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

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1 Application of advection and diffusion to examine movement in fish:

2 A case study of north-eastern Atlantic cod

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26 Abstract

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

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

40 1. Introduction

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

50 stock (SD 22-24), and the eastern Baltic stock (SD 24-32). All ICES units are collectively
51 referred to as ICES areas henceforth.

52 Declining cod stock sizes in the North Sea and Baltic Sea have been a great concern since the
53 1970s and 1980s, respectively. This is particularly evident in the North Sea where the cod
54 stock is currently at similar levels as after the collapse in the early 2000s (Huserbråten et al.
55 2018). In the southern North Sea, the cod is virtually absent due to historically high fishing
56 pressure and continued low recruitment. In the nearby Kattegat, the stock was at a historically
57 low spawning stock biomass (SSB) level in 2020, and ICES currently advises zero catch only
58 (ICES 2021a). In the Baltic Sea, the western Baltic cod stock has experienced low
59 recruitment since the mid-2000s (ICES 2021b). In addition, the eastern Baltic cod stock is in
60 a poor state, partially due to high fishing pressure, low recruitment, and slow growth (Eero et
61 al. 2015, Orio et al. 2019).

62 Several factors may have affected the movement patterns in Atlantic cod stocks, such as
63 changes in stock sizes due to density-dependent behaviour (Fretwell 1969) although
64 cannibalism also plays a role (Neuenfeldt and Köster 2000). As stock sizes increase, density
65 dependent behaviour may cause individuals to adjust their spatial distribution to avoid high
66 density patches as has previously been observed in spawning eastern Baltic cod (Baranova
67 1995). In contrast, reduction in stock sizes has been linked to range contractions. This has
68 previously been observed in capelin (*Mallotus villosus*, Ingvaldsen and Gjøsæter 2013) and
69 pike (*Esox lucius*, Haugen et al. 2006). Furthermore, changes in the environment, such as an
70 increase in hypoxic areas in the past decades in the Baltic Sea (Casini et al. 2016), could
71 potentially have affected movement patterns as well as cod move to more oxygen-rich areas.
72 Additionally, movement may also be variable across stocks due to the presence of two
73 distinct ecotypes of Atlantic cod: more resident inshore and more migratory offshore cod

74 (e.g., see Lear and Green 1984, Robichaud and Rose 2004, Karlsen et al. 2013) and both
75 types can occur in the same area (e.g., Knutsen et al. 2018).

76 Movement patterns of cod in the North Sea and Baltic Sea have been studied using mark-
77 recapture data (e.g., see Otterlind 1985, Aro 1989, Bagge and Steffensen 1989, Bagge and
78 Thurow 1994, Wright et al. 2006a, Righton et al. 2007, Mion et al. in press). The majority of
79 this data, in addition to Danish mark-recapture data from the western Baltic Sea, Sound, and
80 Kattegat, has recently been compiled into a joint database in the Baltic Sea (Mion et al. 2020,
81 2021). Despite the limitations of mark-recapture data, as only the release and recapture
82 location are known, historical mark-recapture studies offer a good opportunity to study
83 temporal movement patterns due to the quantity of data available, making it possible to
84 discern general movement patterns and changes through time.

85 Numerous methods have been used to analyse mark-recapture data in the North Sea and
86 Baltic Sea, including plotting recaptures (Otterlind 1985), employing kernel density
87 distributions (Mion et al. in press, Righton et al. 2007) and generalised additive models
88 (GAMs; Mion et al. in press, Espeland et al. 2008), as well as calculating metrics of
89 movement (Righton et al. 2007). Occasionally, ancillary information such as that provided by
90 otolith microchemistry (Wright et al. 2006b, Svedäng et al. 2010) or genetics (Heath et al.
91 2014, Hemmer-Hansen et al. 2020) have also been used in combination with tagging data to
92 disentangle sub-population stock structuring (e.g., Zemeckis et al. 2014, ICES 2020c). These
93 methods often provide insight on movement behaviour and spatial distribution patterns, but
94 do not provide mathematical links between individual-level movements and population-level
95 patterns. A mathematical approach to assessing movement is the concepts of advection
96 (biased movement) and diffusion (dispersal). When applied to populations, they describe the
97 average movement of a population within a selected time frame and coordinate system and to
98 what extent average movement is directed or appears to be random. For instance, a high

99 advection in one direction indicates the population has an overall tendency to move in this
100 direction, while a high diffusion would indicate the population is characterized by random
101 movement. Together, advection and diffusion can offer a dynamic approach to study
102 movement in tagged fish in space and time and have previously been applied to skipjack tuna
103 (*Katsuwonus pelamis*; Sibert et al. 1999, Faugeras and Maury 2005). To the authors'
104 knowledge, however, this approach has not been applied to Atlantic cod.

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

115 2. Methods

116 2.1 Data overview

117 Mark-recapture data from Danish tagging projects in the North Sea and Baltic Sea ($n = 7,962$)
118 were digitised and incorporated into a database containing mark-recapture data collected
119 between 1955 and 2020 from several countries (Mion et al. 2020, 2021), including Denmark
120 ($n = 325$), Sweden ($n = 4,796$), Poland ($n = 1,794$), Latvia ($n = 113$), Germany ($n = 910$),
121 Finland ($n = 403$), and the United Kingdom ($n = 5,361$). This also included the more recent
122 tagging projects CODYSSEY (Cod spatial dynamics and vertical movements in European

123 waters and implications for fishery management; Righton et al. 2009) and TABACOD
124 (Tagging Baltic Cod; Hüsey et al. 2020) (n = 21,664 in total). Archival tagging data from
125 CODYSSEY and TABACOD were also included but made up <1% of the overall data. The
126 database included detailed information on release and recapture locations and dates, and
127 biological information such as total length (mm) and weight (g). Recaptures were only
128 considered if release and recapture locations and dates were known. Recaptures ≤ 15 days
129 after release were excluded to allow for post-tagging recovery of neutral buoyancy (van der
130 Kooij et al. 2007) and resumption of normal behaviour as cod live at depth. In total, 4,295
131 recaptures were excluded resulting in a dataset of 17,369 recaptures for this study.

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

138 All recaptures were grouped by release ICES areas. Skagerrak (ICES area 20) was grouped
139 with Kattegat (ICES area 21) due to low recapture coverage in Skagerrak (n = 4) and all
140 release locations being on the edge of Kattegat. Henceforth, cod tagged within this area will
141 collectively be referred to as Kattegat-Skagerrak. Overall differences between ICES areas
142 were first considered for all data collected within each ICES area, and the data was further
143 grouped by recapture decades (<1960, 1960-1970, 1971-1980, 1981-1999, 2000-2020) to
144 determine temporal differences within and between ICES areas. Due to low recaptures in all
145 areas in the 1990s (n = 71) and 2000s (n = 256), 1981-1999 and 2000-2020 were grouped to
146 span two decades. Note that recaptures were unavailable for some years (1991-1993, 1997,

147 1998, 2008, 2009, 2012, 2014). For analyses of seasonal movements, we refer to Mion et al.
 148 (in press).

149 2.2 Analysis of movement

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

$$153 \quad \hat{\alpha} = \left(\frac{\sum \Delta x}{\sum \Delta t}, \frac{\sum \Delta y}{\sum \Delta t} \right)' \quad (1)$$

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

$$156 \quad \hat{D} = \frac{1}{4(n-1)} \left(\sum \left(\frac{\Delta x^2}{\Delta t} \right) - \frac{(\sum \Delta x)^2}{\sum \Delta t} + \sum \left(\frac{\Delta y^2}{\Delta t} \right) - \frac{(\sum \Delta y)^2}{\sum \Delta t} \right) \quad (2)$$

157 where Δx and Δy denote the difference between release and recapture coordinates (longitude
 158 and latitude) converted to a geodesic distance (kilometres), Δt the difference between release
 159 and recapture time, and n the number of fish. To visualise the directed movements for each
 160 area, the advection was used to calculate a vector angle and distance, and the time frame was
 161 scaled to per half year by multiplying with 365/2 to see large-scale trends. The advection thus
 162 describes movement through mean changes in kilometres between release and recapture per
 163 half year for the large-scale study that included all ICES areas. Similarly, diffusion (the
 164 variance) describes mean changes in distance from the point of release over $\sqrt{1/2 \text{ year}}$ for the
 165 large-scale study, respectively, and gives a relative indication of the degree of dispersal. To
 166 visualise the dispersal for each area, circles were used, and the radius was determined by the
 167 diffusion coefficient multiplied by 365/2.

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

175 2.3 Movement patterns in offshore and inshore ecotypes

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

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

188 The ecotype case studies were treated and analysed similarly as the large-scale case study
189 (see previous section). To compare overall movement distances between ecotypes (offshore
190 and inshore) in the eastern and western Baltic, distance travelled per month (km month^{-1}) was
191 assessed as a complementary analysis to the advection-diffusion methodology to illustrate

192 pattern detection at even small time scales. Distance travelled per month was calculated as
193 the geodesic distance between release and recapture location to account for the slight
194 curvature of the Earth which was then divided by days at liberty and multiplied by 30.

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

205 However, if the ecotypes were different, the true median difference would be expected to fall
206 outside the bootstrapped distribution.

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

214 All analyses were done in R version 4.0.2 (R Core Team 2020). The packages *sp* (Pebesma
215 and Bivand 2005), *rgeos* (Bivand and Rundel 2020), and *rgdal* (Bivand et al. 2020) were

216 used to create the maps, and *beanplot* (Kampstra 2008) was used for the beanplots. The R
217 script utilized for the analyses is available upon request.

218 3. Results

219 3.1 Data overview

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

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

233 3.2 Analysis of movement

234 3.2.1 The North Sea (ICES areas 4.a-c)

235 The overall advection was low in the northern North Sea (ICES area 4.a) but increased
236 towards the southern part of the North Sea (**Figure 2**). The overall diffusion patterns in the
237 North Sea were much stronger than the adjacent ICES areas (**Figure 3**) and comparable to
238 those observed in the eastern Baltic. Across decades, the advection was strong and towards

239 the north in the central and southern North Sea (ICES area 4.b and 4.c, respectively),
240 although the advection was relatively low in the central North Sea in 1971-1980 (**Figure 4a,**
241 **c**). Diffusion patterns were variable but generally high in both the central and southern North
242 Sea (**Figure 4b, d**). No decadal comparison was possible for the northern North Sea. The
243 bootstrap accuracy analyses generally showed relatively stable estimates aside from the
244 southern North Sea in the 2000s (**Figure 4c, d**).

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

249 3.2.2 The Kattegat-Skagerrak (ICES areas 20-21)

250 Kattegat-Skagerrak exhibited very low overall advection towards the north (**Figure 2**) and no
251 strong historical changes in direction, although advection was slightly greater in 1971-1980
252 (**Figure 4e**). While the overall diffusion was relatively low (**Figure 3**), decadal variation
253 could be observed, with greater diffusion in 1981-1999 compared to 1971-1980 (**Figure 4f**).

254 While the advection estimates were generally characterized by low uncertainty, the diffusion
255 was characterized by wide confidence intervals (**Figure 4f**). The observed patterns suggest a
256 historical high degree of residency in the Kattegat-Skagerrak (see **Table S2-3** for the
257 advection and diffusion values).

258 3.2.3 The Western Baltic Sea (ICES areas 22-24)

259 Advection and diffusion in the western Baltic were relatively low overall but with some
260 decadal variation (**Figure 2, 3, 5**). In the Belt Sea (ICES area 22) the direction of the
261 advection was generally between north and east, and increased north-eastern advection and
262 greater diffusion were observed in 1960-1970 (**Figure 5a, b**). The Sound (ICES area 23)

263 similarly exhibited low advection in earlier years, increasing slightly towards southern
264 Kattegat in 1981-1999 (**Figure 5c**). High degrees of variation in diffusion were observed
265 among decades, with the highest observed in 1981-1999 and 1960-1970 (**Figure 5d**). The
266 Arkona Sea (ICES area 24) was characterized by low advection in opposing directions
267 between 1960-1970 and 1971-1980 and a sharp increase in 2000-2020 towards Bornholm
268 (**Figure 5e**). The extent of diffusion did not change with time (**Figure 5f**). The bootstrap
269 accuracy analyses showed relatively low degrees of accuracy in the Sound and Arkona Basin
270 (**Figure 5c-f**), although the direction of the advection was relatively stable.

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

274 3.2.4 The Eastern Baltic Sea (ICES areas 25-32)

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

286 accurate although the strength of the advection was slightly less certain, particularly in SEBS
287 (**Figure 6c-d**).

288 The Gotland Sea (ICES area 28.2) similarly showed strong advection towards the southern
289 Baltic in 1960-1970 and 1971-1980 (**Figure 6e**). Diffusion was high across both decades but
290 more similar to the patterns in the southern Baltic than the northern Baltic (**Figure 6f**).

291 Comparable patterns were observed in the Archipelago Sea (ICES area 29) with very strong
292 advection towards the southern Baltic across all decades although lower in 1960-1970
293 compared to <1960 and 1981-1999 (**Figure 7a**). A high degree of diffusion was observed,
294 with the lowest observed in 1960-1970 (**Figure 7b**). The Bothnian Sea (ICES area 30) also
295 exhibited strong advection towards the southern Baltic in 1981-1999 (**Figure 2**). Diffusion
296 was very high albeit with relatively wide 95% confidence intervals (**Figure 3**), indicating a
297 high degree of uncertainty. However, due to low recaptures in other decades, no temporal
298 comparison was possible for this area either. The Gulf of Finland (ICES area 32) showed low
299 advection towards the north-west, with slightly higher advection in 1971-1980 compared to
300 1981-1999 (**Figure 7c**). Diffusion was greatly variable and was much higher in 1971-1980
301 compared to 1981-1999 (**Figure 7d**). While the bootstrap accuracy analyses showed fairly
302 stable estimates in the Gotland Sea and Gulf of Finland (**Figure 6e, f, 7c, d**), the Archipelago
303 Sea was characterized by high uncertainty (**Figure 7a, b**).

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

310 3.3 Movement patterns in inshore and offshore ecotypes

311 3.3.1 Western Baltic - Aabenraa Fjord vs. southern Belt Sea (SBS)

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

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

326 3.3.2 Eastern Baltic - Gulf of Finland vs. south-eastern Baltic Sea (SEBS)

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

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

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

347 3.3.3 Decadal variation in movement patterns within ecotypes

348 Clear variation in decadal movement patterns were observed within Aabenraa Fjord, SBS,
349 and Gulf of Finland. The bootstrap test on the median differences showed that tagged cod in
350 Aabenraa Fjord moved significantly farther in 1960-1970 compared to <1960 (**Figure 10a**),
351 despite the recapture lengths and months being similar between the two time periods (median
352 = 400 and 410 mm, and June and May in <1960 and 1960-1970, respectively). Similar
353 patterns were observed in SBS (**Figure 10b**), although the recapture lengths seemed to differ
354 slightly more (median = 365 and 440 mm in <1960 and 1960-1970, respectively) with
355 recaptures mainly occurring in early spring (median = March for both decades). In contrast,
356 the true median difference for Gulf of Finland was negative and below the bootstrapped

357 distribution, suggesting cod moved slightly less in 1981-1999 vs. 1970-1980 (**Figure 10c**).
358 Recapture lengths were slightly higher in 1981-1999 vs. 1970-1980 (median = 570 and 650
359 mm) and cod were recaptured slightly earlier in the year in 1981-1999 (median = July vs.
360 May). No clear variation was observed across decades for SEBS as the true median
361 differences fell within the distribution of the bootstrapped decadal median differences across
362 all decades.

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

365 4. Discussion

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

374 In the North Sea, tagging data has shown mixing between the southern and central North Sea,
375 with limited mixing between these areas and the northern North Sea (e.g. see Bedford 1966,
376 Righton et al. 2007). Indeed, cod in the northern North Sea appear to be relatively stationary
377 (e.g., see Wright et al. 2006, Nedreaas et al. 2008, Neat et al. 2014). In contrast, recent
378 studies in the Baltic Sea by Mion et al. (in press) using kernel density distributions and
379 GAMs showed greater movement distances in northern and central Baltic cod compared to
380 cod in the southern Baltic (Mion et al. in press, Mion et al. 2020). In addition, other studies

381 have identified the migration routes between spawning and feeding areas in the Baltic Sea
382 using tagging data (e.g., see Otterlind 1985, Aro 1989, Bagge and Steffensen 1989, Bagge
383 and Thurow 1994). In general, these studies all agree that eastern Baltic cod migrate to the
384 southern Baltic to spawn, whereas cod in the western part of the Baltic use spawning areas
385 that cover most of the Belt Sea (Otterlind 1985, Hüsey 2011). Furthermore, Mion et al. (in
386 press) showed seasonal patterns in movements with variations in home ranges during the
387 spawning and feeding seasons and suggested a potential link to ecotype behaviour.

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

397 Inshore ecotypes in Aabenraa Fjord and Gulf of Finland had remarkably restricted movement
398 patterns compared to offshore ecotypes in the southern Belt Sea and south-eastern Baltic Sea,
399 respectively. This aligns with earlier studies where inshore cod have been found to be
400 relatively resident (Jakobsen 1987, Salvanes et al. 2004, Espeland et al. 2008) while offshore
401 ecotypes appear to be more migratory (Robichaud and Rose 2004). For example, a study over
402 two years on Icelandic cod using data storage tags showed consistent behavioural patterns
403 across inshore and offshore cod, with offshore cod migrating up to four times the depth of
404 inshore cod to feed at thermal fronts (Thorsteinsson et al. 2012). Additionally, ecotypes can
405 vary even within a single spawning ground (Thorsteinsson et al. 2012), as has been observed

406 in Norwegian and Skagerrak cod (Godø and Michalsen 2000, Espeland et al. 2008). Our
407 findings highlight the diversification of cod behaviour within even single stocks.
408 Furthermore, the additional possibility of looking at shorter time scales and areas (as shown
409 here in the ecotype case studies) could offer insights into movement within spawning and
410 feeding seasons, respectively, although this requires a lot of data for bootstrapping to estimate
411 accuracy. However, it should be noted that the movement behaviour of cod in Gulf of Finland
412 may not have been properly captured, as the nearest spawning ground is further away than the
413 local spawning grounds in the Belt Sea, possibly suggesting more migratory behaviour (Bleil
414 et al. 2009).

415 The existence of different ecotypes within stock components at even small scales, as
416 illustrated by the Aabenraa case study, poses challenges for the stocks in light of climate
417 change. More resident cod in fjords and inlets (e.g., Aabenraa Fjord and Gulf of Finland)
418 have largely disappeared over the years and whether it is due to an inability to adapt to more
419 migratory behaviour or whether it is due to failure of reproduction caused by changes in
420 biotic and abiotic factors is currently unknown. Cod are very sensitive to temperature changes
421 and an increase of only 2.5°C in water temperature has been shown to cause an increase of
422 15-30% in metabolic rate (Claireaux et al. 1995). As Atlantic cod prefer to stay in colder
423 deeper water during the day and warmer shallower water at night (Claireaux et al. 1995), it is
424 possible that environmental changes in fjords have inferred a great metabolic cost to resident
425 cod populations and affected reproduction. While low oxygen levels have a negative effect on
426 egg survival in Baltic cod, lower oxygen levels are tolerated at low temperatures (Wieland et
427 al. 1994) which has also been shown in Pacific cod where eggs tolerate low levels of oxygen
428 as long as temperatures are between 3-5°C (Alderdice and Forrester 1971). Warm conditions
429 caused by a marine heatwave have been shown to persist for at least 4 years in the deeper
430 layers of a fjord (Jackson et al. 2018) and with the historical warming of the Baltic Sea

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

438 The results presented here indicate clear differences in movement behaviour within ICES
439 areas and across ecotypes. However, it should be noted that some of the observed variation
440 may be attributed to other factors to a certain degree, especially across decades. The
441 environment in the Baltic Sea and North Sea has greatly changed between 1955 and 2020,
442 such as a historical rise in sea surface and bottom temperature (Carstensen et al. 2014) and an
443 expansion in hypoxic and anoxic areas (Kabel et al. 2012, Casini et al. 2016), which could
444 have influenced the movement patterns. Fishing effort was also not accounted for in this
445 study, and some of the observed movement patterns may not properly represent the true
446 migratory behaviour of the population as fishing boats focus on areas with a higher
447 abundance. This has been shown to be informative to the analysis of mark-recapture data
448 (Solmundsson et al. 2005, Wright et al. 2006a), and, when coupled with differences in the
449 reporting and return rates of tags (Taylor et al. 2011, Konrad et al. 2016), may influence our
450 understanding of movement patterns. Additionally, the main fishing grounds for Atlantic cod
451 are not evenly distributed over the habitat range and have likely changed through time
452 (Engelhard et al. 2014). For instance, in the central North Sea the observed patterns in the
453 1970s are likely affected by the strong presence of fisheries on the western coast of the
454 Danish Jutland peninsula during this time period. Furthermore, the analyses suggested that a
455 high proportion of cod did not move far, if at all, between release and recapture. This

456 apparent lack of movement is most likely a combination of true movement behaviour and the
457 nature of mark-recapture experiments missing information between release and recapture,
458 particularly for individuals with long time intervals between release and recapture. The
459 presence of seasonal movements in Atlantic cod will also influence the observed movement
460 patterns, as will differences in body size and life stage (Mion et al. in press, Righton et al.
461 2007, Griffiths et al. 2018).

462 Conclusions

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

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

480 Atlantic cod will react to the changes in environmental conditions entrained by climate
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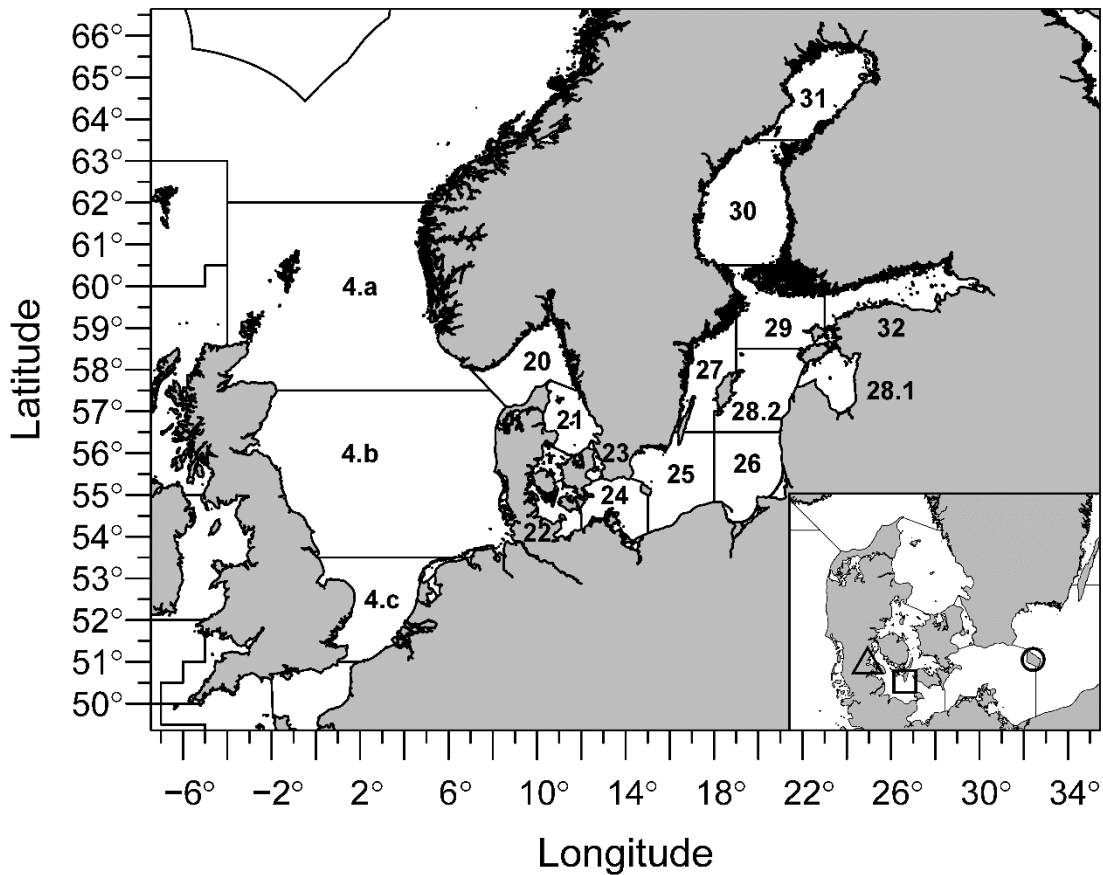
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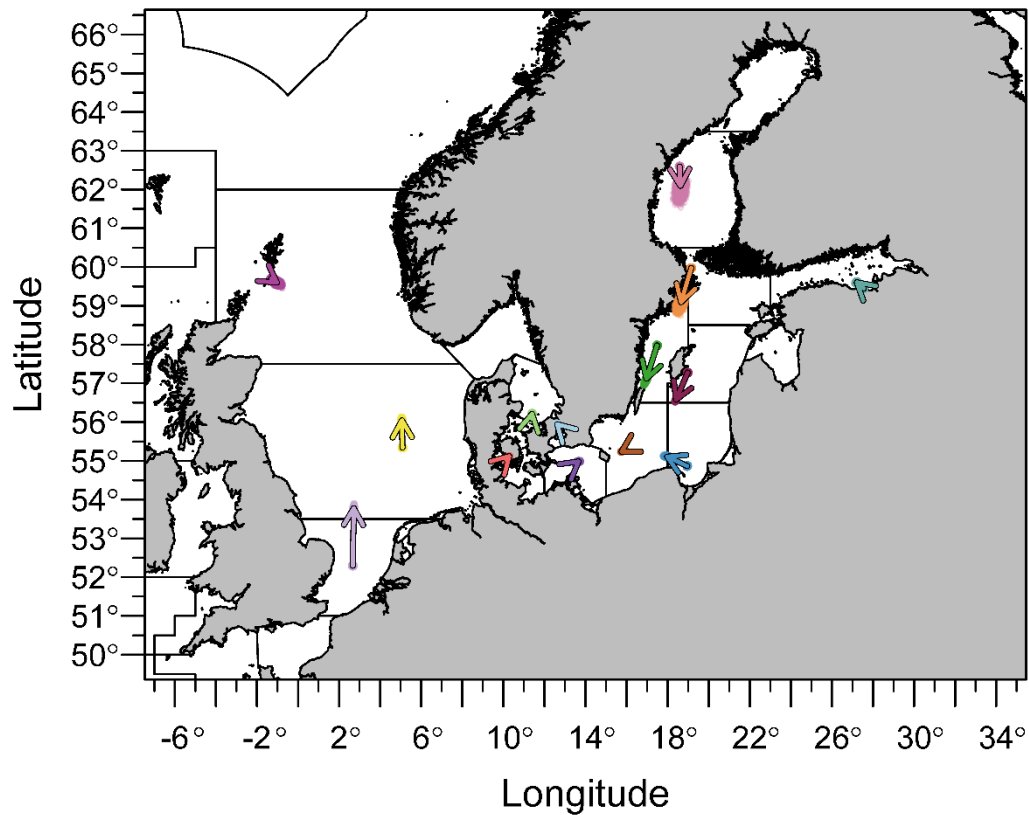
668 7. Appendix



669

670 Fig. 1. Map of the North Sea and the Baltic Sea showing ICES areas. ICES area indicated by
 671 numbers: 4.a-c: The North Sea, 20: Skagerrak, 21: Kattegat, 22: Belt Sea, 23: The
 672 Sound/Øresund, 24: Arkona Sea, 25: Bornholm Sea, 26: south-eastern Baltic Sea (SEBS), 27:
 673 The Western Gotland Basin, 28.1: Gulf of Riga, 28.2: Gotland Sea, 29: The Archipelago Sea,
 674 30: Bothnian Sea, 31: Bothnian Bay, 32: Gulf of Finland. The relevant stocks are as follows:
 675 North Sea stock (ICES areas 4.a-c, 7.d, 20), the Kattegat stock (21), the western Baltic stock
 676 (22-24), and the eastern Baltic stock (24-32). Map inset shows noteworthy local locations. Δ
 677 = Aabenraa Fjord. \square = Bagenkop. \circ = Bornholm.

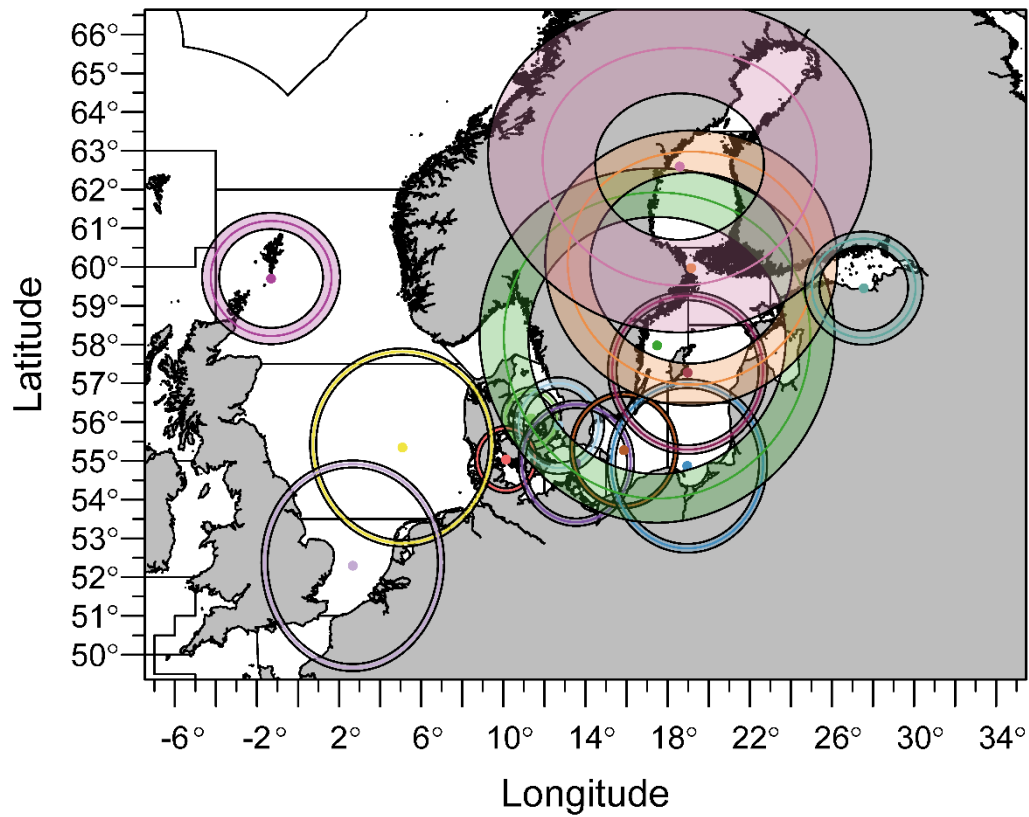
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679

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

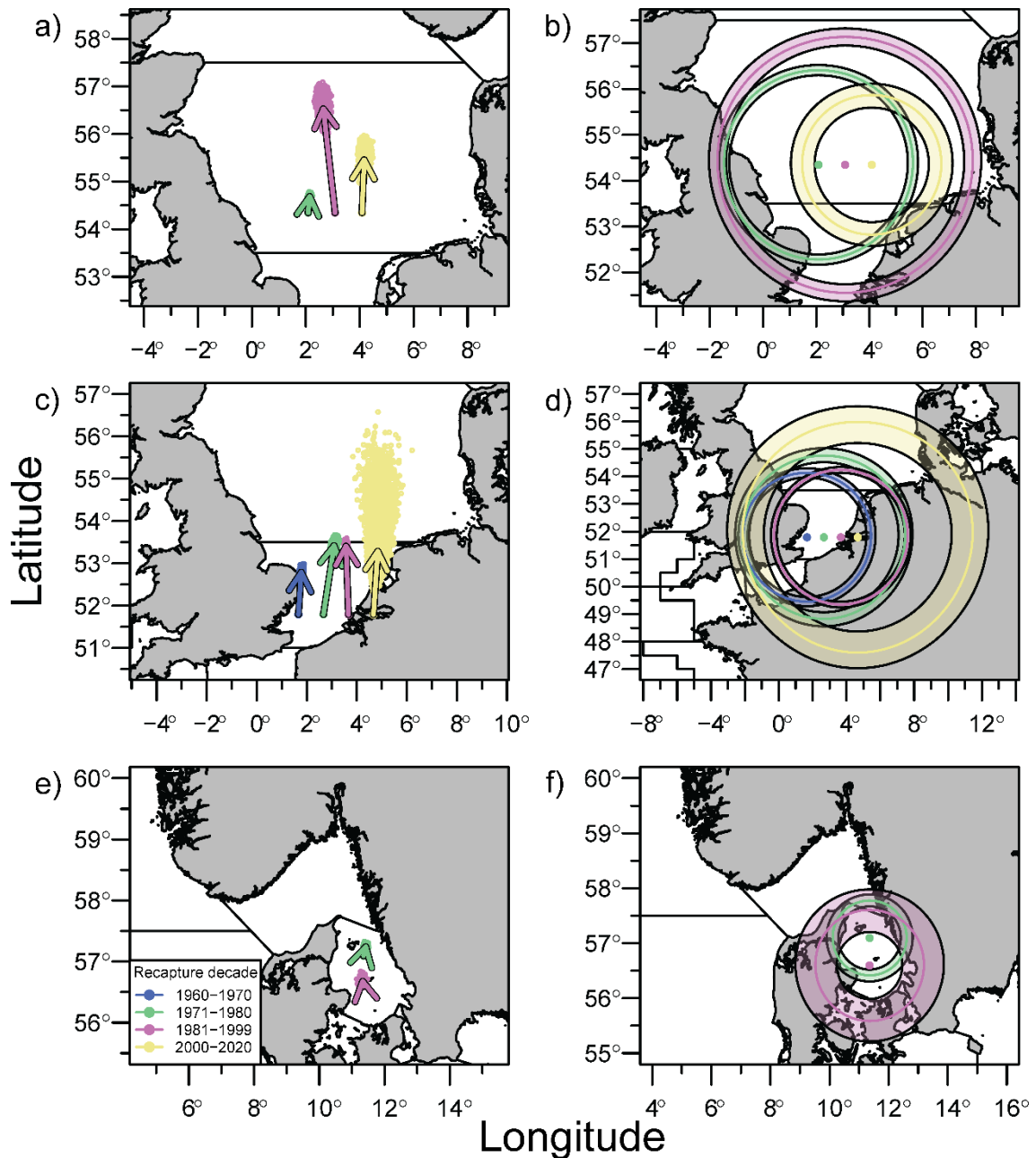
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687

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

693

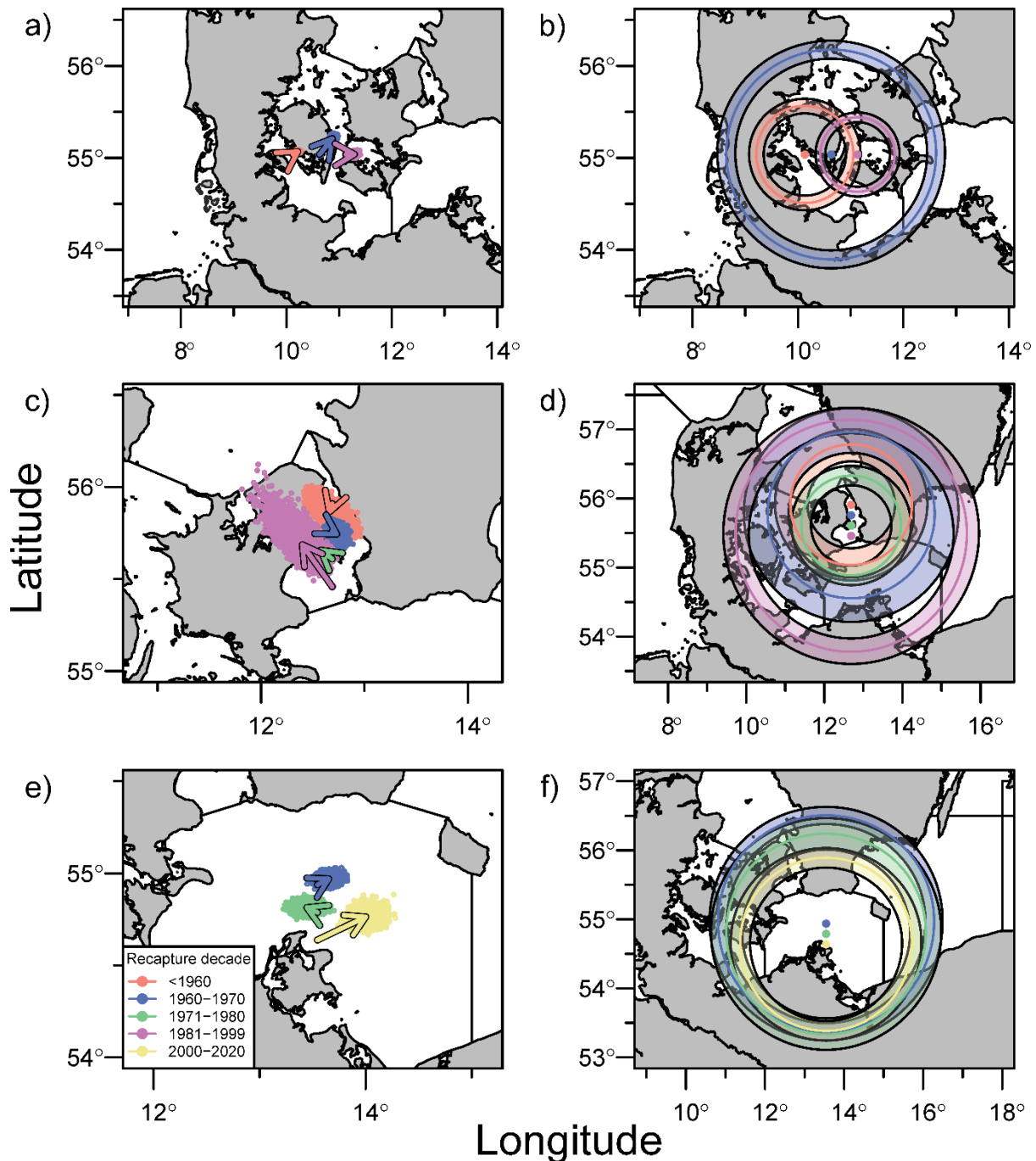


694

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

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

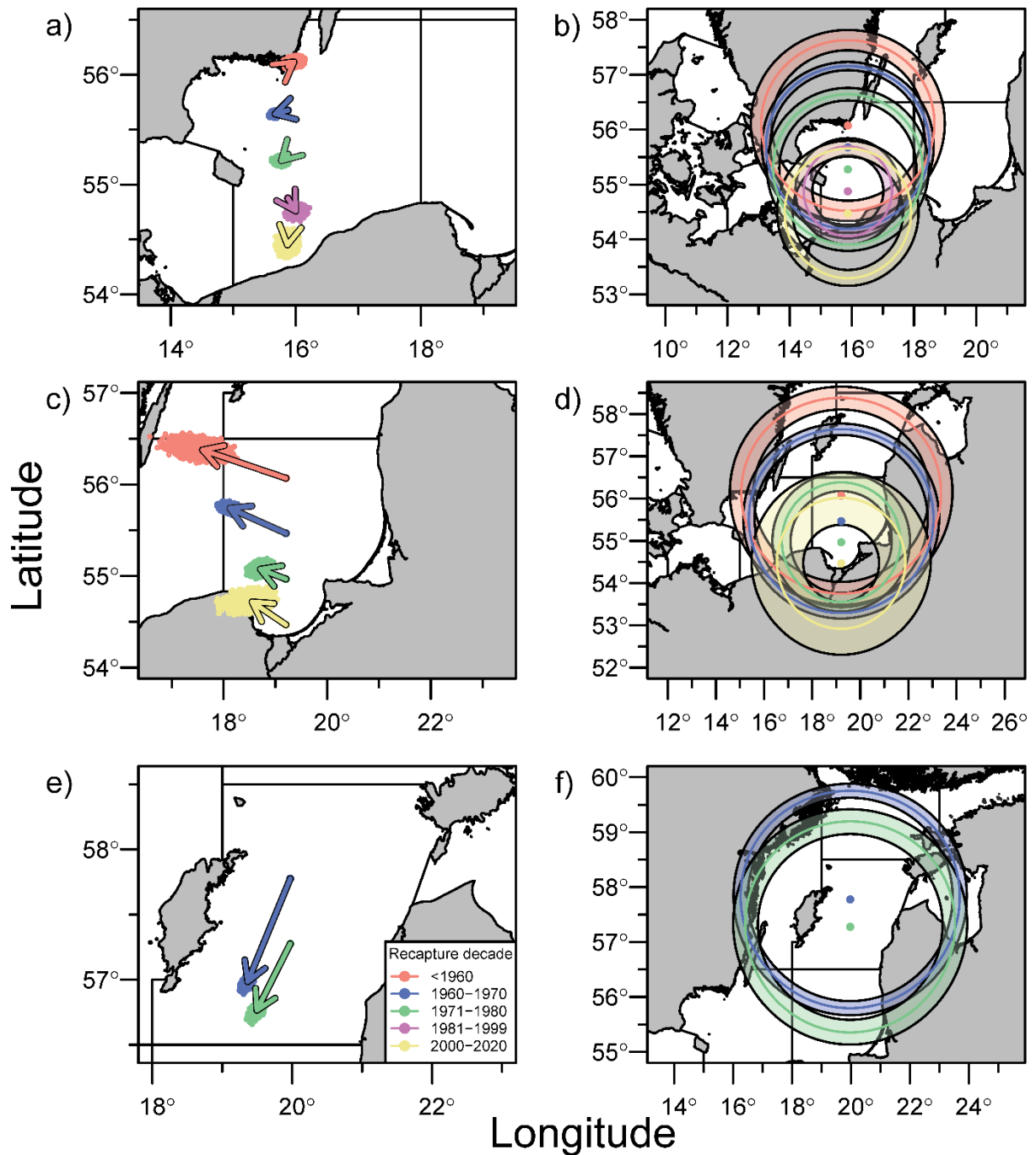
707



708

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

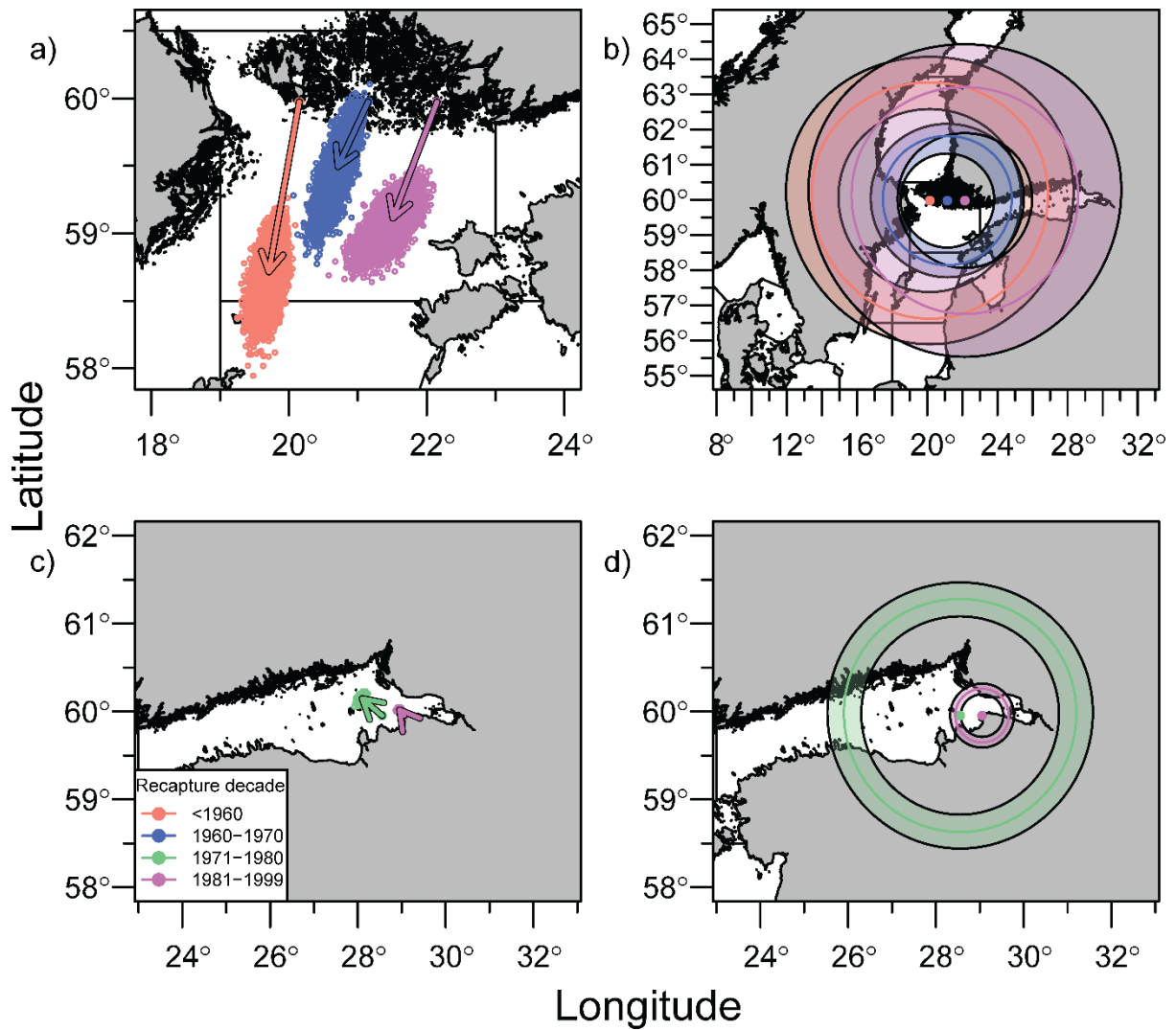
715 difference between release and recapture positions and the size of the circles indicates the
716 relative strength and degree of diffusion in individual areas. The small points denote the end
717 points of 10,000 advection arrows calculated for each area from bootstrapped datasets to
718 show accuracy.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



721

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

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

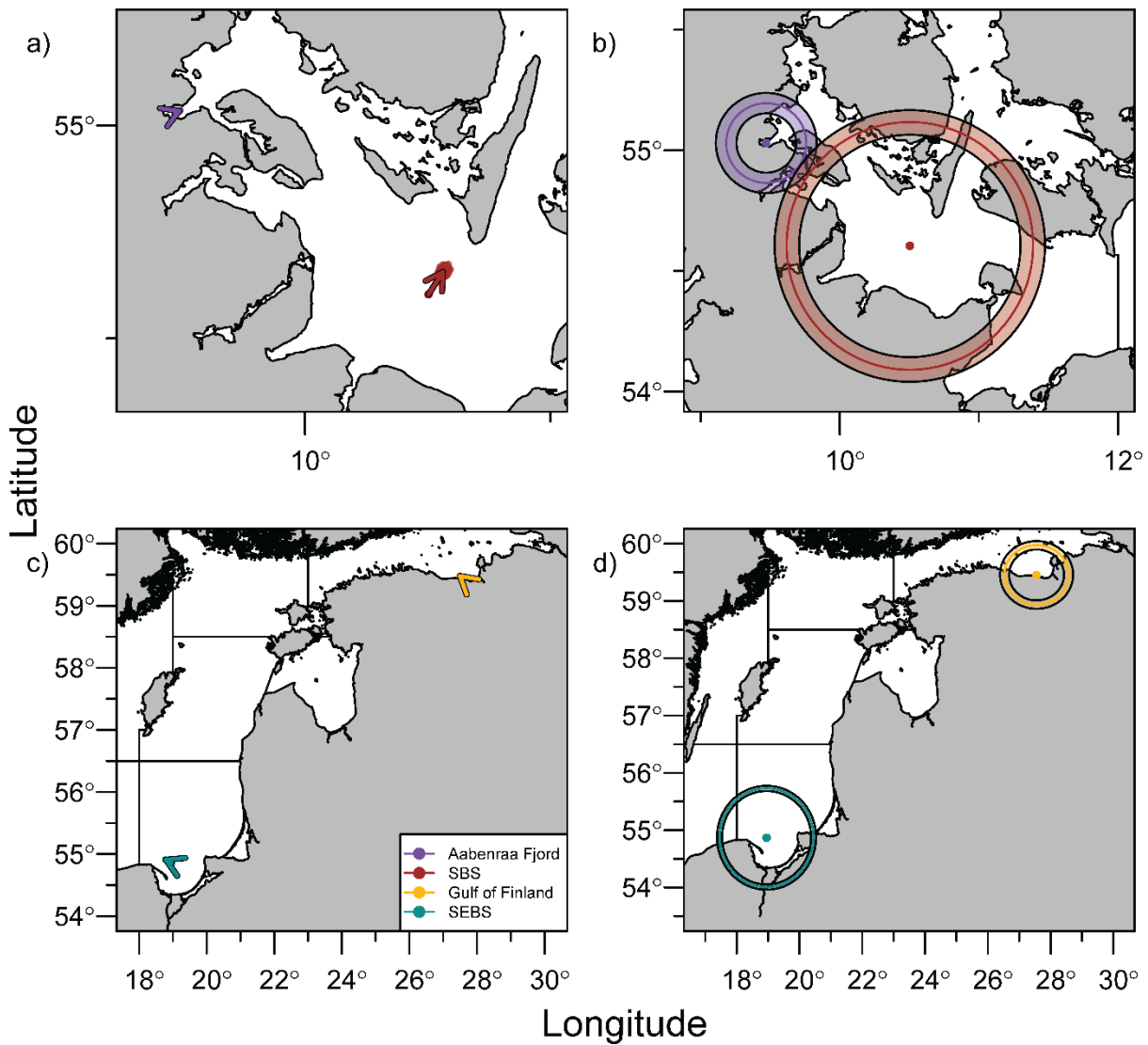


734

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

Advection-diffusion patterns in Atlantic cod

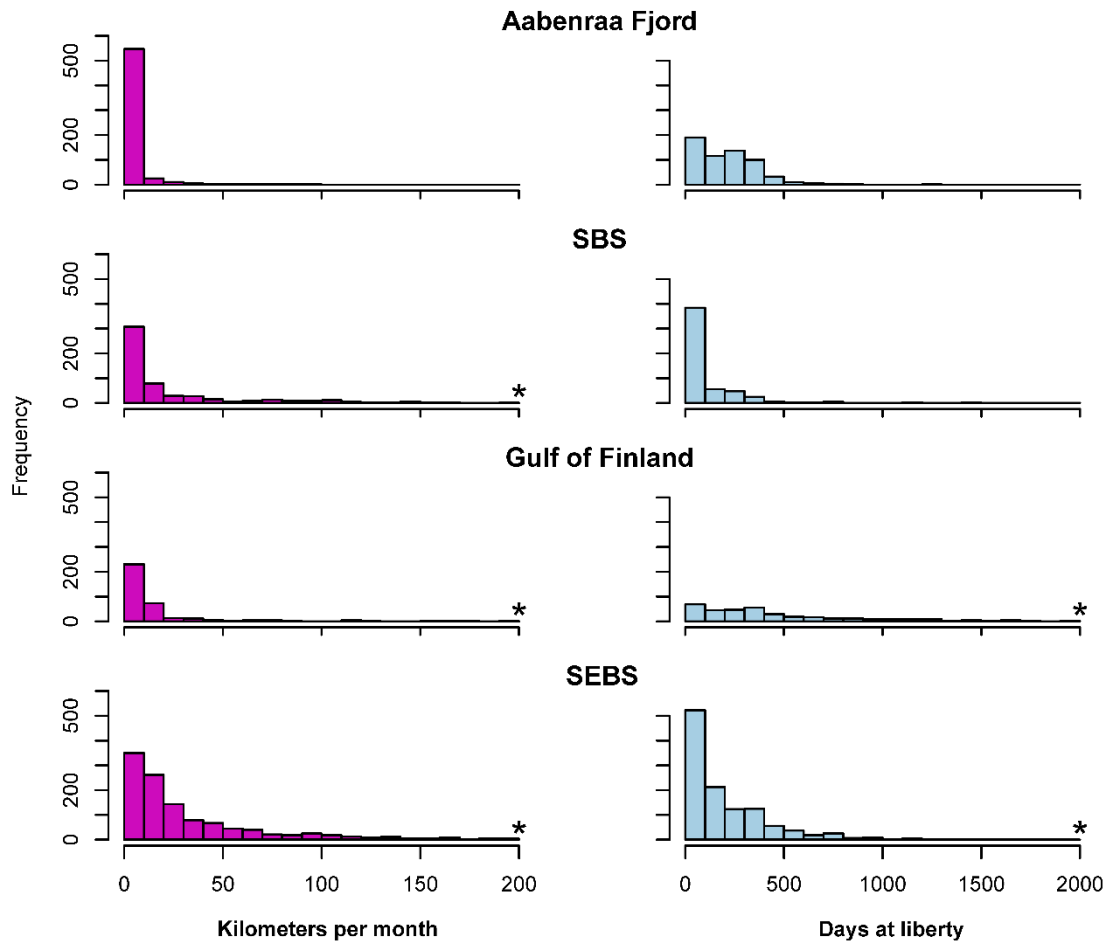
- 744 in each circle indicates the diffusion calculated from the raw data and the outer limits the
- 745 95% confidence intervals calculated from the bootstrapped datasets.



746

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

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

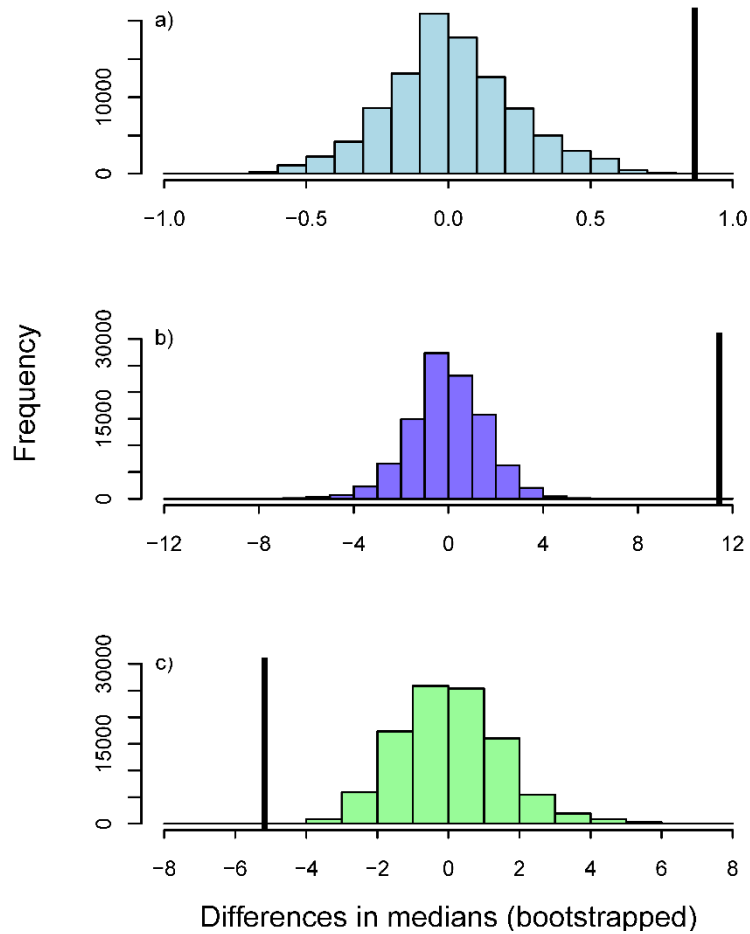


759

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

764

765



766

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

774

775