Examining fish movement in terms of advection or diffusion: a case study of northeastern Atlantic cod

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Application of advection and diffusion to examine movement in fish: A case study of north-eastern Atlantic cod

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Abstract

Advection (directional movement) and diffusion (dispersed movement) were applied for the first time to describe movement patterns in Atlantic cod in the North Sea and Baltic Sea between 1955 and 2020. The advection-diffusion approach provided more detailed estimates of movement that corresponded to previously observed patterns using different analytical techniques. Spatial patterns were evident with greater movement distances in cod from the North Sea and eastern Baltic Sea compared to the western Baltic and Kattegat-Skagerrak. Furthermore, comparative case studies on different ecotypes in the western and eastern Baltic suggested that inshore cod were more resident compared to offshore cod. This preliminary study highlights the usefulness of the advection-diffusion method to describe movements in fish populations and can be further expanded by incorporating information on environment and mortality and providing information to spatially explicit population models.

Key words: Atlantic cod, movement, advection-diffusion, mark-recapture, Baltic Sea, North Sea

1. Introduction

The north Atlantic cod (*Gadus morhua*) is a commercially important fish species found across the Atlantic Ocean. It is one of the most heavily fished species which has led to several populations collapsing. In the north-eastern Atlantic, the Atlantic cod can be found from the North Sea to the Baltic Sea and the Barents Sea. The North Sea, located between Great Britain and the western coast of Europe, connects to the Baltic Sea through the straits Skagerrak and Kattegat. For management purposes, these adjacent seas are divided into units known as International Council for the Exploration of the Sea (ICES) subareas, divisions, and subdivisions (SD; **Figure 1**), and the populations are managed as the following stocks: the North Sea stock (Division 4.a-c, 7.d, SD 20), the Kattegat stock (SD 21), the western Baltic stock (SD 22-24), and the eastern Baltic stock (SD 24-32). All ICES units are collectively referred to as ICES areas henceforth.

Declining cod stock sizes in the North Sea and Baltic Sea have been a great concern since the 1970s and 1980s, respectively. This is particularly evident in the North Sea where the cod stock is currently at similar levels as after the collapse in the early 2000s (Huserbråten et al. 2018). In the southern North Sea, the cod is virtually absent due to historically high fishing pressure and continued low recruitment. In the nearby Kattegat, the stock was at a historically low spawning stock biomass (SSB) level in 2020, and ICES currently advises zero catch only (ICES 2021a). In the Baltic Sea, the western Baltic cod stock has experienced low recruitment since the mid-2000s (ICES 2021b). In addition, the eastern Baltic cod stock is in a poor state, partially due to high fishing pressure, low recruitment, and slow growth (Eero et al. 2015, Orio et al. 2019).

Several factors may have affected the movement patterns in Atlantic cod stocks, such as changes in stock sizes due to density-dependent behaviour (Fretwell 1969) although cannibalism also plays a role (Neuenfeldt and Köster 2000). As stock sizes increase, density dependent behaviour may cause individuals to adjust their spatial distribution to avoid high density patches as has previously been observed in spawning eastern Baltic cod (Baranova 1995). In contrast, reduction in stock sizes has been linked to range contractions. This has previously been observed in capelin (*Mallotus villosus*, Ingvaldsen and Gjøsæter 2013) and pike (*Esox lucius*, Haugen et al. 2006). Furthermore, changes in the environment, such as an increase in hypoxic areas in the past decades in the Baltic Sea (Casini et al. 2016), could potentially have affected movement patterns as well as cod move to more oxygen-rich areas. Additionally, movement may also be variable across stocks due to the presence of two distinct ecotypes of Atlantic cod: more resident inshore and more migratory offshore cod (e.g., see Lear and Green 1984, Robichaud and Rose 2004, Karlsen et al. 2013) and both types can occur in the same area (e.g., Knutsen et al. 2018).

Movement patterns of cod in the North Sea and Baltic Sea have been studied using mark-recapture data (e.g., see Otterlind 1985, Aro 1989, Bagge and Steffensen 1989, Bagge and Thurow 1994, Wright et al. 2006a, Righton et al. 2007, Mion et al. in press). The majority of this data, in addition to Danish mark-recapture data from the western Baltic Sea, Sound, and Kattegat, has recently been compiled into a joint database in the Baltic Sea (Mion et al. 2020, 2021). Despite the limitations of mark-recapture data, as only the release and recapture location are known, historical mark-recapture studies offer a good opportunity to study temporal movement patterns due to the quantity of data available, making it possible to discern general movement patterns and changes through time.

Numerous methods have been used to analyse mark-recapture data in the North Sea and Baltic Sea, including plotting recaptures (Otterlind 1985), employing kernel density distributions (Mion et al. in press, Righton et al. 2007) and generalised additive models (GAMs; Mion et al. in press, Espeland et al. 2008), as well as calculating metrics of movement (Righton et al. 2007). Occasionally, ancillary information such as that provided by otolith microchemistry (Wright et al. 2006b, Svedäng et al. 2010) or genetics (Heath et al. 2014, Hemmer-Hansen et al. 2020) have also been used in combination with tagging data to disentangle sub-population stock structuring (e.g., Zemeckis et al. 2014, ICES 2020c). These methods often provide insight on movement behaviour and spatial distribution patterns, but do not provide mathematical links between individual-level movements and population-level patterns. A mathematical approach to assessing movement is the concepts of advection (biased movement) and diffusion (dispersal). When applied to populations, they describe the average movement of a population within a selected time frame and coordinate system and to what extent average movement is directed or appears to be random. For instance, a high advection in one direction indicates the population has an overall tendency to move in this direction, while a high diffusion would indicate the population is characterized by random movement. Together, advection and diffusion can offer a dynamic approach to study movement in tagged fish in space and time and have previously been applied to skipjack tuna (*Katsuwonus pelamis*; Sibert et al. 1999, Faugeras and Maury 2005). To the authors' knowledge, however, this approach has not been applied to Atlantic cod.

The main aim of this study was to gain preliminary insights into overall movement patterns in Atlantic cod in the North Sea and Baltic Sea based on mark-recapture data from 1955 to 2020 by applying the advection-diffusion approach and to test the applicability of this approach to reproduce movement patterns obtained by other methods, such as the kernel density distribution analyses done by Mion et al. (in press) which also addressed seasonality in movements. Specifically, the objectives of this study were to compare spatial and temporal patterns in advection and diffusion of Atlantic cod between the North Sea, Kattegat-Skagerrak, western Baltic, and eastern Baltic. Additionally, we examined if movement distances were higher in offshore ecotypes in comparison to inshore ecotypes in the eastern and western Baltic Sea.

2. Methods

2.1 Data overview

Mark-recapture data from Danish tagging projects in the North Sea and Baltic Sea (n = 7,962) were digitised and incorporated into a database containing mark-recapture data collected between 1955 and 2020 from several countries (Mion et al. 2020, 2021), including Denmark (n = 325), Sweden (n = 4,796), Poland (n = 1,794), Latvia (n = 113), Germany (n = 910), Finland (n = 403), and the United Kingdom (n = 5,361). This also included the more recent tagging projects CODYSSEY (Cod spatial dynamics and vertical movements in European waters and implications for fishery management; Righton et al. 2009) and TABACOD (Tagging Baltic Cod; Hüssy et al. 2020) (n = 21,664 in total). Archival tagging data from CODYSSEY and TABACOD were also included but made up <1% of the overall data. The database included detailed information on release and recapture locations and dates, and biological information such as total length (mm) and weight (g). Recaptures were only considered if release and recapture locations and dates were known. Recaptures ≤15 days after release were excluded to allow for post-tagging recovery of neutral buoyancy (van der Kooij et al. 2007) and resumption of normal behaviour as cod live at depth. In total, 4,295 recaptures were excluded resulting in a dataset of 17,369 recaptures for this study.

All Atlantic cod were tagged and released within the distribution areas of the North Sea stock (ICES area 4.a, 4.b, 4.c, 20), the Kattegat stock (ICES area 21), the western Baltic stock (ICES area 22-24), and the eastern Baltic stock (ICES area 24-32, except 28.1 and 31) (see **Figure 1** for ICES areas and figure text for important local area names), and the most common tag types were Lea, alcathene, and t-bars. Information on total release numbers was not available due to a lack of available information within the historical part of the database.

All recaptures were grouped by release ICES areas. Skagerrak (ICES area 20) was grouped with Kattegat (ICES area 21) due to low recapture coverage in Skagerrak (n = 4) and all release locations being on the edge of Kattegat. Henceforth, cod tagged within this area will collectively be referred to as Kattegat-Skagerrak. Overall differences between ICES areas were first considered for all data collected within each ICES area, and the data was further grouped by recapture decades (<1960, 1960-1970, 1971-1980, 1981-1999, 2000-2020) to determine temporal differences within and between ICES areas. Due to low recaptures in all areas in the 1990s (n = 71) and 2000s (n = 256), 1981-1999 and 2000-2020 were grouped to span two decades. Note that recaptures were unavailable for some years (1991-1993, 1997, 1998, 2008, 2009, 2012, 2014). For analyses of seasonal movements, we refer to Mion et al. (in press).

2.2 Analysis of movement

Assuming individuals move independently of each other, the direction-driven (anisotropic) movement from the release point was illustrated using advection (mean movement vector), $\hat{\alpha}$, and estimated for each release ICES area by (Nielsen 2004):

$$\hat{\alpha} = \left(\frac{\sum \Delta x}{\sum \Delta t}, \frac{\sum \Delta y}{\sum \Delta t}\right)' \quad (1)$$

and assuming non-directional movement is the same in every direction (isotropic) from the release point, the isotropic diffusion coefficient, $\widehat{D}$, was estimated by (Nielsen 2004):

$$\widehat{D} = \frac{1}{4(n-1)}\left(\sum\left(\frac{\Delta x^2}{\Delta t}\right) - \frac{(\sum \Delta x)^2}{\sum \Delta t} + \sum\left(\frac{\Delta y^2}{\Delta t}\right) - \frac{(\sum \Delta y)^2}{\sum \Delta t}\right) \quad (2)$$

where Δx and Δy denote the difference between release and recapture coordinates (longitude and latitude) converted to a geodesic distance (kilometres), Δt the difference between release and recapture time, and n the number of fish. To visualise the directed movements for each area, the advection was used to calculate a vector angle and distance, and the time frame was scaled to per half year by multiplying with 365/2 to see large-scale trends. The advection thus describes movement through mean changes in kilometres between release and recapture per half year for the large-scale study that included all ICES areas. Similarly, diffusion (the variance) describes mean changes in distance from the point of release over $\sqrt{½\ year}$ for the large-scale study, respectively, and gives a relative indication of the degree of dispersal. To visualise the dispersal for each area, circles were used, and the radius was determined by the diffusion coefficient multiplied by 365/2.

To account for statistical uncertainty and assign a measure of accuracy to the observed patterns, each ICES area group was bootstrapped to create new datasets (n = 10,000) by randomly sampling the original dataset for the respective ICES area group and allowing duplicate data entries. These new datasets were used to calculate bootstrapped $\hat{\alpha}$ and $\widehat{D}$ values to use as confidence intervals to determine the stability of the $\hat{\alpha}$ and $\widehat{D}$ estimates from the raw data for each release ICES area group. Subsets per ICES area per decade with less than 30 recaptures were ignored for the bootstrap accuracy analyses due to low sample size.

2.3 Movement patterns in offshore and inshore ecotypes

In the western Baltic Sea, stock components in the Aabenraa Fjord and southern Belt Sea (SBS) were chosen to represent inshore and offshore ecotypes, respectively, based on the proximity to land (**Figure 1**). Aabenraa Fjord is a short fjord located in the western part of the Baltic Sea and is constrained by land. In comparison, the southern Belt Sea is one of the more offshore areas in the western Baltic. This group included all releases south of Bagenkop (see **Figure 1** for locations).

Stock components in the eastern Baltic (the Gulf of Finland and south-eastern Baltic Sea (SEBS)) were similarly chosen to represent inshore and offshore ecotypes, respectively. The Gulf of Finland is a large inlet located in the easternmost Baltic Sea and is relatively constrained by land. This ecotype group included all releases in ICES area 32 (**Figure 1**). In contrast, the south-eastern Baltic Sea is an offshore area, and this group included all releases in ICES area 26 (**Figure 1**).

The ecotype case studies were treated and analysed similarly as the large-scale case study (see previous section). To compare overall movement distances between ecotypes (offshore and inshore) in the eastern and western Baltic, distance travelled per month (km month^{-1}) was assessed as a complementary analysis to the advection-diffusion methodology to illustrate pattern detection at even small time scales. Distance travelled per month was calculated as the geodesic distance between release and recapture location to account for the slight curvature of the Earth which was then divided by days at liberty and multiplied by 30.

Distance per month between inshore and offshore ecotypes was compared using a pairwise bootstrap test on the median differences. The median was chosen as the test metric due to its robustness to outliers. For each group comparison (Aabenraa Fjord vs. SBS, Gulf of Finland vs. SEBS), the groups were combined into one dataset which was used to construct two new datasets through sampling with replacement. The datasets would then represent the inshore and offshore group, respectively, and be of the same size as the original datasets. The median difference was calculated by subtracting the distance per month median for the inshore population from the offshore population. This was repeated 100,000 times to compare to the true median difference between the ecotypes. If the ecotypes were statistically similar, the true median difference would be expected to fall within the bootstrapped distribution. However, if the ecotypes were different, the true median difference would be expected to fall outside the bootstrapped distribution.

Finally, a pairwise bootstrap test was performed to test for temporal differences within the areas based on recapture decade (Aabenraa Fjord = 1950s vs. 1960s; SBS = 1950s vs. 1960s; Gulf of Finland = 1970s vs. 1980s; SEBS = 1950 vs. 1960s vs. 1970s vs. 2010s). The median difference was calculated by subtracting the distance per month median for the oldest decade from the youngest. The results of the tests were subsequently compared to recapture lengths and months to check for biases. Subsets per ecotype group per decade with less than 30 recaptures were ignored for the bootstrap analyses due to low sample size.

All analyses were done in R version 4.0.2 (R Core Team 2020). The packages *sp* (Pebesma and Bivand 2005), *rgeos* (Bivand and Rundel 2020), and *rgdal* (Bivand et al. 2020) were used to create the maps, and *beanplot* (Kampstra 2008) was used for the beanplots. The R script utilized for the analyses is available upon request.

3. Results

3.1 Data overview

Cod were both released and recaptured in different months across the years (**Table S1**) indicating both spawning and feeding seasonal movements were represented. However, release numbers were lower for June-September and recapture numbers slightly lower for August-December compared to the rest of the year (**Table S1**). In the case of recaptures, this is likely due to differences in fishing pressure. The number of recaptures was variable among ICES areas (**Figure S1**). Most areas were well represented across decades although the northern North Sea (ICES area 4.a) and northern Baltic Sea (ICES areas 29, 30, 32) were mainly represented by few recaptures across one or two decades. Most releases were recaptured within the same decade. Days at liberty were similarly variable for each release area (**Figure S2**) with most cod being recaptured within the first 100 days after release.

In general, release and recapture lengths across the four stocks were similar with a median total length around 400 mm and 450 mm, respectively (**Figure S3**), with the largest sizes observed in the North Sea.

3.2 Analysis of movement

3.2.1 The North Sea (ICES areas 4.a-c)

The overall advection was low in the northern North Sea (ICES area 4.a) but increased towards the southern part of the North Sea (**Figure 2**). The overall diffusion patterns in the North Sea were much stronger than the adjacent ICES areas (**Figure 3**) and comparable to those observed in the eastern Baltic. Across decades, the advection was strong and towards the north in the central and southern North Sea (ICES area 4.b and 4.c, respectively), although the advection was relatively low in the central North Sea in 1971-1980 (**Figure 4a, c**). Diffusion patterns were variable but generally high in both the central and southern North Sea (**Figure 4b, d**). No decadal comparison was possible for the northern North Sea. The bootstrap accuracy analyses generally showed relatively stable estimates aside from the southern North Sea in the 2000s (**Figure 4c, d**).

Overall, the patterns suggest high degrees of movement in a northerly direction in the central and southern North Sea with some decadal variation. In contrast, the patterns suggest a relatively high degree of movement in the northern North Sea but with no clear direction (see **Table S2-3** for the advection and diffusion values).

3.2.2 The Kattegat-Skagerrak (ICES areas 20-21)

Kattegat-Skagerrak exhibited very low overall advection towards the north (**Figure 2**) and no strong historical changes in direction, although advection was slightly greater in 1971-1980 (**Figure 4e**). While the overall diffusion was relatively low (**Figure 3**), decadal variation could be observed, with greater diffusion in 1981-1999 compared to 1971-1980 (**Figure 4f**). While the advection estimates were generally characterized by low uncertainty, the diffusion was characterized by wide confidence intervals (**Figure 4f**). The observed patterns suggest a historical high degree of residency in the Kattegat-Skagerrak (see **Table S2-3** for the advection and diffusion values).

3.2.3 The Western Baltic Sea (ICES areas 22-24)

Advection and diffusion in the western Baltic were relatively low overall but with some decadal variation (**Figure 2, 3, 5**). In the Belt Sea (ICES area 22) the direction of the advection was generally between north and east, and increased north-eastern advection and greater diffusion were observed in 1960-1970 (**Figure 5a, b**). The Sound (ICES area 23) similarly exhibited low advection in earlier years, increasing slightly towards southern Kattegat in 1981-1999 (**Figure 5c**). High degrees of variation in diffusion were observed among decades, with the highest observed in 1981-1999 and 1960-1970 (**Figure 5d**). The Arkona Sea (ICES area 24) was characterized by low advection in opposing directions between 1960-1970 and 1971-1980 and a sharp increase in 2000-2020 towards Bornholm (**Figure 5e**). The extent of diffusion did not change with time (**Figure 5f**). The bootstrap accuracy analyses showed relatively low degrees of accuracy in the Sound and Arkona Basin (**Figure 5c-f**), although the direction of the advection was relatively stable.

Overall patterns in the western Baltic suggest a relatively low degree of movement with a higher degree of movement towards the southern Kattegat since the 1970s (see **Table S2-3** for the advection and diffusion values).

3.2.4 The Eastern Baltic Sea (ICES areas 25-32)

The eastern Baltic Sea generally exhibited high rates of advection and diffusion in the northern part compared to slightly lower rates in the Gulf of Finland (ICES area 32) and central Baltic (ICES areas 25-26; **Figure 2, 3, 6-7**). The Bornholm Sea (ICES area 25) was characterized by overall low advection in variable directions towards west and east over time (**Figure 6a**). Diffusion was relatively high but in the lower end for the eastern Baltic Sea, with a general decadal decrease in diffusion rates (**Figure 6b**). In comparison, SEBS (ICES area 26) had strong overall advection west towards the Bornholm Sea and high diffusion, with highest rates observed <1960 (**Figure 6c, d**). The Western Gotland Basin (ICES area 27) exhibited very strong advection in a southerly direction towards the southern Baltic and similarly strong diffusion in 1960-1970 (**Figure 2-3**). However, due to low recaptures in other decades, a temporal comparison was not possible. The estimates were relatively accurate although the strength of the advection was slightly less certain, particularly in SEBS (**Figure 6c-d**).

The Gotland Sea (ICES area 28.2) similarly showed strong advection towards the southern Baltic in 1960-1970 and 1971-1980 (**Figure 6e**). Diffusion was high across both decades but more similar to the patterns in the southern Baltic than the northern Baltic (**Figure 6f**). Comparable patterns were observed in the Archipelago Sea (ICES area 29) with very strong advection towards the southern Baltic across all decades although lower in 1960-1970 compared to <1960 and 1981-1999 (**Figure 7a**). A high degree of diffusion was observed, with the lowest observed in 1960-1970 (**Figure 7b**). The Bothnian Sea (ICES area 30) also exhibited strong advection towards the southern Baltic in 1981-1999 (**Figure 2**). Diffusion was very high albeit with relatively wide 95% confidence intervals (**Figure 3**), indicating a high degree of uncertainty. However, due to low recaptures in other decades, no temporal comparison was possible for this area either. The Gulf of Finland (ICES area 32) showed low advection towards the north-west, with slightly higher advection in 1971-1980 compared to 1981-1999 (**Figure 7c**). Diffusion was greatly variable and was much higher in 1971-1980 compared to 1981-1999 (**Figure 7d**). While the bootstrap accuracy analyses showed fairly stable estimates in the Gotland Sea and Gulf of Finland (**Figure 6e, f, 7c, d**), the Archipelago Sea was characterized by high uncertainty (**Figure 7a, b**).

Overall patterns in the eastern Baltic Sea suggest high degrees of movement from the northern part towards the southern Baltic. The decadal patterns suggest generally higher degrees of movement before 1980s compared to more recent decades. In comparison, movement in the Gulf of Finland and east and south of Gotland appear to be lower but still higher or similar to the western Baltic Sea (see **Table S2-3** for the advection and diffusion values).

3.3 Movement patterns in inshore and offshore ecotypes

3.3.1 Western Baltic - Aabenraa Fjord vs. southern Belt Sea (SBS)

Ecotypes in Aabenraa Fjord (inshore) and SBS (offshore) exhibited different movement patterns and both methodologies produced similar results with relatively accurate estimates (**Figure 8a, b, 9**). While most cod in both areas swam less than 10 km month^{-1} (**Figure 9**), movement distances greater than 10 km month^{-1} were more common in offshore cod in SBS compared to inshore cod in Aabenraa Fjord, suggesting more resident behaviour in Aabenraa Fjord. The advection and diffusion (**Table S4**), and distance medians suggested similar patterns (0.67 km month^{-1} and 7.32 km month^{-1} for Aabenraa Fjord and SBS, respectively).

The bootstrap test on the median differences between Aabenraa Fjord and SBS supported this difference in behaviour as the true difference between the medians (6.65 km month^{-1}) was significantly higher than the bootstrapped distribution (**Figure S4a**). Recapture lengths were similar between populations (**Figure S4c**) but releases in Aabenraa Fjord were generally recaptured throughout the year compared to SBS that was dominated by recaptures early in the year (**Figure S4e**). Days at liberty were variable in both ecotypes although the majority were caught within 100 days of release, especially in SBS (**Figure 9**).

3.3.2 Eastern Baltic - Gulf of Finland vs. south-eastern Baltic Sea (SEBS)

Similar patterns were observed in ecotypes in the Gulf of Finland (inshore) and SEBS (offshore; **Figure 8c, d, 9**). Inshore cod in the Gulf of Finland generally swam <20 km month^{-1} while a relatively small proportion of offshore cod in SEBS swam >50 km month^{-1}. The advection and diffusion, and distance medians similarly suggested more resident behaviour in cod in the Gulf of Finland (6.26 km month^{-1}) compared to SEBS (17.79 km month^{-1}) (**Table S4, Figure 8c, d**).

As for the western Baltic ecotypes, the bootstrap test on the median differences between Gulf of Finland and SEBS further supported this distinction in behaviour as the true difference between the medians (11.53 km month^{-1}) was significantly higher than the bootstrapped distribution (**Figure S4b**). Overall recapture lengths were lower in SEBS compared to Gulf of Finland (**Figure S4d**) and releases in SEBS were generally recaptured early on in the year while releases in Gulf of Finland were recaptured throughout the year with peaks in spring and autumn (**Figure S4f**). The majority of releases in SEBS were recaptured within 100 days of release while days at liberty were more evenly distributed in Gulf of Finland within the first 500 days (**Figure 9**).

Overall, both case studies suggested a higher degree of resident behaviour in the inshore ecotypes in contrast to a more mobile behaviour in offshore ecotypes regardless of which stock they belonged to. Additionally, the offshore component in SBS resembled the inshore component in the Gulf of Finland (median = 7.32 km month^{-1} and 6.26 km month^{-1}, respectively), although Gulf of Finland cod were slightly more resident (**Figure 9**).

3.3.3 Decadal variation in movement patterns within ecotypes

Clear variation in decadal movement patterns were observed within Aabenraa Fjord, SBS, and Gulf of Finland. The bootstrap test on the median differences showed that tagged cod in Aabenraa Fjord moved significantly farther in 1960-1970 compared to <1960 (**Figure 10a**), despite the recapture lengths and months being similar between the two time periods (median = 400 and 410 mm, and June and May in <1960 and 1960-1970, respectively). Similar patterns were observed in SBS (**Figure 10b**), although the recapture lengths seemed to differ slightly more (median = 365 and 440 mm in <1960 and 1960-1970, respectively) with recaptures mainly occurring in early spring (median = March for both decades). In contrast, the true median difference for Gulf of Finland was negative and below the bootstrapped distribution, suggesting cod moved slightly less in 1981-1999 vs. 1970-1980 (**Figure 10c**). Recapture lengths were slightly higher in 1981-1999 vs. 1970-1980 (median = 570 and 650 mm) and cod were recaptured slightly earlier in the year in 1981-1999 (median = July vs. May). No clear variation was observed across decades for SEBS as the true median differences fell within the distribution of the bootstrapped decadal median differences across all decades.

Overall, these patterns show clear decadal variation in movement patterns across both ecotypes.

4. Discussion

In the present study, we successfully applied the advection-diffusion methodology to study movement patterns in Atlantic cod in the North Sea and Baltic Sea for the first time. We surmised that the North Sea is most likely dominated by the more migratory offshore ecotype and the combination of an expansive coastal area and offshore areas in the Baltic region suggested a mix of both the offshore and resident ecotypes. These patterns were evident from our data; however, in order to evaluate the usefulness of this method to analyse movement in cod, it is essential to compare our results to previous analyses of tagging data while also acknowledging the limitations of this methodology.

In the North Sea, tagging data has shown mixing between the southern and central North Sea, with limited mixing between these areas and the northern North Sea (e.g. see Bedford 1966, Righton et al. 2007). Indeed, cod in the northern North Sea appear to be relatively stationary (e.g., see Wright et al. 2006, Nedreaas et al. 2008, Neat et al. 2014). In contrast, recent studies in the Baltic Sea by Mion et al. (in press) using kernel density distributions and GAMs showed greater movement distances in northern and central Baltic cod compared to cod in the southern Baltic (Mion et al. in press, Mion et al. 2020). In addition, other studies have identified the migration routes between spawning and feeding areas in the Baltic Sea using tagging data (e.g., see Otterlind 1985, Aro 1989, Bagge and Steffensen 1989, Bagge and Thurow 1994). In general, these studies all agree that eastern Baltic cod migrate to the southern Baltic to spawn, whereas cod in the western part of the Baltic use spawning areas that cover most of the Belt Sea (Otterlind 1985, Hüssy 2011). Furthermore, Mion et al. (in press) showed seasonal patterns in movements with variations in home ranges during the spawning and feeding seasons and suggested a potential link to ecotype behaviour.

Our findings in the North Sea and the Baltic Sea aligned well with these earlier results, highlighting the usefulness of this method. We expanded upon these results by presenting tools to separate movement into direction-driven and dispersed movement and assigning a measure of accuracy, providing more detailed analyses of movement. As an example, while northern North Sea cod have been shown to be relatively stationary, we showed that this movement was characterized by relatively high dispersal rather than being direction-driven. Similarly, combined with the kernel density distributions as presented in Mion et al. (in press), we further showed that movements in the eastern Baltic cod were overall characterized by both strong southerly advection and diffusion.

Inshore ecotypes in Aabenraa Fjord and Gulf of Finland had remarkably restricted movement patterns compared to offshore ecotypes in the southern Belt Sea and south-eastern Baltic Sea, respectively. This aligns with earlier studies where inshore cod have been found to be relatively resident (Jakobsen 1987, Salvanes et al. 2004, Espeland et al. 2008) while offshore ecotypes appear to be more migratory (Robichaud and Rose 2004). For example, a study over two years on Icelandic cod using data storage tags showed consistent behavioural patterns across inshore and offshore cod, with offshore cod migrating up to four times the depth of inshore cod to feed at thermal fronts (Thorsteinsson et al. 2012). Additionally, ecotypes can vary even within a single spawning ground (Thorsteinsson et al. 2012), as has been observed in Norwegian and Skagerrak cod (Godø and Michalsen 2000, Espeland et al. 2008). Our findings highlight the diversification of cod behaviour within even single stocks. Furthermore, the additional possibility of looking at shorter time scales and areas (as shown here in the ecotype case studies) could offer insights into movement within spawning and feeding seasons, respectively, although this requires a lot of data for bootstrapping to estimate accuracy. However, it should be noted that the movement behaviour of cod in Gulf of Finland may not have been properly captured, as the nearest spawning ground is further away than the local spawning grounds in the Belt Sea, possibly suggesting more migratory behaviour (Bleil et al. 2009).

The existence of different ecotypes within stock components at even small scales, as illustrated by the Aabenraa case study, poses challenges for the stocks in light of climate change. More resident cod in fjords and inlets (e.g., Aabenraa Fjord and Gulf of Finland) have largely disappeared over the years and whether it is due to an inability to adapt to more migratory behaviour or whether it is due to failure of reproduction caused by changes in biotic and abiotic factors is currently unknown. Cod are very sensitive to temperature changes and an increase of only 2.5°C in water temperature has been shown to cause an increase of 15-30% in metabolic rate (Claireaux et al. 1995). As Atlantic cod prefer to stay in colder deeper water during the day and warmer shallower water at night (Claireaux et al. 1995), it is possible that environmental changes in fjords have inferred a great metabolic cost to resident cod populations and affected reproduction. While low oxygen levels have a negative effect on egg survival in Baltic cod, lower oxygen levels are tolerated at low temperatures (Wieland et al. 1994) which has also been shown in Pacific cod where eggs tolerate low levels of oxygen as long as temperatures are between 3-5°C (Alderdice and Forrester 1971). Warm conditions caused by a marine heatwave have been shown to persist for at least 4 years in the deeper layers of a fjord (Jackson et al. 2018) and with the historical warming of the Baltic Sea

(Siegel et al. 2006, Hinrichsen et al. 2007) and an increase in the extent of hypoxic coastal areas (Conley et al. 2011), it is likely that temperature and hypoxia have been factors in the disappearance of resident ecotypes. In comparison, stocks with highly migratory stock components are more likely to survive when conditions change, although range shifts will cause local socio-economic consequences. Indeed, future studies into cod population dynamics should take behavioural ecotypes into consideration, possibly using genetics and otolith analyses.

The results presented here indicate clear differences in movement behaviour within ICES areas and across ecotypes. However, it should be noted that some of the observed variation may be attributed to other factors to a certain degree, especially across decades. The environment in the Baltic Sea and North Sea has greatly changed between 1955 and 2020, such as a historical rise in sea surface and bottom temperature (Carstensen et al. 2014) and an expansion in hypoxic and anoxic areas (Kabel et al. 2012, Casini et al. 2016), which could have influenced the movement patterns. Fishing effort was also not accounted for in this study, and some of the observed movement patterns may not properly represent the true migratory behaviour of the population as fishing boats focus on areas with a higher abundance. This has been shown to be informative to the analysis of mark-recapture data (Solmundsson et al. 2005, Wright et al. 2006a), and, when coupled with differences in the reporting and return rates of tags (Taylor et al. 2011, Konrad et al. 2016), may influence our understanding of movement patterns. Additionally, the main fishing grounds for Atlantic cod are not evenly distributed over the habitat range and have likely changed through time (Engelhard et al. 2014). For instance, in the central North Sea the observed patterns in the 1970s are likely affected by the strong presence of fisheries on the western coast of the Danish Jutland peninsula during this time period. Furthermore, the analyses suggested that a high proportion of cod did not move far, if at all, between release and recapture. This apparent lack of movement is most likely a combination of true movement behaviour and the nature of mark-recapture experiments missing information between release and recapture, particularly for individuals with long time intervals between release and recapture. The presence of seasonal movements in Atlantic cod will also influence the observed movement patterns, as will differences in body size and life stage (Mion et al. in press, Righton et al. 2007, Griffiths et al. 2018).

Conclusions

The concepts of advection and diffusion have been demonstrated to be simple and useful tools for analysing dynamics of cod population movements. In conjunction with other methods, such as bootstrapping for accuracy analysis, movement can be described in greater detail by addressing both directional and dispersed movement at a predetermined time scale. Indeed, this approach can easily be applied to the majority of available tagging data sets for other studies to give a dynamic and in-depth description of movement patterns in fish at even finer time scales. We demonstrated this in the present study and our results agreed with previous analyses of tagging data, demonstrating the value of this simple method.

More advanced applications of the advection-diffusion approach may incorporate estimates of mortality or habitat indices to study how environmental conditions (e.g. temperature, salinity, and oxygen) affect movement patterns on a much finer spatiotemporal scale than the preliminary results shown in the present study. Applications of this linked methodology approach have been utilized greatly in population dynamics models such as the Spatial Ecosystem And Population Dynamics Model (SEAPODYM, Lehodey et al. 2008). In order to expand the methodology used in this study, efforts are currently ongoing to examine the link between changes in movement patterns through time and changes in environmental factors by incorporating hydrographic data. These will provide useful information on how

Atlantic cod will react to the changes in environmental conditions entrained by climate change.

5. Acknowledgements

We thank everyone involved with the tagging projects utilized in this study for their hard work in carrying out the projects. We thank all fishers who have submitted recapture data throughout the decades. This study was funded by the European Maritime and Fisheries Fund (EMFF) and the Danish Fisheries Agency through the project "Management of mixed cod stocks in the transition zone between the North Sea and the Baltic Sea: How can this be achieved most efficiently?" (FABBIO). Funding was also provided by BalticSea2020 (http://balti csea2 020.org) through the project "Tagging Baltic Cod" (TABACOD).

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7. Appendix

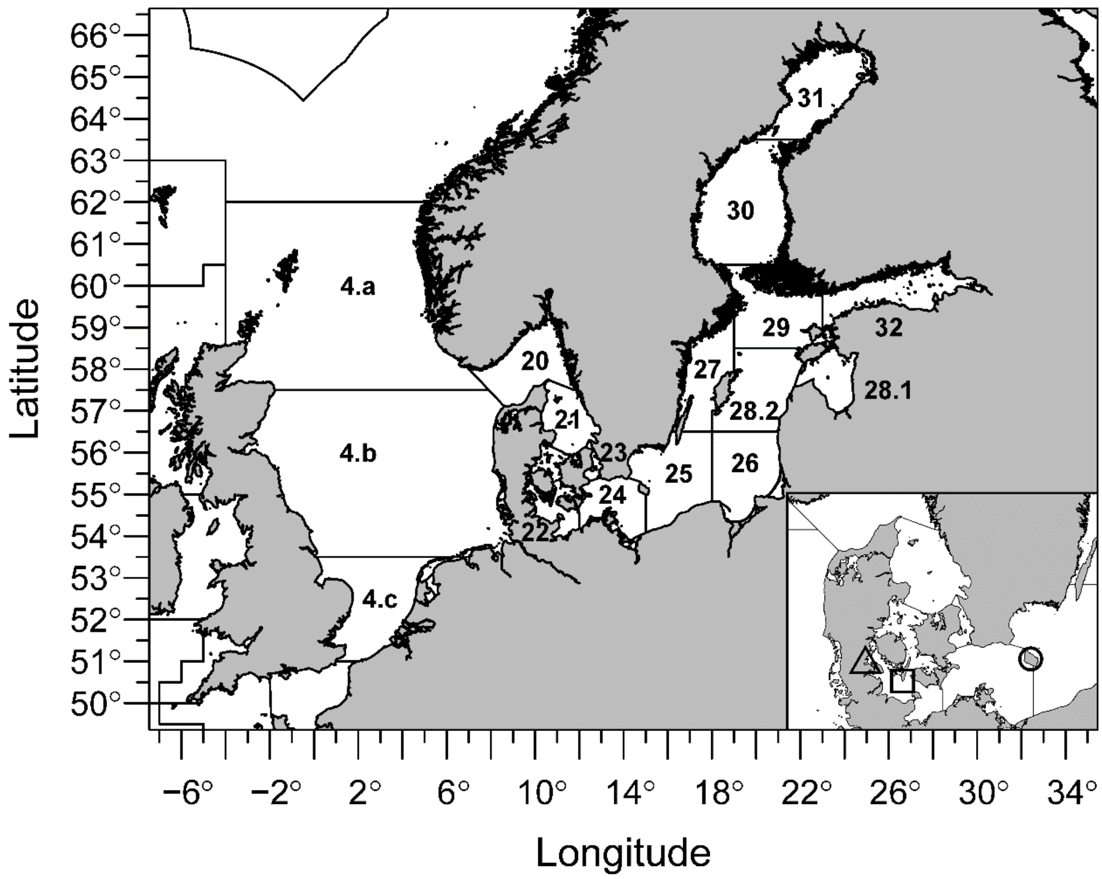

Fig. 1. Map of the North Sea and the Baltic Sea showing ICES areas. ICES area indicated by numbers: 4.a-c: The North Sea, 20: Skagerrak, 21: Kattegat, 22: Belt Sea, 23: The Sound/Øresund, 24: Arkona Sea, 25: Bornholm Sea, 26: south-eastern Baltic Sea (SEBS), 27: The Western Gotland Basin, 28.1: Gulf of Riga, 28.2: Gotland Sea, 29: The Archipelago Sea, 30: Bothnian Sea, 31: Bothnian Bay, 32: Gulf of Finland. The relevant stocks are as follows: North Sea stock (ICEs area 4.a-c, 7.d, 20), the Kattegat stock (21), the western Baltic stock (22-24), and the eastern Baltic stock (24-32). Map inset shows noteworthy local locations. △ = Aabenraa Fjord. □ = Bagenkop. ○ = Bornholm.

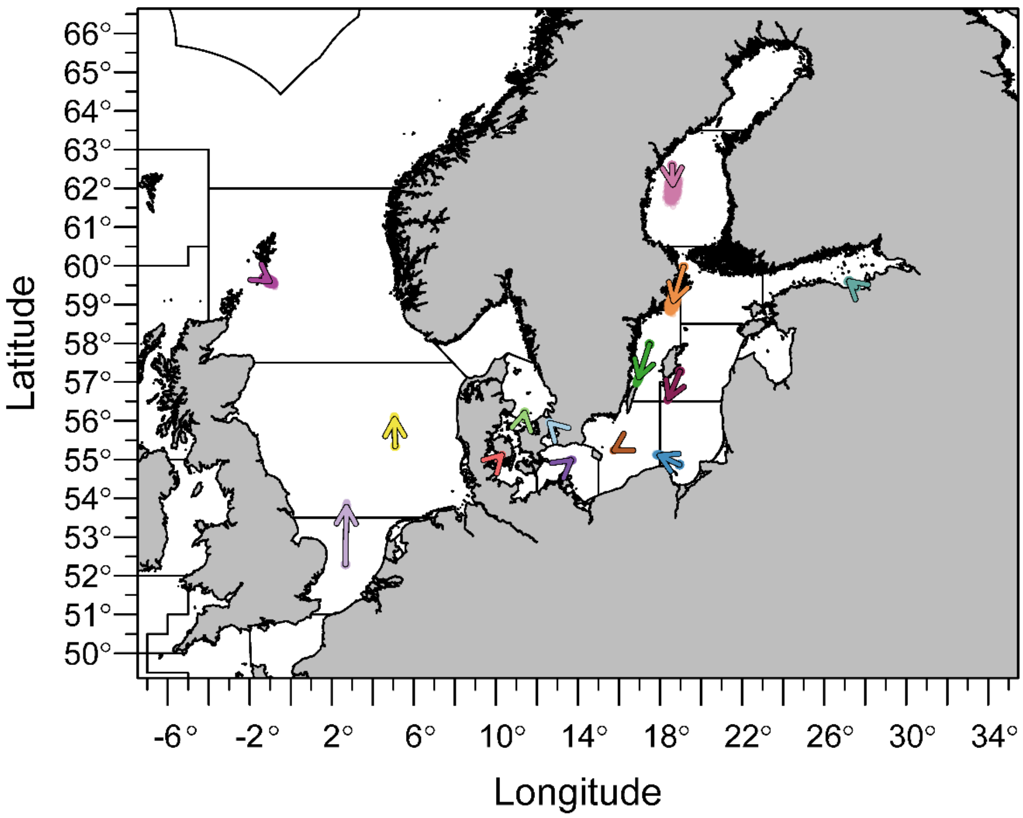

Fig. 2. Semi-annual advection patterns for each area for all years combined. Each arrow represents the advection in individual areas calculated from the raw datasets. The length of the arrow denotes the strength of the advection based on the difference between release and recapture positions. The start point of the arrow is the mean of the release coordinates. The small points denote the end points of 10,000 advection arrows calculated for each area from bootstrapped datasets to show accuracy.

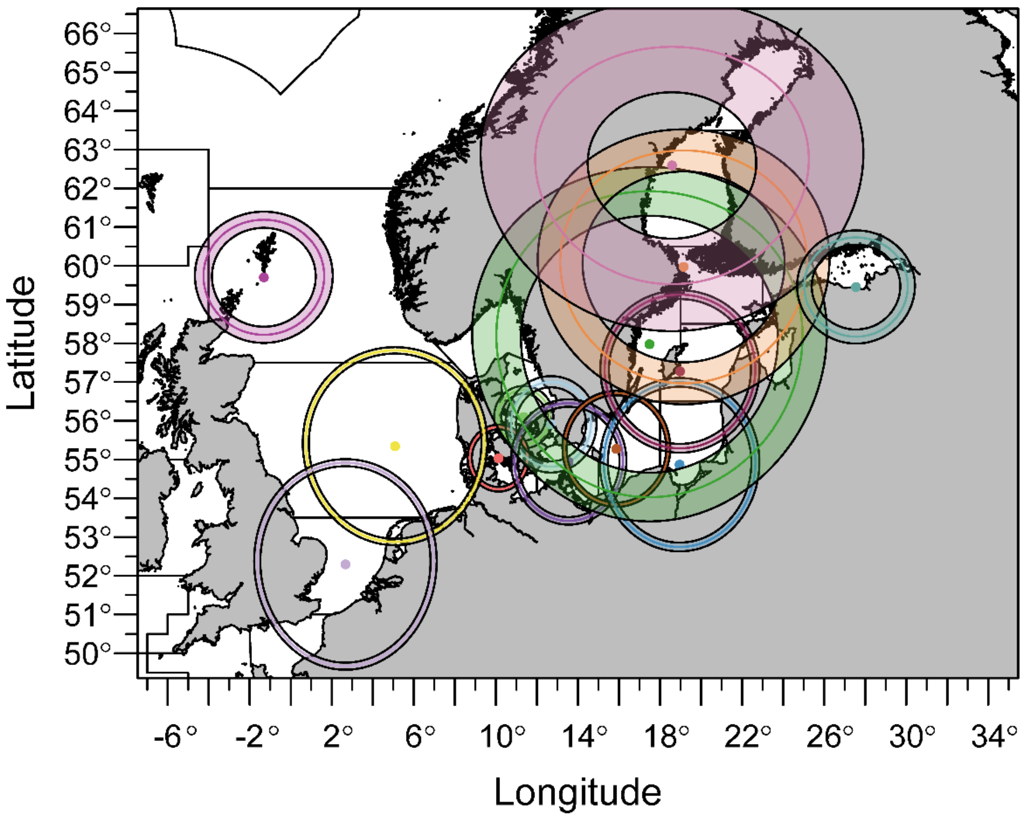

Fig. 3. Semi-annual diffusion patterns for each area for all years combined. The size of the circles indicates the relative strength and degree of diffusion in individual areas. The centre of the circle is the mean of the release coordinates. The middle line in each circle indicates the diffusion calculated from the raw data and the outer limits the 95% confidence intervals calculated from the bootstrapped datasets.

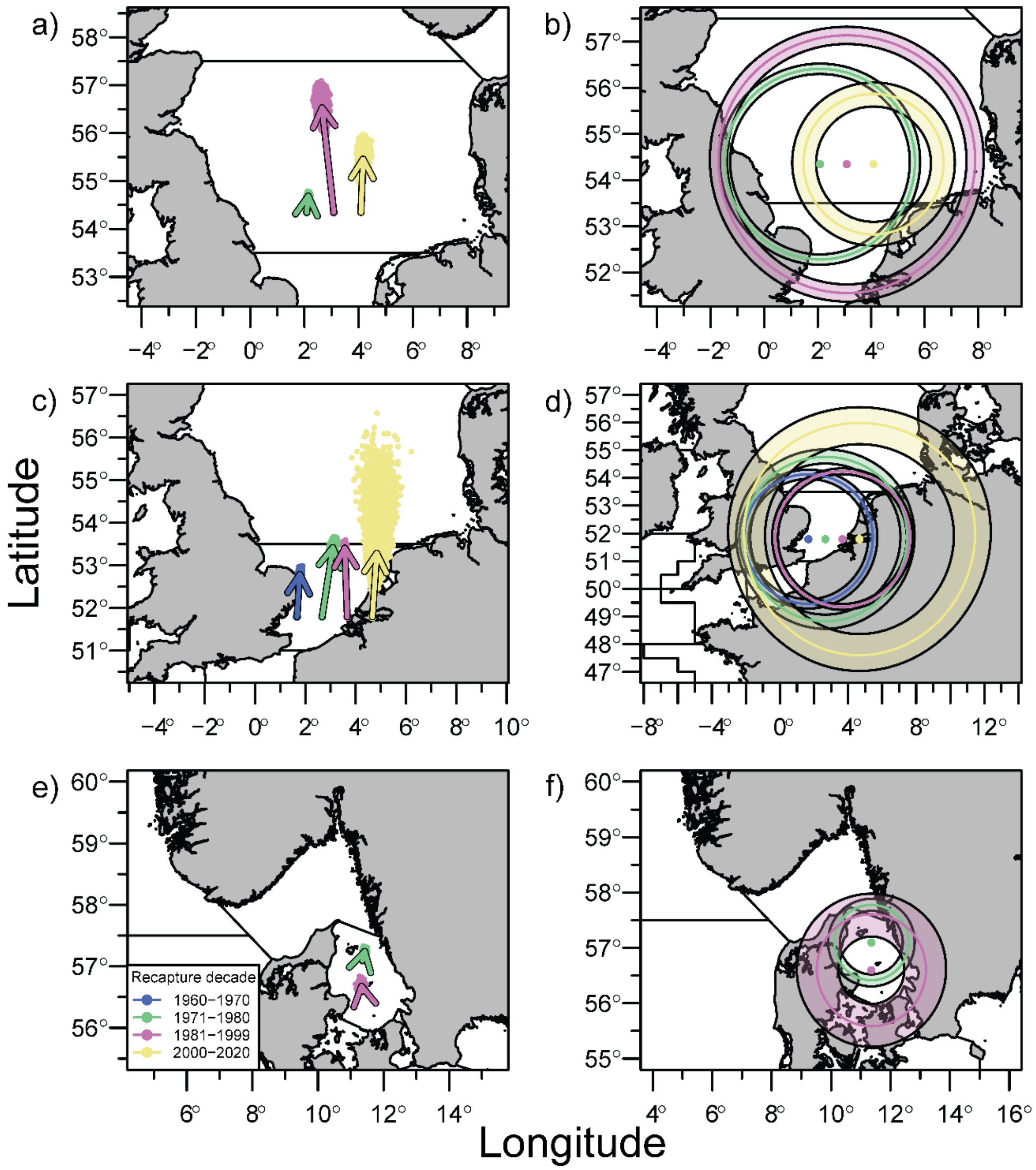

Fig. 4. Semi-annual advection and diffusion patterns across decades in the central and southern North Sea and Kattegat-Skagerrak. a-b) Advection and diffusion in the central North Sea (ICES area 4.b), c-d) in the southern North Sea (ICES area 4.c), and e-f) in Kattegat-Skagerrak (ICES area 20+21). Each arrow and circle represent the advection and diffusion in individual areas calculated from the raw datasets, respectively. The start point of the arrow and centre of the circles do not represent release locations. The length of the arrow denotes the strength of the advection based on the difference between release and recapture positions

and the size of the circles indicates the relative strength and degree of diffusion in individual areas. The small points denote the end points of 10,000 advection arrows calculated for each area from bootstrapped datasets to show accuracy. The middle line in each circle indicates the diffusion calculated from the raw data and the outer limits the 95% confidence intervals calculated from the bootstrapped datasets.

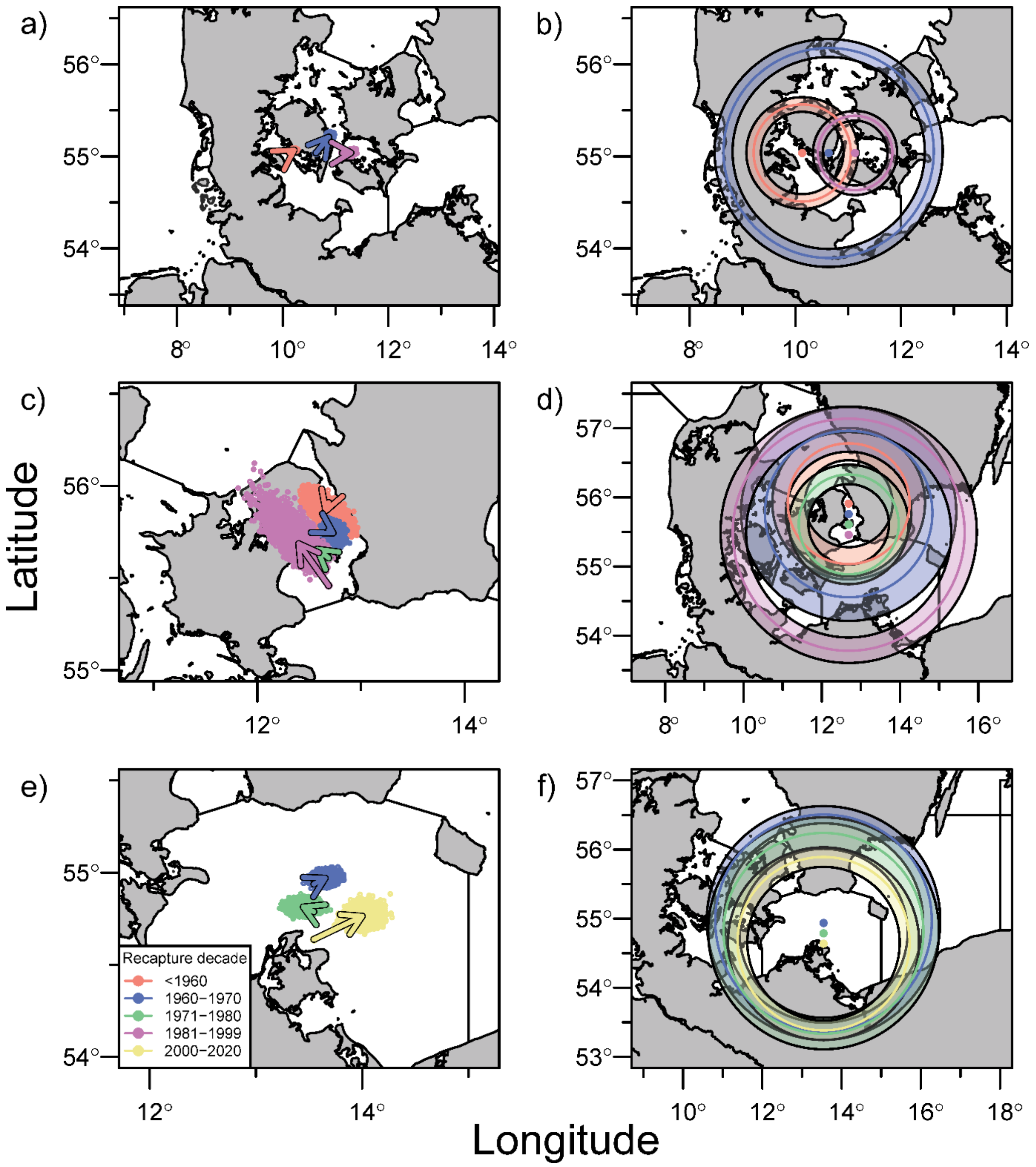

Fig. 5. Semi-annual advection and diffusion patterns across decades in the Belt Sea, the Sound, and the Arkona Sea. a-b) Advection and diffusion in the Belt Sea (ICES area 22), c-d) in the Sound (ICES area 23), and e-f) in the Arkona Sea (ICES area 24). Each arrow and circle represent the advection and diffusion in individual areas calculated from the raw datasets, respectively. The start point of the arrow and centre of the circles do not represent release locations. The length of the arrow denotes the strength of the advection based on the

difference between release and recapture positions and the size of the circles indicates the relative strength and degree of diffusion in individual areas. The small points denote the end points of 10,000 advection arrows calculated for each area from bootstrapped datasets to show accuracy. The middle line in each circle indicates the diffusion calculated from the raw data and the outer limits the 95% confidence intervals calculated from the bootstrapped datasets.

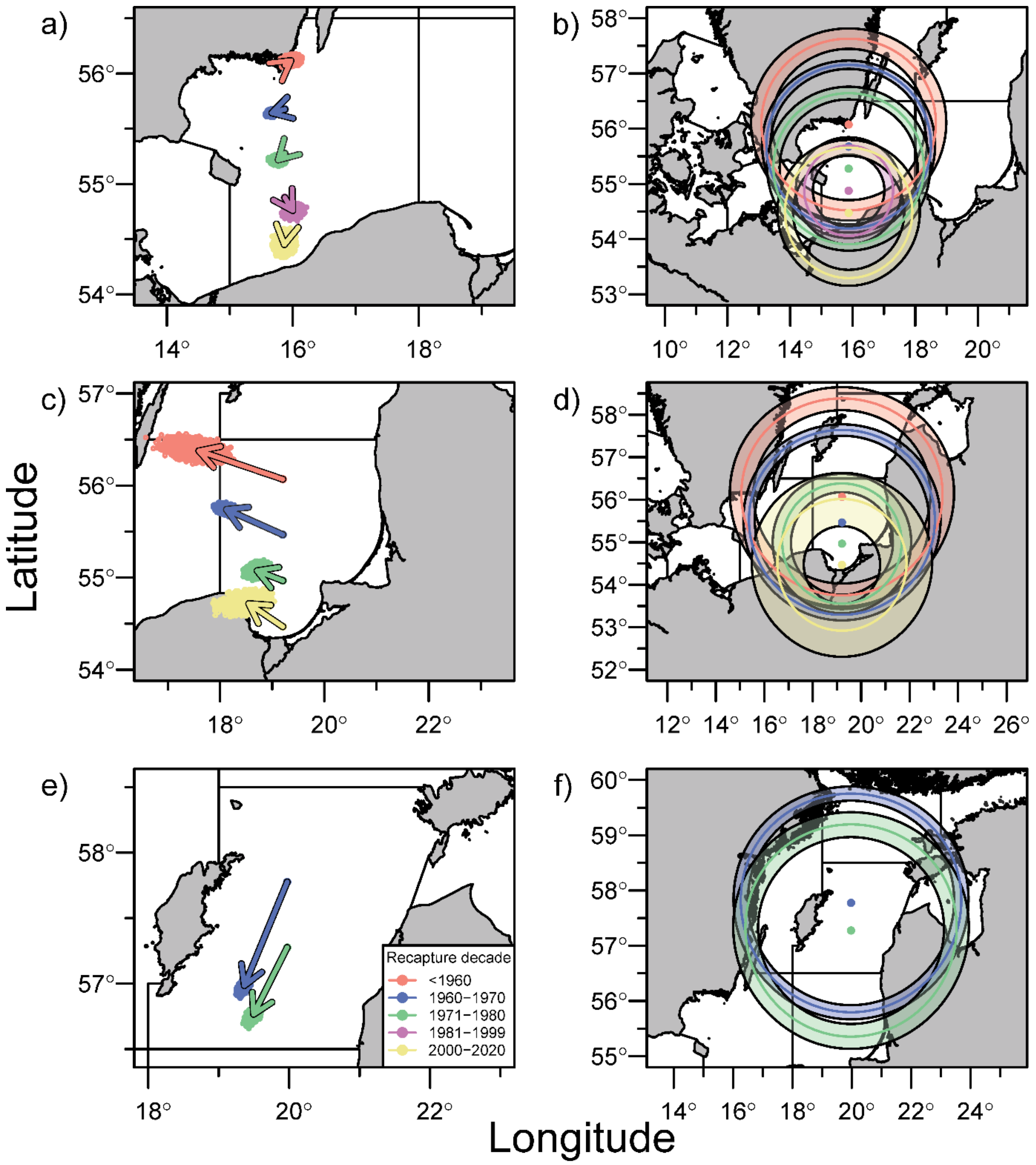

Fig. 6. Semi-annual advection and diffusion patterns across decades in the Bornholm Sea, south-eastern Baltic Sea (SEBS), and the Gotland Sea. a-b) Advection and diffusion in the Bornholm Sea (ICES area 25), c-d) in SEBS (ICES area 26), and e-f) in the Gotland Sea (ICES area 28.2). Each arrow and circle represent the advection and diffusion in individual areas calculated from the raw datasets, respectively. The start point of the arrow and centre of the circles do not represent release locations. The length of the arrow denotes the strength of

the advection based on the difference between release and recapture positions and the size of the circles indicates the relative strength and degree of diffusion in individual areas. The small points denote the end points of 10,000 advection arrows calculated for each area from bootstrapped datasets to show accuracy. The middle line in each circle indicates the diffusion calculated from the raw data and the outer limits the 95% confidence intervals calculated from the bootstrapped datasets.

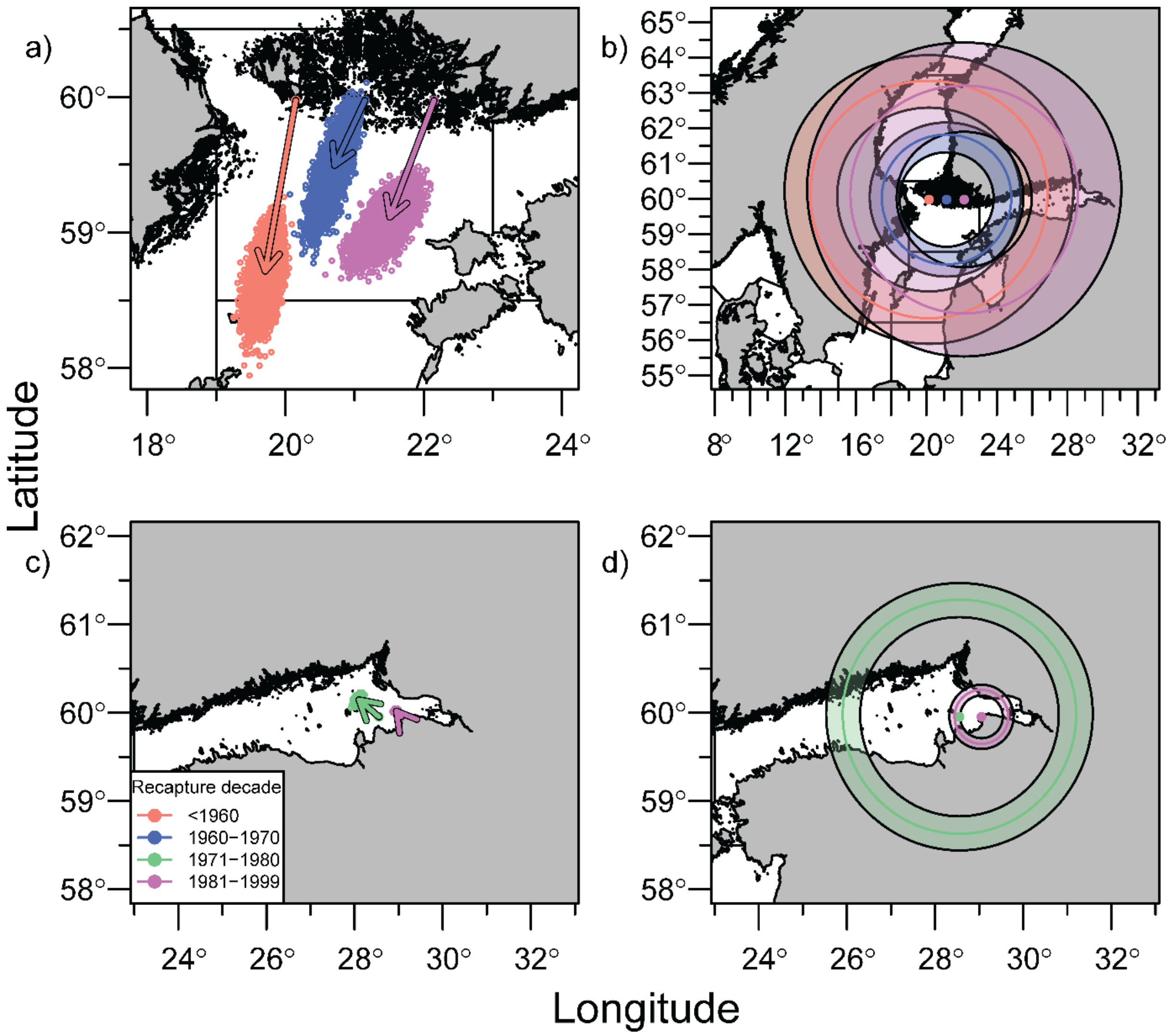

Fig. 7. Semi-annual advection and diffusion patterns across decades in the Archipelago Sea and the Gulf of Finland. a-b) Advection and diffusion in the Archipelago Sea (ICES area 29), and c-d) in the Gulf of Finland (ICES area 32). Each arrow and circle represent the advection and diffusion in individual areas calculated from the raw datasets, respectively. The start point of the arrow and centre of the circles do not represent release locations. The length of the arrow denotes the strength of the advection based on the difference between release and recapture positions and the size of the circles indicates the relative strength and degree of diffusion in individual areas. The small points denote the end points of 10,000 advection arrows calculated for each area from bootstrapped datasets to show accuracy. The middle line

in each circle indicates the diffusion calculated from the raw data and the outer limits the 95% confidence intervals calculated from the bootstrapped datasets.

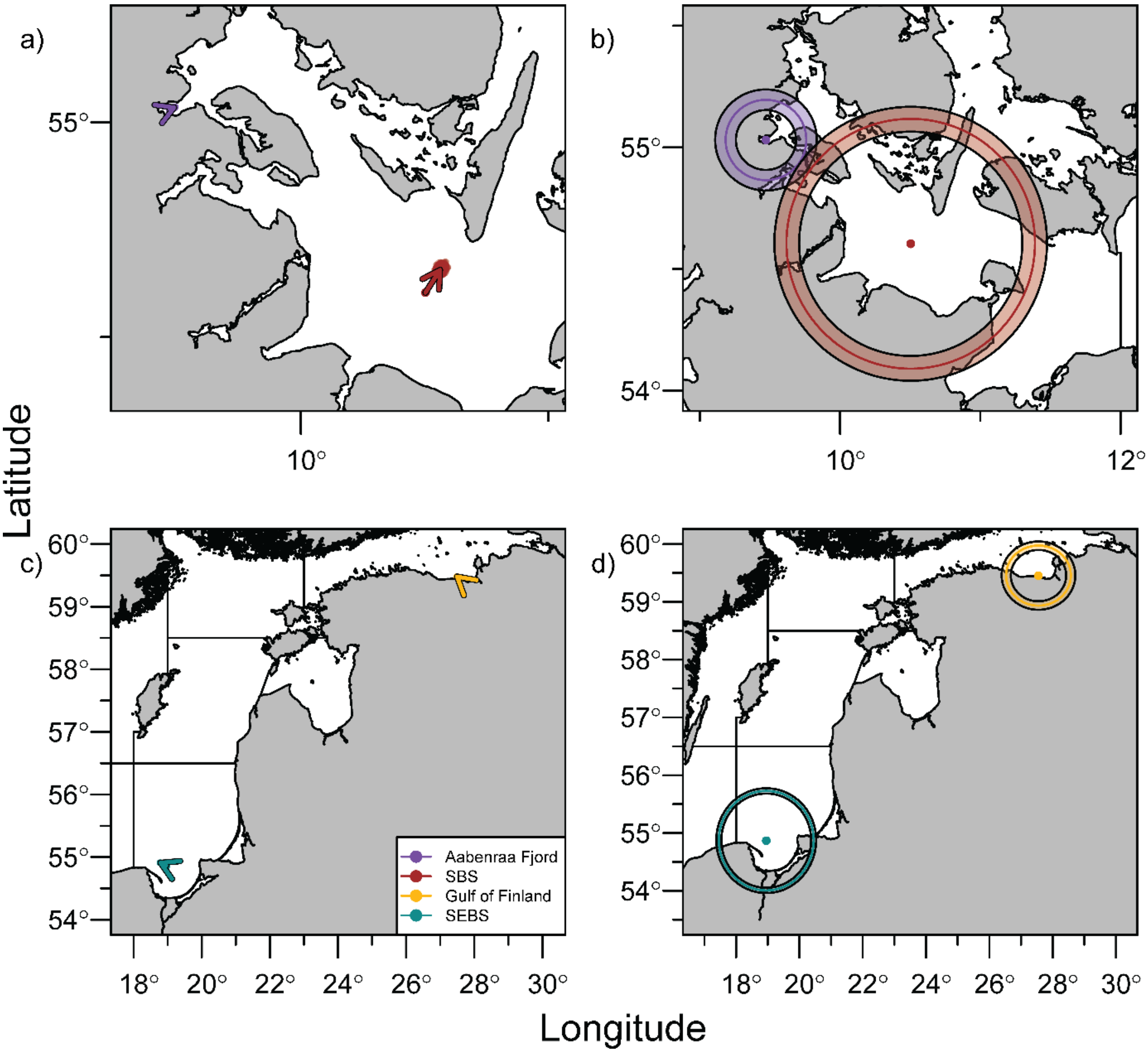

Fig. 8. Monthly advection and diffusion patterns in the western Baltic Sea and eastern Baltic Sea. a) Advection patterns in the western Baltic Sea. b) Diffusion patterns in the western Baltic Sea. c) Advection patterns in the eastern Baltic Sea. d) Diffusion patterns in the eastern Baltic Sea. Each arrow and circle represent the advection and diffusion in individual areas calculated from the raw datasets, respectively. The start point of the arrow and centre of the circles do not represent release locations. The length of the arrow denotes the strength of the advection based on the difference between release and recapture positions and the size of the circles indicates the relative strength and degree of diffusion in individual areas. The small points denote the end points of 10,000 advection arrows calculated for each area from bootstrapped datasets to show accuracy. The middle line in each circle indicates the diffusion

calculated from the raw data and the outer limits the 95% confidence intervals calculated from the bootstrapped datasets. SBS = southern Belt Sea; SEBS = south-eastern Baltic Sea.

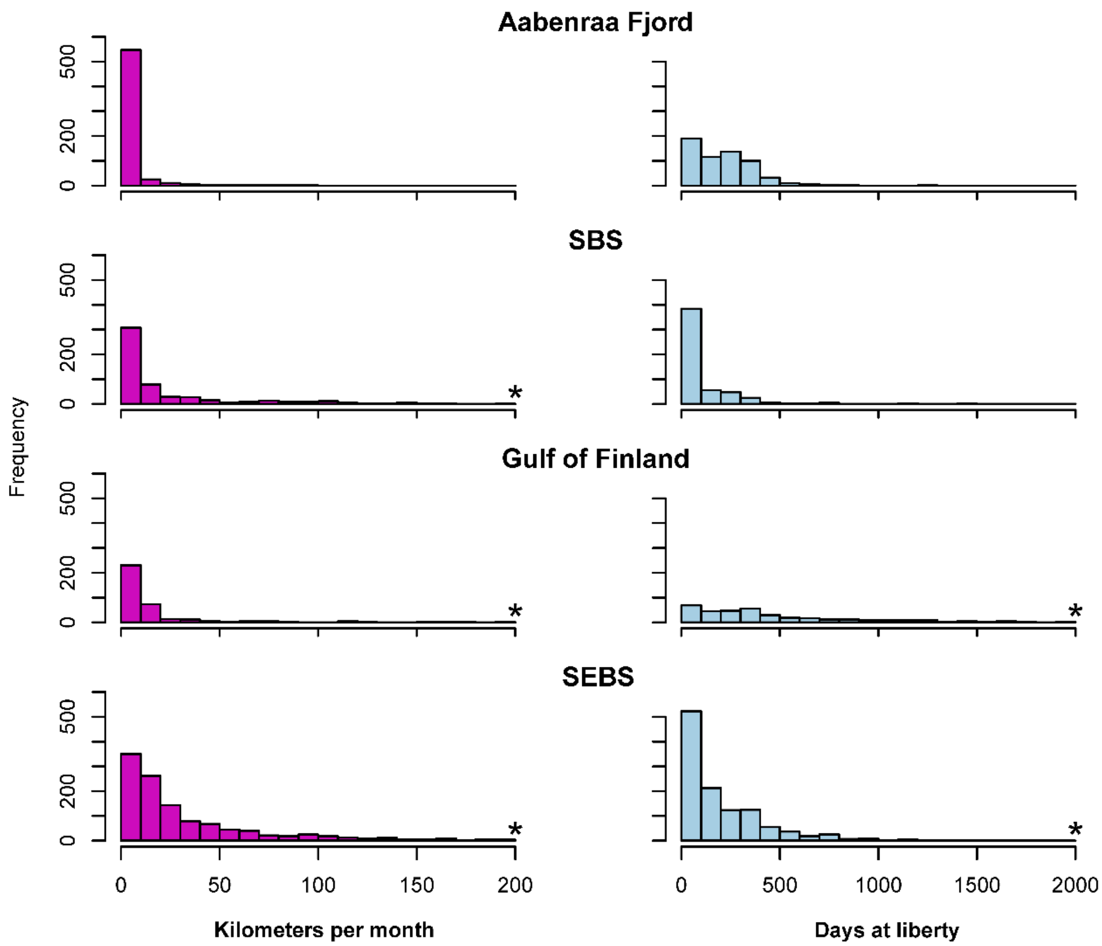

Fig. 9. Movement distances and days at liberty for recaptures released in Aabenraa Fjord, southern Belt Sea (SBS), Gulf of Finland, and south-eastern Baltic Sea (SEBS). Left column = distance travelled (km month^{-1}); right column = days at liberty. Asterisks (*) indicate values above 3 km and 2000 days, respectively.

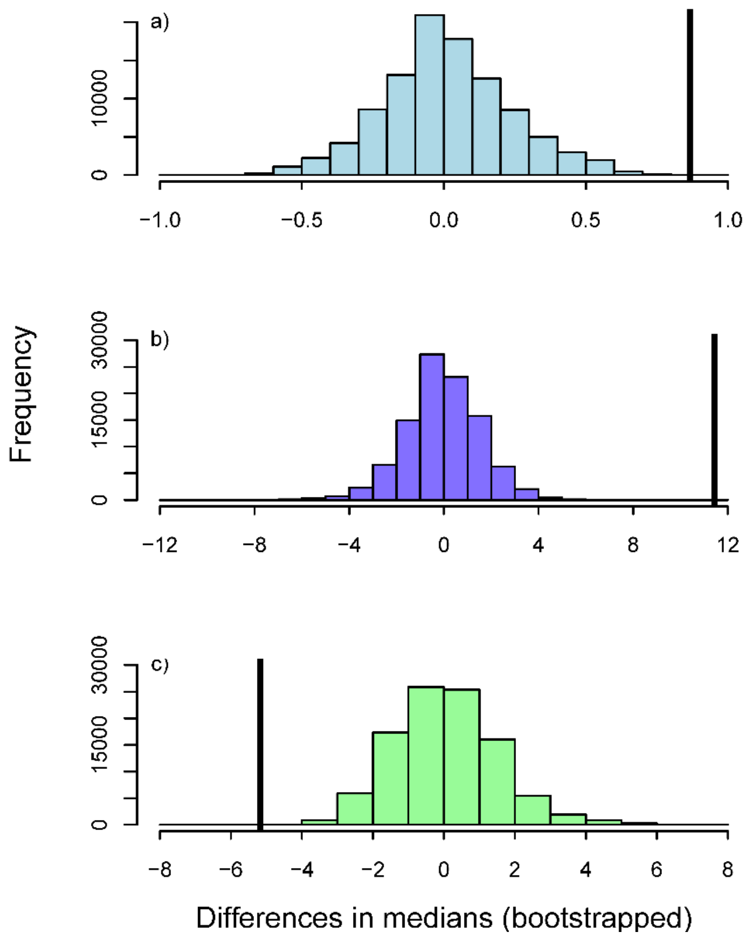

Fig. 10. Distributions of bootstrapped decadal median differences for swimming distances (km month^{-1}) for recaptures released in Aabenraa Fjord, the southern Belt Sea (SBS), and the Gulf of Finland. a) Aabenraa Fjord (<1960 vs. 1960-1970), b) SBS (<1960 vs. 1960-1970), and c) Gulf of Finland (1970-1980 vs. 1981-1999). Median differences were calculated from bootstrapped datasets (n = 100,000). Thick black lines indicate true median values for respective populations. Due to a lack of differences across decades, southern Baltic Sea (SEBS) is not shown.