release and treatment of *DAL* as a continuous variable allowed us to capture possible effects of seasonality (movements between spawning and feeding grounds) on *d*. A gamma distribution with a logarithmic link function was used for the GAMs because it best represented the distribution of *d*.

To improve consistency and representation of the datasets, the GAMs were fitted to restricted data. Only cod with a *DAL* between 30 and 550 days and a $Length_{rl}$ between 25 and 70 cm (n = 1,202 for cod released in quarter 2; n = 1,981 for cod released in quarter 4) were considered. To avoid taking the log of zero, all zero distances were given the value of the lowest observed distance (~1 km). All GAMs were implemented using the "mgcv" library in R (Wood 2006). Model fit was assessed by visual inspection of the residuals (see Fig. S4).

3. Results

The average *d* for cod released in the southern Baltic area (SDs 24-26) was ~80 km for both historical and contemporary datasets, and for both recapture seasons (Fig. 5). In the historical dataset, seasonal patterns in average *d* were observed. In particular, cod released in the northern and central Baltic Sea (SDs 27-32) exhibited greater *d* during the spawning season compared to the feeding season (Fig. 5; average *d* of 235 km and 135 km, respectively). In addition, for the northern areas (SDs 29 and 30) the variation in *d* was higher than in the southern SDs in both the historical and contemporary datasets (Fig. 5; Table S2).

3.1 Movement patterns in the spawning season with Kernel Density Estimation

In the historical dataset, cod released in the southern Baltic areas (SDs 24-26), were mostly recaptured in the same SD of release, however, some variation was observed (Table 1; Fig. 6). For example, core areas of cod released in SD 26 and SD 24 extended into SD 25 during the spawning season. Similarly, cod released in SD 24 had a home range during the spawning season that extended in a western direction into SD 21. Moreover, cod released in SD 25 had a home range that extended in an eastern direction into SD 26.

In the contemporary dataset, recaptures during the spawning season mostly occurred in the same SD of release (Fig. 7; Table 1). These findings are consistent with the historical dataset from the southern Baltic areas with high home range overlaps of ~ 50 % (Fig. 8; Table 2). However, some differences between the datasets occurred in the southern Baltic area. In the contemporary dataset, core areas and home ranges in SD 24 and 25 occurred in close proximity to Bornholm Island on the boundary between the two SDs (Fig. 8), while in the historical dataset the home range extended towards the western or eastern direction depending on if cod were released in SD 24 or 25, respectively. In addition, cod re-leased in SD 26 had two core spawning areas in the historical period, (SD 25 and 26) while in the contemporary dataset cod were mainly recaptured in SD 26 (Fig. 8). In the historical dataset, recaptures during the spawning season of cod released in the northern and central areas (SDs 27-32) were mainly found in SD 25 and to some extent in SD 26, or in the SD of release (Fig. 6; Table 1). One exception to this pattern occurred in SD 32, where cod were found to have core area and home range within SD 32.

3.2 Movement patterns in the feeding season with Kernel Density Estimation

In general, both home ranges and core areas during the feeding season were similar to the home ranges and core areas detected during the spawning season, irrespective of the dataset (Fig. 6 and 7; Table 2). In the historical dataset, there was a general trend of recapture close to the area of release, albeit some notable exceptions were observed. For example, cod released in SD 29 had core feeding areas that were limited to the northern Baltic, while in the spawning season a core area was also detected in the southern Baltic. Cod released in SD 26 had a core feeding area in SD 26, and an extended home range, which spanned SD 25, SD 26 and SD 28.2. During the feeding season of cod released in the southern Baltic areas, the overlap in core areas and home ranges between historical and contemporary datasets was higher than in the spawning season (Fig. 8; Table 2). This high overlap was especially true for cod released in SD 24 (home range overlap ~91 %) but less so in SDs 25 and 26 (home range overlap ~55 % and 78 %, respectively; Table 2). Visually, foraging areas appeared to be constricted in the contemporary period (Fig. 8).

3.3 Movement patterns with Generalised Additive Models

GAM models applied to the historical dataset for cod released in quarter 2 and 4 explained 15.5 % and 15.7 % of the deviance of the overall model, respectively (see Tables S3 and S4 for model summaries). For cod released in quarter 2 (spawning period) in SD 24, 26, 29 and 32, *DAL* had no significant effect on the distance between release and recapture positions, while for cod released in SD 25, 27 and 28.2 the effect was significant showing that *d* slightly increased over time and reached an asymptote (Table S3, Fig. S5). For cod released in quarter 4 (feeding period) for most of the SD_{rl} the *DAL* had a significant effect on *d* (Table S4, Fig. S6). In particular, a positive, almost linear effect of *DAL* on *d* was found for cod released in SD 25 and 29. In comparison, cod released in SD 24, 26, 27 and 28.2 displayed a positive nonlinear relationship between *DAL* and *d*, whereby *d* increased to a point but then declined to a minimum at around 300 to 350 *DAL*, and then increased thereafter (Table S4, Fig. S6). There was no significant effect of *DAL* on *d* for cod released in SD 32 (Table S4, Fig. S6).

A significant positive nearly linear effect of $Length_{rl}$ on *d* was found for cod released both in quarter 2 and 4, with cod displaying an increase in *d* with increasing body size (Tables S3 and S4, Fig. S5 and S6). Therefore, larger cod tended to be recaptured at more distant locations, whereas smaller cod tended to be recaptured closer to the point of release.

4. Discussion

The re-analysis of historical tagging data combined with contemporary data enabled the description of movement patterns and area utilisation of EBC for both time periods. In agreement with our expectations, this study has shown that in the historical period, cod released in the central and northern area of the Baltic generally travelled greater distances than cod released in the southern Baltic. Furthermore, data from the recent tagging experiment indicated that the historical movement patterns in the southern Baltic have been generally maintained over time. The results from the kernel density dstimation analysis confirmed the patterns described in previous research (Aro 1989, 2002, Bagge & Steffensen 1989, Robichaud & Rose 2004), highlighting two types of movement behaviours for EBC: sedentary (i.e. cod recaptured year-round within the area of release) and migratory (i.e. cod covering larger distances, probably linked to spawning in areas separated from the feeding grounds).

The data show that management boundaries between SD 24 and 25 are crossed all year round, both in the historical and in the contemporary period. However, this study also suggests that the percentage of cod released in SD 25 and recaptured in SD 24 has increased in the recent period. In the historical period, 6 % and 7 % of cod released in SD 25 were recaptured in SD 24 during the spawning and feeding seasons, respectively. On the other hand, in the recent period 30 % and 41 % of cod released in SD 25 were recaptured in SD 24 during the spawning and feeding seasons, respectively. These findings suggest that the use of SD 24 by EBC has increased in the recent period, an observation that supports our expectations on higher utilisation of southern areas and could result in an increased likelihood of mixing between EBC and WBC in SD 24. There can be limitations to the use of tagging data to quantify the degree of mixing in different areas and these need to be acknowledged. For instance, differences in tagging location might influence the likelihood of recapture in a different area from that of release. In fact, in the recent tagging experiment, cod in SD 25 were mainly tagged in proximity to the border with SD 24, thus potentially increasing the possibility of cod released in SD 25 being recaptured in SD 24. However, these results are in line with recent increases in the occurrence of EBC in SD 24, as estimated by shape analysis of archived otoliths (Hüssy et al. 2016). The KDE analysis results also support this finding. In the historical period, during the spawning season, core areas suggested that cod released in SDs 24 and 25 were mainly recaptured in the Arkona Basin (i.e. spawning area of WBC), and in the Bornholm Basin (i.e. main spawning area for the EBC), respectively. The bimodal core areas observed for cod released in SD 26 indicate utilisation of both the Bornholm Basin and Gdansk Deep as the main spawning areas, with cod likely moving between the two. In the contemporary period, the home ranges were similar to the historical period, although core areas of cod released in SDs 24 and 25 were concentrated around Bornholm Island (SDs 24 and 25) during the spawning season, whilst in the past, core areas concentrated mainly in the respective area of release. Since EBC currently inhabit also SD 24 (Hüssy et al. 2016), these results could add evidence that, contrary to historical assumptions (Bagge et al. 1994), EBC spawn in the Arkona Sea as shown by Hüssy et al. 2016 and Hemmer-Hansen et al. 2019.

Recaptures from the historical period indicate long distance movements from the northern and central Baltic towards the southern Baltic, which are probably linked to spawning in the Bornholm basin, (i.e. the main EBC spawning area). These movements are not observed in the contemporary dataset, as individuals appear to remain in the south. As recent tagging was only conducted in the south, no clear conclusions on changes in movement rates of EBC, or a loss of his migratory pathway to the north can be made. Thus, further work will be needed to test our hypothesis around changes in movement rates of EBC, in particular, there is a need to tag EBC in northern and central areas.

One interesting finding during the historical period is the presence of sedentary groups in the northern and central Baltic. A year-round resident population in the northern Baltic could be explained by the presence of juveniles (i.e. individuals that have not reached sexual maturity) that do not participate in a spawning migration. In fact, GAM results suggested that smaller fish tended to be recovered at locations closer to their release positions than larger cod. However, 56 % of cod that stayed in this area had a length at release that exceeded the average length at maturation (i.e. 40 cm), indicating that individuals with sedentary behaviour also included adults. In addition, fish species are thought to skip spawning when in low body condition as they may lack the necessary energetic reserves to successfully migrate or spawn (Jørgensen et al. 2006). Due to the low salinity, fertilisation of the eggs was deemed impossible in the Åland Sea and further north. Previously, it was assumed that recruitment to these northern areas took place mostly through larval drift and the passive transport of young cod at times of strong influxes of water from the south (Otterlind 1983, 1984), rather than recruitment from a local population (Hinrichsen et al. 2017). However, spawning events have previously been observed in the Åland Sea (Otterlind 1976, Vallin et al. 1999), suggesting the presence of a locally reproducing population.

Some active migration northward of young cod can probably take place, although migration of cod from the central and southern parts of the Baltic proper to the Åland Sea was negligible according to the historical tagging results. Due to biological problems (i.e., high tagging mortality of smaller fish), it was not possible to effectively tag cod smaller than 20 cm in total length, therefore, northern active migration of young cod could have been missed in the historical period. More information is needed on oceanographic processes, larval drift and possible active adult migration towards the Åland Sea to understand the possible connectivity between these areas. Preliminary results indicate that some individuals from the Åland Sea have higher successful fertilisation at lower salinities compared to cod from the Gotland and Bornholm areas (Bergström et al. unpublished). Thus, although the results of our study for the northern Baltic area are restricted to the historical period, they could contribute evidence to the presence of a sub-population of cod that remain and spawn in the Åland Sea. Preliminary genetic studies showed some level of separation, although not very distinct, of cod in this area (Bergström et al. unpublished). Further genetic studies are needed to confirm the possible presence of a resident population in the area of the Åland Sea.

For cod released in SD 32 (Gulf of Finland), home range analyses indicate a year-round spatial distinction from the home ranges of cod released in other Baltic areas. These cod are found to exhibit a sedentary behaviour and are recaptured mainly in SD 32 during both feeding and spawning seasons. However, in other studies the migration of adult cod southwards was evident and linked to spawning (Aro & Sjöblom 1983, Otterlind, 1985). These differences are likely due to the fact that in the present study tagging experiments in SD 32 were limited compared to previous evaluations. This is because the present study does not include transportation experiments of marked cod to other locations (Aro & Sjöblom 1983, Otterlind 1985). Further work to digitise additional historical records from this area would be required to examine this discrepancy.

Generalized additive models were used to account for the effect of *DAL* on the movement patterns of cod during the historical period. Different patterns were found for cod released during the spawning or feeding periods, probably linked to the proximity to spawning grounds and presence of differing behavioural strategies (i.e. sedentary and migratory). Cod released during the spawning period (quarter 2) in SDs 25, 26 and 28.2 were potentially already in proximity to EBC spawning grounds, while cod released in SD 24 were in proximity to one of the WBC spawning grounds (Bleil & Oeberst 2002). The results indicate that cod released during the spawning period in SDs 24, 26, 29 and 32 were recaptured closer to positions of release all year round. These findings suggest that these cod were sedentary, probably spawning in the area of release or not participating in a spawning migration (e.g. cod released during spawning period in SD 29). For cod released during the spawning period in SDs 25, 27 and 28.2, the distance between release and recapture positions increased through time, suggesting that cod moved away from the area of release but did not necessarily return.

Cod released during the feeding period (quarter 4) in SDs 24, 26, 27 and 28.2 showed approximately an annual pattern in the distance moved from the release. The presence of this relationship between *d* and *DAL* indicates that cod moved away from the area of release, probably to reach spawning grounds, and then returned a year later, suggesting homing behaviour to both feeding and spawning areas. Cod released in SDs 25 and 29 during the feeding period moved away from the area of release but did not appear to return.

In a true migratory population, a clear cyclical signal would be expected as individuals move away and return. This is lacking in some areas, and this could be due to the presence of different movement behaviours, as indicated by the KDE analysis of the historical dataset. Since conventional tagging data consist of only two positions, release and recapture, GAM may have low power when describing temporal cyclic patterns of migration, especially when a mix of behaviours is present (Espeland et al. 2008). Individuals that alternate between spawning and feeding seasons, as well as those that display sedentary behaviour, would obscure this pattern (Espeland et al. 2008).

Our findings, using quantitative methods to re-analyse historical tagging data combined with contemporary data, provide additional information on general movement patterns between different areas of the Baltic Sea. However, caution is advised regarding some limitations of our analysis. Unfortunately, as is the case for many historical tagging studies, there is a lack of spatially-resolved fisheries effort data. Historical catch data does show lower catches in the northern Baltic Sea compared to the south. This could have prevented a full detection of a northward migration of cod due to a lower probability of recapture in the northern Baltic Sea. In addition, if fishing effort is higher in one area (e.g. SD 24) compared to others, it might explain any lack of change in the movements of tagged cod. Further work is needed to account for spatio-temporal patterns in fishing effort within our analysis, which might result in an overrepresentation of some recapture locations (Wright et al. 2006). In addition, conventional mark-recapture data are restricted to information on release and recapture but nothing is known about movement between these two points. Application of dynamic migration models may enhance our knowledge of movements on a smaller time scale. Data-storage tags also offer an advanced method for gathering high-resolution data on demersal fish movements in both the horizontal and vertical dimension (Griffiths et al. 2018) and allow behaviour to be related to the physical environment (Patterson et al. 2009). Combining results from conventional tagging data with fine-scale movement patterns of individual cod would facilitate further study on migration and how it might be related to changes in the environment.

Failure to incorporate information on the meta-population dynamics of marine fishes in fishery management risks the depletion of local sub-populations that may eventually contribute to stock collapse (Hilborn et al. 2003; Kritzer & Sale 2004; Heath et al. 2008, Neat et al. 2014). Our study suggests that possible meta-populations in the Baltic Sea (e.g. northern and southern Baltic cod) may have existed in the historical period with individuals experiencing different patterns of movement. This means that cod from different areas of the Baltic may have experienced different salinity, oxygen and temperature conditions (Mion et al., 2021). The applied implications of this are that the removal of individuals in one area could be more costly than in other areas, therefore a spatial adjustment of exploitation strategies, such as the setting of a maximum sustainable yield for each spatial unit, may be required to ensure sustainable harvesting (Holmes et al. 2014). Future management of fisheries, especially where meta-populations exist or where mixing between different stocks occur, should implement the use of tagging data in area-based assessment models (e.g. Stock Synthesis; Methot & Wetzel, 2013) to provide a more reliable estimation of stock status.

Our results show that re-analysing historical conventional tagging data can still provide important insights on movement patterns and area utilisation that can be readily compared with contemporary data. In doing so, the biological knowledge of a stock, or multiple stocks, is increased, which could inform future management actions.

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Figures

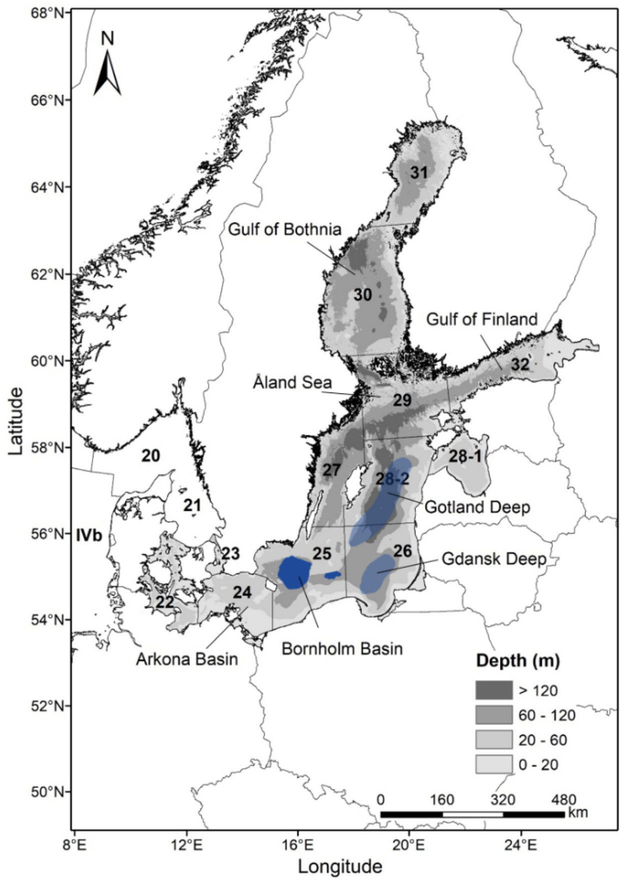

Figure 1. Map of the Baltic Sea with ICES subdivisions. The former spawning grounds of the Gotland Deep and Gdansk Deep are shaded in blue, while the active spawning ground of the Bornholm Basin is marked in blue (Modified after Cardinale and Svedäng, 2011).

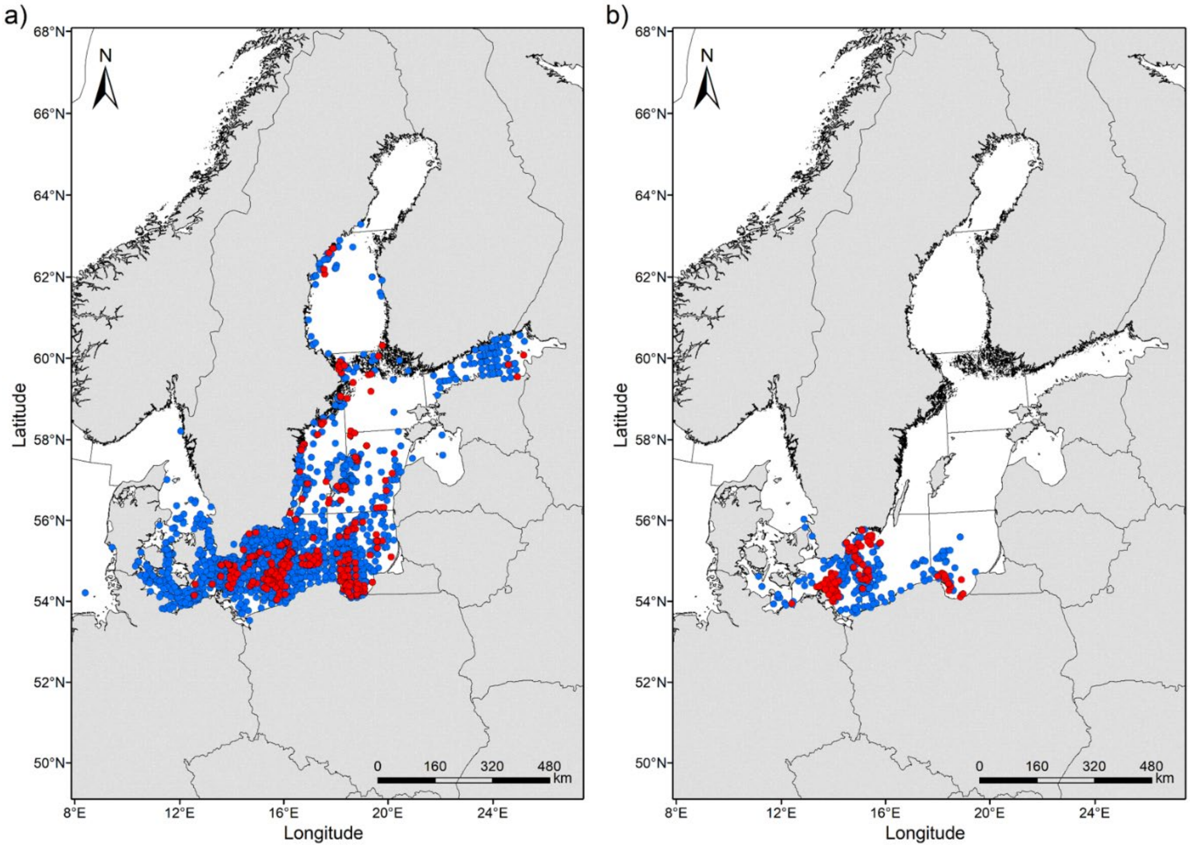

Figure 2. Map of the Baltic Sea with release positions (red dots) and recapture positions (blue dots) for the historical (a) and the contemporary tagging experiments (b). See Figure 1 for a map of the Baltic Sea with ICES subdivisions.

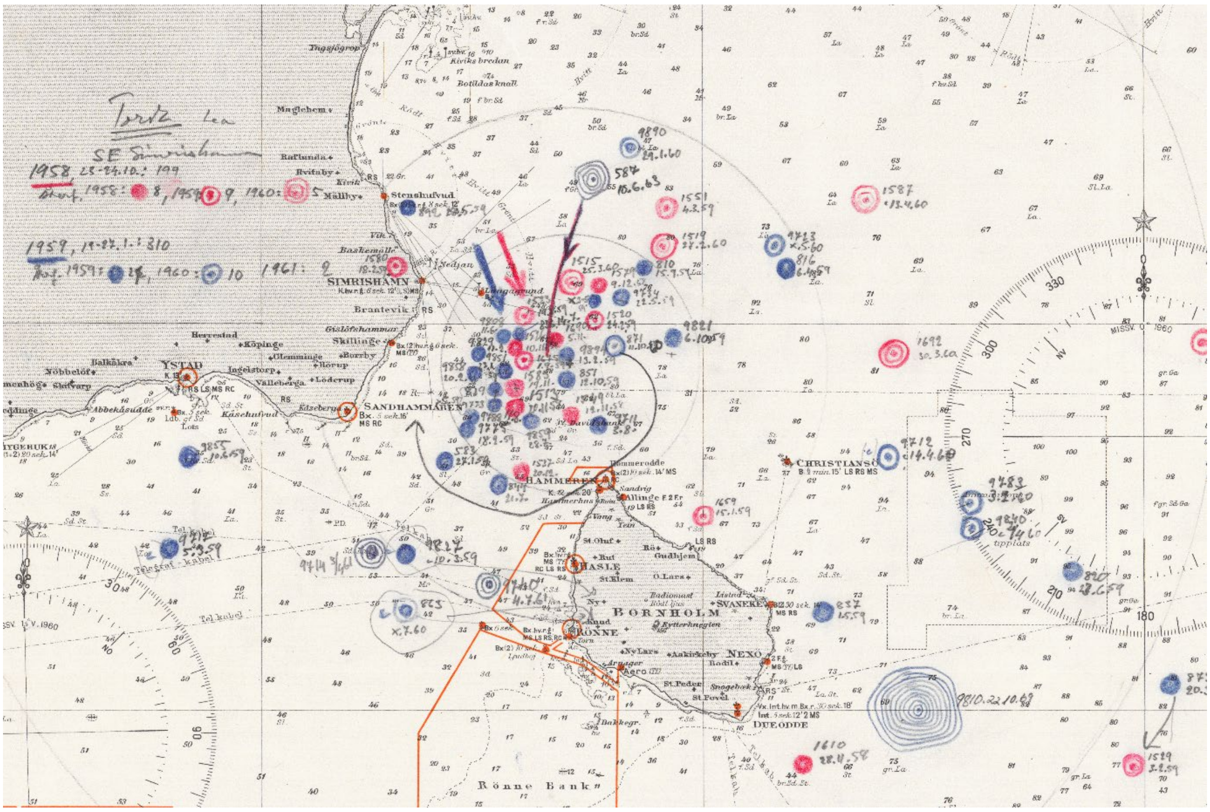

Figure 3. Example of an historical map visualising Swedish tagging experiments carried out in 1958 (red) and 1959 (blue) in the Baltic Sea (nearby Bornholm Island). Arrows indicate the release and dots the recapture locations of cod. Filled dots represent cod that were recaptured within a year of release, while additional years (>1) from release are represented as circles surrounding a recapture location. For example, in the bottom right of the map, a cod is recaptured after 10 years and its recapture location is illustrated as a blue dot surrounded by nine circles.

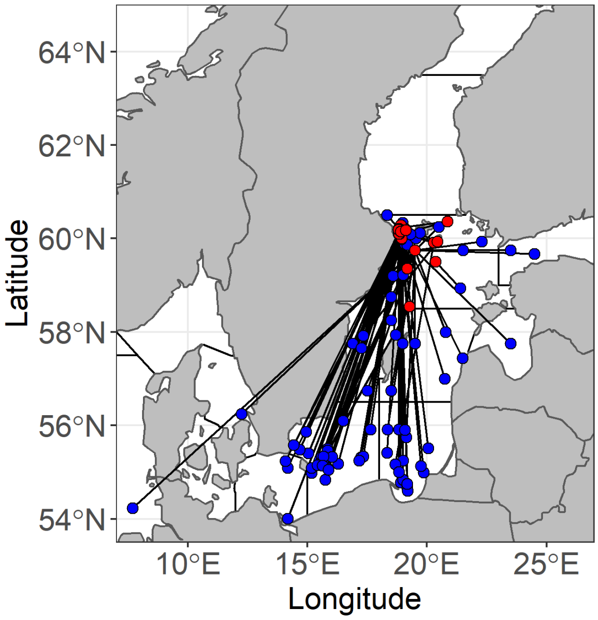

Figure 4. Example of straight-line trajectories (black lines) between release (red dots) and recapture (blue dots) positions for fish released in SD 29 (Åland Sea) during the historical tagging experiments.

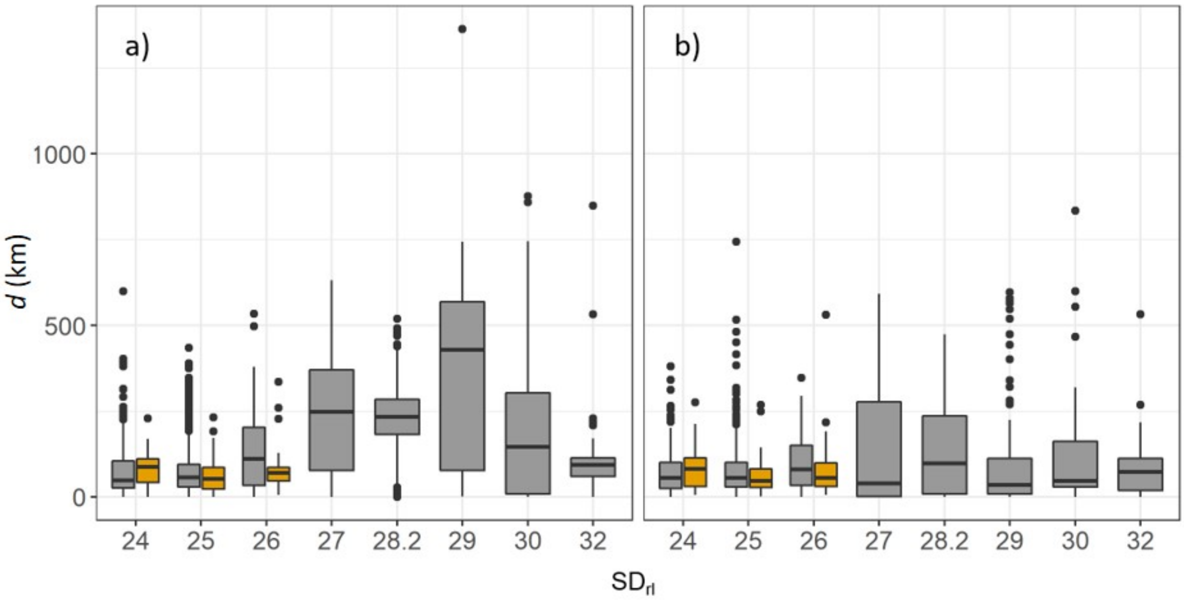

Figure 5. Box plots of the distance between release and recapture (*d*) during spawning (a) and feeding (b) seasons by subdivision of release (SD_{rl}) for the historical (grey) and contemporary (orange) periods. Spawning and feeding seasons are assigned based on recapture time. Thick line: median; box: 25th and 75th percentiles; whiskers: 1.5 times the interquartile range; black dots: outliers).

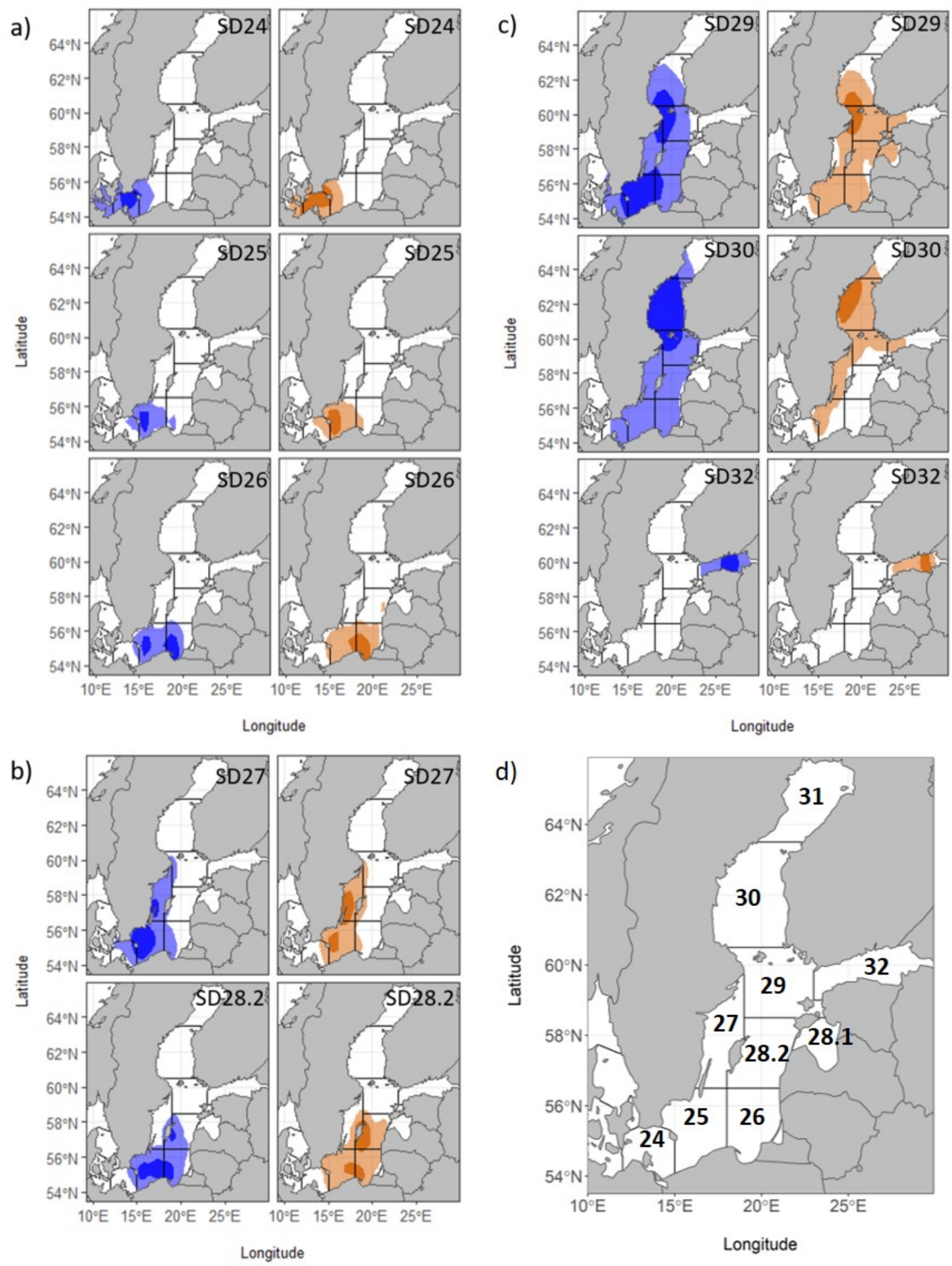

Figure 6. Maps showing the 95% kernel home ranges (shaded colour) and 50% kernel core areas (bold colour) for each subdivision (SD) of release written on the top right corner of each map in the southern (a), central (b) and northern (c) Baltic areas for the historical dataset. d) Map of the Baltic Sea with ICES subdivisions. Data shown are for cod recaptured during the spawning season (January to June; blue, left panels) and the feeding season (July to December; orange, right panels).

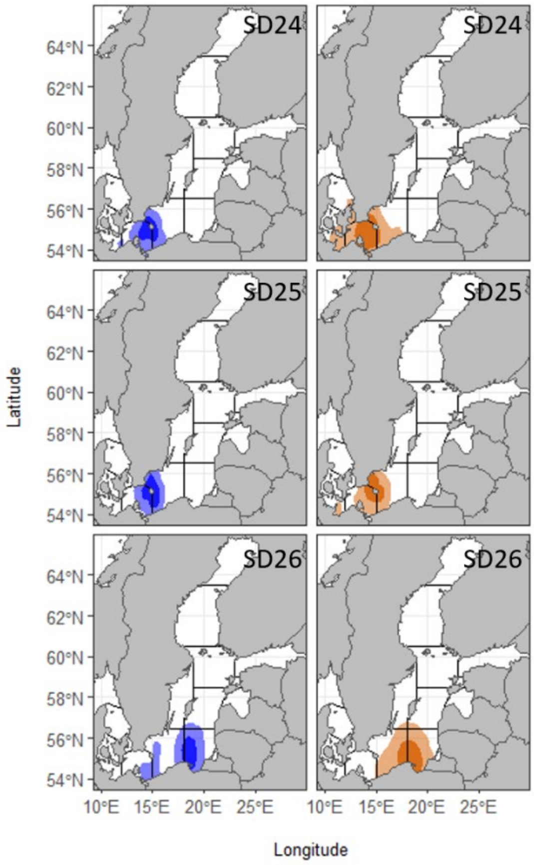

Figure 7. a) Maps showing the 95% kernel home ranges (shaded colour) and 50% kernel core areas (bold colour) for each subdivision (SD) of release written on the top right corner of each map for the contemporary dataset. Data shown are for cod recaptured during the spawning season (April to September; blue, left panels) and the feeding season (October to March; orange, right panels). See Figure 6d for a map of the Baltic Sea with ICES subdivisions.

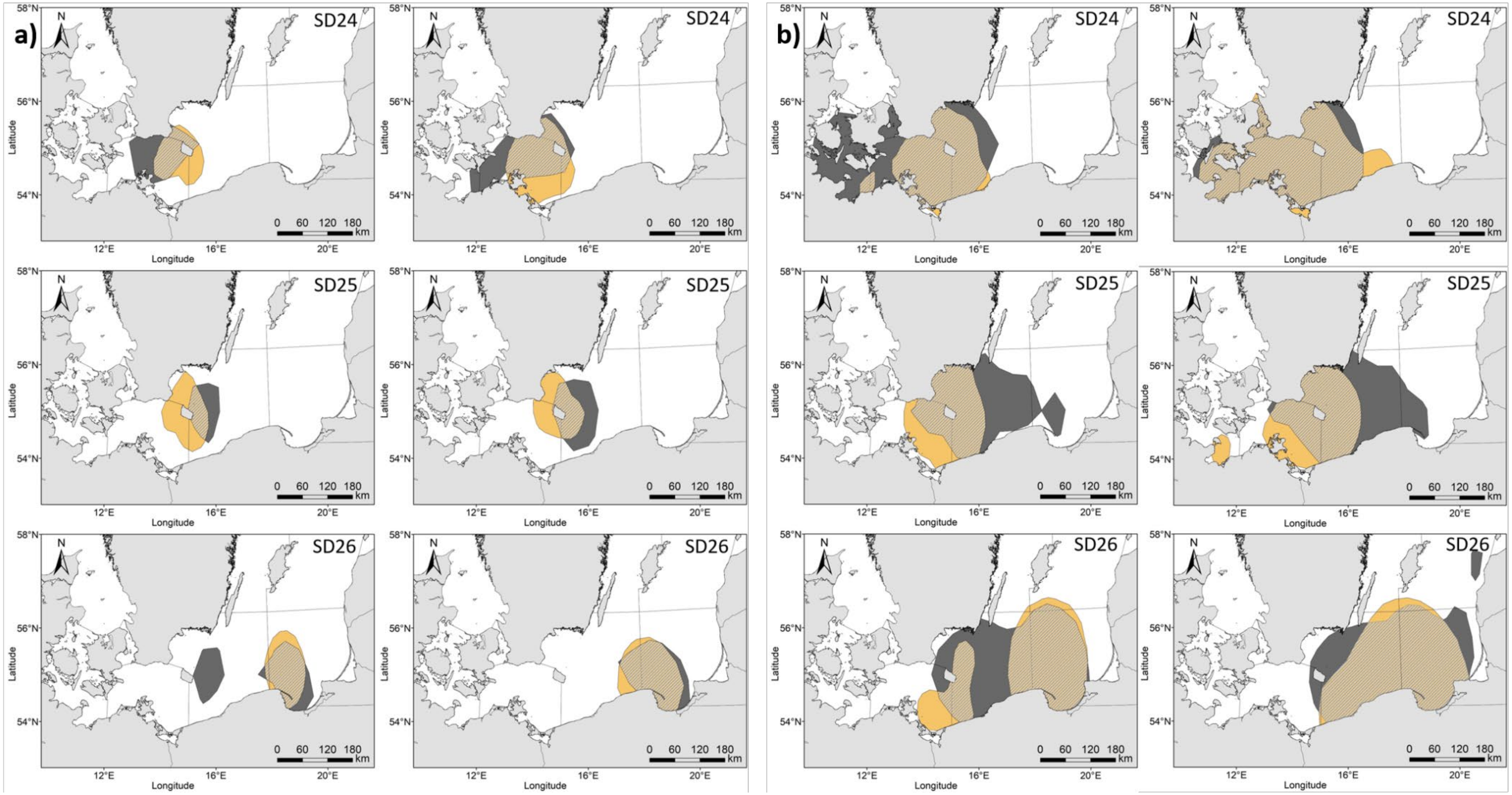

Figure 8. Overlap between the historical (grey) and contemporary (orange) data for cod recaptured during the spawning season (left panels) and the feeding season (right panels). The 50% kernel core areas are shown in panel (a) and the 95% kernel home ranges are shown in panel (b) for cod tagged in subdivision (SD; written in bold) 24, 25 and 26. See Figure 6d for a map of the Baltic Sea with ICES subdivisions.

Table 1. Percentage and total number (in brackets) of cod recaptured by subdivision of release (SD_{rl}) and subdivision of recapture (SD_{rc}) during the spawning and feeding seasons for the historical and contemporary (Contemp) datasets. Percentage and total number of recaptures in the same SD_{rl} are in bold.

a)		Spawning													
		SDrc													
Dataset	*SDr*l	IVb	20	21	22	23	24	25	26	27	28	29	30	31	32
Historical	24	0.1 (1)	1.5 (11)		16.1 (119)	1.4 (10)	**61.6 (458)**	18.4 (137)	0.5 (4)		0.4 (3)				
	25		0.3 (6)		1.0 (18)	0.2 (4)	6.0 (111)	**87.6 (1622)**	4.7 (86)	0.1 (1)	0.2 (3)				
	26				0.3 (2)		2. 9 (21)	43.6 (317)	**52.4 (381)**	0.1 (1)	0.7 (5)				
	27		0.5 (1)		0.5 (1)	0.5 (1)	3.6 (8)	63.4 (140)	4.1 (9)	**27.2 (60)**		0.5 (1)			
	28					0.1 (1)	1.4 (11)	52.9 (427)	27.2 (220)	0.4 (3)	**18.1 (146)**				
	29	1.0 (1)	1.0 (1)				3.03 (3)	32.3 (32)	13.11 (13)	8.1 (8)	9.1 (9)	**32.4 (32)**			
	30							9.1 (2)	9.1 (2)	4.6 (1)		22.7 (5)	**54.6 (12)**		
	32							2.5(4)	2.47 (4)						**95.1 (154)**
Contemp.	24				2.1 (2)		**54.3 (51)**	43.7 (41)							
	25					1.9 (1)	29.6 (16)	**66.7 (36)**	1.9 (1)						
	26						4 (1)	20 (5)	**76 (19)**						

b)		Feeding													
		SDrc													
Dateset	*SDrl*	IVb	20	21	22	23	24	25	26	27	28	29	30	31	32
Historical	24	0.3 (1)	1.2 (4)		13.2 (43)	2.8 (9)	**54.8 (178)**	26.5 (86)	1.2 (4)						
	25		0.3 (2)		0.4 (3)	0.1 (1)	7.0 (50)	**85.8 (609)**	5.1 (35)	0.7 (5)	0.6 (4)		0.1 (1)		
	26						0.7 (2)	33.5 (90)	**61.0 (164)**		4.9 (18)				
	27				0.5 (1)		0.5 (1)	34.6 (72)	1.4 (3)	**61.1 (127)**	1.0 (2)	1.0 (2)			
	28							27.5 (101)	16.6 (61)	1.6 (6)	**54.2 (199)**				
	29							7.4 (5)	7.4 (5)	2.9 (2)	4.4 (3)	**73.5 (50)**	1.5 (1)		2.9 (2)
	30							2.2 (1)		4.4 (2)		8.9 (4)	**80.0 (36)**	2.2 (1)	2.2 (1)
	32								1.7 (3)		0.6 (1)				**97.7 (169)**
Contemp.	24			3.7 (2)	9.3 (5)		**63.0 (34)**	24.0 (13)							
	25				4.5 (2)		40.9 (18)	**54.5 (24)**							
	26				3.3 (1)			30.0 (9)	**66.7 (20)**						

Table 2. 95% kernel density estimation (KDE) home ranges (x1000 km^2) and 50% KDE core areas (x1000 km^2) for the historical and contemporary datasets during the spawning and feeding seasons by subdivision of release (SD_{rl}). Spatial overlap between historical and contemporary data is reported in %.

KDE 50 %					
Season	SD_{rl}	Historical (km^2)	Contemporary (km^2)	Overlap (km^2)	Historical overlaps Contemporary %
Spawning	24	12.7	11.4	6.9	54.4
	25	7.8	13.1	3.8	48.5
	26	19.4	12.8	10.2	52.5
	27	31.4			
	28	29.2			
	29	93.5			
	30	78.5			
	32	12			
Feeding	24	21.7	20.9	13.8	63.5
	25	13.5	12.6	6.2	45.9
	26	18	18.3	15.9	88.0
	27	21.9			
	28	25.5			
	29	21.7			
	30	24.6			
	32	7.1			
KDE 95 %					
Season	SD_{rl}	Historical (km^2)	Contemporary (km^2)	Overlap (km^2)	Historical overlaps Contemporary %
Spawning	24	61.6	35.5	34.6	56.2
	25	48.4	32.8	24.6	50.7
	26	69.6	55	45.8	65.8
	27	94.9			
	28	88.7			
	29	240.3			
	30	264.9			
	32	28.2			
Feeding	24	57.8	57.8	52.4	90.6
	25	56	40.5	30.9	55.2
	26	75.9	62.6	58.8	77.5
	27	77.7			
	28	113.2			
	29	200.1			
	30	113.8			
	32	21.1			