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

- 3
- 4 Monica Mion<sup>1</sup>\*, Christopher A. Griffiths<sup>1,2,3</sup>, Valerio Bartolino<sup>1</sup>, Stefanie Haase<sup>4</sup>, Annelie Hil-
- 5 varsson<sup>1</sup>, Karin Hüssy<sup>5</sup>, Maria Krüger-Johnsen<sup>5</sup>, Uwe Krumme<sup>4</sup>, Regitze Benedicte Carlstedt
- 6 Lundgreen<sup>5</sup>, Johan Lövgren<sup>1</sup>, Kate McQueen<sup>4,6</sup>, Maris Plikshs<sup>7</sup>, Krzysztof Radtke<sup>8</sup>, Jari Raitaniemi<sup>9</sup>,
- 7 Michele Casini<sup>1,10</sup>.
- 8
- <sup>9</sup> <sup>1</sup>Swedish University of Agricultural Sciences, Department of Aquatic Resources, Turistgatan 5,
- 10 45330 Lysekil, Sweden.
- <sup>11</sup> <sup>2</sup>University of Sheffield, Department of Animal and Plant Sciences, Western Bank, Sheffield, S10

12 2TN, UK.

- <sup>13</sup> <sup>3</sup>Centre for Environment Fisheries and Aquaculture Science, Lowestoft, NR33 0HT, UK.
- <sup>4</sup>Thünen Institute of Baltic Sea Fisheries, Alter Hafen Süd 2, 18069 Rostock, Germany.
- <sup>15</sup> <sup>5</sup>Technical University of Denmark, National Institute of Aquatic Resources, Kemitorvet, DK 2800
- 16 Kgs. Lyngby, Denmark.
- <sup>6</sup>Institute of Marine Research, P.O. Box 1870 Nordnes, 5817 Bergen, Norway.
- 18 <sup>7</sup>Fish Resource Research Department, Institute of Food Safety, Animal Health and Environment, 3
- 19 Lejupes Street, LV-1076 Riga, Latvia.
- 20 <sup>8</sup>National Marine Fisheries Research Institute, Ul. Kołłątaja 1, 81-332 Gdynia, Poland.
- 21 <sup>9</sup>Natural Resources Institute Finland, Luke, Itäinen Pitkäkatu 4 A, FI-20520 Turku, Finland.
- <sup>10</sup>University of Bologna, Department of Biological, Geological and Environmental Sciences, Via
- 23 Selmi 3, 40126 Bologna, Italy.
- 24
- 25 \*corresponding author e-mail: <u>monica.mion@slu.se</u>
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#### 29 Eastern Baltic cod movement patterns

# 30 Abstract

Knowledge of the movement patterns and area utilisation of commercially important fish stocks is critical to management. The Eastern Baltic cod (*Gadus morhua*) has been one of the most commercially and ecologically important stocks in the Baltic Sea but is currently one of the most severely impacted fish stocks in Europe. During the last two decades, this stock has experienced drastic decreases in pop-

35 ulation size, distributional range, individual growth, and body condition, all of which could have af-

36 fected the stock's movements between different areas of the Baltic Sea.

37 In this study, we investigated the seasonal movement patterns of Eastern Baltic cod by re-analysing

38 historical tagging data collected by the countries surrounding the Baltic Sea (1955-1988), and compared

39 historical patterns with contemporary data from a recent international tagging experiment (2016-2019).

40 Our re-analyses of historical data showed the presence of different movement behaviours, resident and

41 seasonally migratory, with larger distances moved by cod released in the northern and central Baltic

42 areas compared to cod released in the southern Baltic areas. Furthermore, trends from the recent tagging

43 experiment indicate a persistent resident strategy in the southern Baltic area.

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

46

47 Keywords: Baltic Sea, Gadus morhua, fish movement, mark-recapture, historical data, home range,

48 kernel density estimation, generalized additive model

## 50 1. Introduction

- 51 Fish often undertake regular migrations between areas of feeding and spawning in order to maximize
- 52 the benefits available from certain habitats for a particular activity or life-stage (Metcalfe, 2006). As a
- 53 consequence, knowledge of migration and dispersal behaviour, termed "movement patterns", is funda-
- 54 mental for managing commercially fished populations, especially in areas where population mixing
- 55 takes place (Rose & Rowe 2015, Neat et al. 2014, Zemeckis et al. 2014), where environmental condi-
- tions are subject to change (Drinkwater 2005, 2015, Engelhard et al. 2014) or where ontogenetic move-
- 57 ments generate marked differences in the spatial distribution of different age groups.
- 58 One of the most widely applied methods to study the movements of wild animals is to use individual 59 markers. Particularly, conventional tagging experiments, which provide information on release and re-60 capture positions, and are used for investigating broad-scale patterns such as area of utilisation and
- 61 movement patterns of individuals (e.g., Righton & Metcalfe 2019).
- 62 The movements of Atlantic cod (Gadus morhua) have been studied extensively with tagging experi-63 ments (Robichaud & Rose 2004). Cod migratory behaviour has been shown to vary markedly with 64 respect to area, season, and major environmental factors (Pálsson & Thorsteinsson 2003). Cod of the 65 same population may adopt different migration routes between areas and their speed of travel can vary 66 considerably during and between journeys (Righton & Metcalfe 2019). Differences in migratory strat-67 egies have also been identified, with some cod remaining relatively stationary, while others redistribute 68 over vast spatial distances that exceed 1000 km (Robichaud & Rose 2004). Cod migratory patterns 69 therefore appear to be complex and there are cases where populations of predominantly migratory and 70 predominantly sedentary cod overlap in certain areas and at certain times of the year (e.g., cod at the 71 Lofoten Islands, Nordeide 1998).
- Baltic Sea cod inhabit an area that differs from most of the other areas where the species is found. The Baltic Sea is, in fact, one of the largest brackish areas in the world, where severe changes in biotic and environmental conditions have occurred in the past hundred years (Reusch et al. 2018). Two genetically distinct cod populations are present in this area: the western Baltic cod (WBC) stock in ICES subdivi-
- sions (SD) 22-24, and the Eastern Baltic cod (EBC) stock in SD 24-32 (Fig.1) with mixing of the two
- 57 stocks occurring in SD 24 (Hüssy et al. 2016, ICES 2021).
- 78 In this extreme environment, the EBC have uniquely adapted to survive and successfully reproduce in 79 the low salinity and low oxygen conditions of the eastern Baltic Sea (Andersen et al. 2009, Nissling et 80 al. 1994), experiencing temperatures and salinities at the upper and lower tolerance limits of Atlantic 81 cod, respectively (Köster et al. 2005, Mackenzie et al. 2007). Historically, cod have been one of the 82 most important commercial species in the Baltic Sea (Bagge et al. 1994; ICES 2014) and, as a major 83 piscivorous fish, play an important structuring role in the ecosystem (Casini et al. 2009). However, the 84 EBC stock is currently one of the most severely threatened fish stocks in Europe (ICES 2020) and since 85 2019 the scientific advice has recommended a complete closure of the EBC fishery (ICES 2021).

86 The EBC stock size has changed considerably, with a peak in the early 1980s (ca. 200,000 tonnes) and 87 a subsequent decline (Eero et al. 2015). Concurrent with the decline in stock size, a number of changes 88 have been observed in the EBC stock, which include reduced body condition, maturation at a smaller 89 size, shift in the timing of peak spawning, reduced growth, increased parasite infestation and thiamine 90 deficiency (Eero et al. 2015, Mion et al. 2021, Engelhardt et al. 2020, Horbowy et al. 2016). After the 91 late 1980s, the decline in cod abundance was also accompanied by a spatial contraction of the stock, 92 primarily to the southern Baltic Sea (SD 25) (Eero et al. 2012, Bartolino et al. 2017, Orio et al. 2019, 93 Wieland et al. 2000). This contraction has been linked to different biotic and abiotic conditions, which caused some areas to become "cod hostile" (Möllmann et al. 2009, Casini et al. 2009). In fact, in the 94 95 last 40 years, the extent of hypoxic areas in the Baltic Sea has increased 5-fold (Carstensen et al. 2014, 96 Meier et al. 2018). In addition, since the mid-1980s, the hydrographic conditions in the eastern spawn-97 ing areas (in SDs 26 and 28) were thought to be no longer suitable for survival of cod eggs, and SD 25 98 is now considered the only area supporting successful reproduction of EBC (Köster et al. 2017, Fig.1). 99 All of these dramatic changes in the marine environment, biology and distribution of the EBC stock 100 may have resulted in changes in the movement patterns of the stock.

- 101 Extensive conventional tagging experiments were conducted from the 1950s to the 1980s to study the 102 movement patterns of cod in the Baltic Sea and adjacent areas. The results of these historical tagging 103 experiments have been summarised by a number of authors (Aro 1989, 2002, Bagge & Steffensen 1989, 104 Robichaud & Rose 2004). Briefly, these studies showed that both sedentary and migratory behaviours were present in the EBC stock and that generally EBC exhibited strong migratory tendencies towards 105 106 the southern Baltic. However, these studies only presented a description of the general movements, 107 rather than a quantitative analysis, and a comparison with contemporary data in light of the deteriorated 108 situation of the EBC stock is lacking.
- 109 In the studies of Mion et al. 2020, 2021, data from most of these historical tagging experiments, together 110 with recent tagging experiments carried out in the southern Baltic Sea in 2016-2019, were digitised and 111 collated for the first time in a unique database. This database provides a perfect opportunity to reanalyse 112 historical data and investigate how the movement patterns of EBC may have changed through time. To 113 achieve this quantitatively, kernel density estimation and generalized additive models were used to ex-114 plore seasonal movement patterns and area utilisation of EBC in different areas of the Baltic Sea. Based 115 on previous research (Aro 1989, 2002, Bagge & Steffensen 1989, Robichaud & Rose 2004), we hy-116 pothesise that during the historic period EBC will exhibit both migratory and sedentary movement strat-117 egies, with distance travelled and area utilisation varying based on release area. Conversely, in the con-118 temporary data, we might expect that changing biotic and abiotic conditions in the northern and central 119 Baltic, as well as contractions in the spatial distribution of EBC towards the south, may have impacted 120 movement rates and area utilisation. Consequently, we hypothesise that recently tagged EBC will show 121 a greater utilisation of southern areas, as northern and central areas are no longer suitable for spawning 122 and are now considered "cod hostile". Any changes in movement patterns or area utilisation of EBC

123 could impact the level of mixing with the WBC stock in the southern Baltic, with potential implications124 for management and future stock recovery.

# 125 2. Materials & Methods

126 Data from historical cod tagging experiments performed between the 1950s and 1980s covering the 127 main historical distribution area of the EBC stock (SDs 24-32), and the more recent TABACOD dataset 128 (2016-2019) covering the main current distribution area of the EBC stock (SDs 24-26), were extracted 129 from the database compiled in Mion et al. (2020, 2021). All records were quality checked for movement 130 analyses, selecting only the records where release and recapture dates and geographical positions as 131 well as total body length measurements at release (*Length<sub>rl</sub>*, cm) were present. Any recaptures of cod 132 that occurred within 30 days of release were excluded. This was to ensure that all cod in this study had 133 sufficient time to recover from the tagging procedure and move to different areas following release. A 134 summary of the different tagging procedures and detailed information on releases and recaptures for 135 these datasets can be found in Mion et al. (2020, 2021) and Hüssy et al. (2020).

#### 136 2.1 Historical data

137 In total, there were 6,798 records suitable for movement analyses. Each record consisted of release and 138 recapture dates and geographical positions (Fig. 2, S1a) as well as measurements of *Length*<sub>rl</sub> (Fig. S1c). 139 Tagging efforts were focused in SDs 24-32 (Fig. 2. S2) and the recaptures were mainly reported by commercial fishers from their catches. The precision of the reported recapture locations varied largely 140 141 between fishers. When only a location name was given (e.g., 4 nm south-east of Dueodde lighthouse), 142 a geographical position was assigned as precisely as possible. In some cases, historical maps of the 143 tagging experiments were used to confirm the position of a particular location name (an example is 144 provided in Fig. 3).

145 Records for tagged cod spanned the mid-1950s to the 1980s, with 65% of cod recaptured during the

146 1970s (Fig. S1a). Cod were released year-round, but with reduced effort in quarter 3 (July-September).

147 Tagging effort was likely reduced in the warmer months of quarter 3 as the thermocline is more pro-

- nounced and less tolerated by cod during the tag and release process (Otterlind 1984, Table S1a).
- 149 Tagging effort varied in space and time. In the southern Baltic areas, in particular the Bornholm basin
- 150 (SD 25), tagging occurred throughout the historical period, whereas in the central and northern Baltic
- areas, tagging effort was more concentrated in certain time periods (Fig. S2).
- 152 The time between release and recapture (days at liberty, *DAL*) ranged between 30 and 3,928 days (me-
- dian: 174 days; Fig S1b). The historical dataset consisted of a mix of adults and juveniles with a Length<sub>rl</sub>
- range from 17 to 98 cm (median: 40 cm; Fig. S1c; size at sexual maturation in the historical period was

- 155 45 to 50 cm for females and 37 to 41 cm for males; Cardinale & Modin, 1999). The return rate (i.e., the
- 156 % of tagged cod that were recaptured and returned to the research institutes) was on average 11.8%
- 157 (Mion et al. 2021).

#### 158 2.2 Contemporary data

159 The contemporary dataset consists of 301 records suitable for movement analyses from the TABACOD project (Hüssy et al. 2020), spanning the years 2016 to 2019. Again, each record consisted of release 160 161 and recapture dates and geographical positions (Fig. 2, S1a) as well as measurements of Lengthr. Cod 162 were released year-round, but with limited numbers in quarter 3 (Table S1b). Tagging efforts were 163 concentrated in SDs 24-26 (Fig. 2), covering the main current distribution area of the stock (Orio et al. 164 2019). The contemporary dataset consisted mainly of adults with a Length<sub>rl</sub> range from 18 to 55 cm (median: 39 cm; current size at sexual maturation is 19 cm; Köster et al. 2017; Fig. S1c). DAL ranged 165 between 30 and 927 days (median: 220 days) (Fig. S1b). The return rate of tagged cod from the TABA-166 167 COD project was 1.5% (Mion et al. 2021).

#### 168 2.3 Analyses of fish movement

169 Due to changes in the main distribution of the Baltic Sea cod stock (Orio et al. 2019 and references 170 therein), the spatial coverage differed by dataset (Fig. 1). The historical data contained records spanning

171 almost the entire Baltic Sea (SDs 24-32), whereas the contemporary dataset contained records restricted

to the southern Baltic Sea (SDs 24-26) where cod concentrate nowadays.

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

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

#### 185 2.3.1 Kernel Density Estimation

186 Kernel Density Estimation (KDE) was used to describe the main distributional areas of EBC tagged in 187 different SDrl. Assuming a homogenous fishing effort, this analysis provides a visualisation of the prob-188 ability of recapturing a tagged individual in a given location (Worton, 1987), conditional on the group-189 ing factors applied ( $SD_{rl}$ , season of recapture and time period) and the constraints of the data (DAL >190 30 days). All KDEs were calculated assuming a bivariate normal kernel using the kernel probability 191 density function from the adehabitatHR package (Calenge 2015) in R. A detailed description of this 192 approach can be found in Calenge (2015) and Griffiths (2019) and has been previous used to describe 193 the area utilisation of Atlantic cod in the Gulf of Maine (Dean et al. 2014) and in the waters surrounding 194 the United Kingdom (Righton et al. 2007; Neat et al. 2014). For clarity, the default 'reference band-195 width' approach was used to estimate the smoothing parameter h for each KDE. Moreover, as is com-196 mon in the movement ecology literature, the 95% and 50% probability contours were extracted from 197 each KDE and assumed to represent the population's 2-dimensional "home range" and "core area", 198 respectively (Worton 1989, Seaman & Powell 1996, Sólmundsson et al. 2015). Home range identifies 199 the area occupied by the majority of cod in their normal activities of spawning and feeding, and the core 200 area identifies the most intensively used areas within an animal's home range (Burt 1943, Powell 2000).

201 For each  $SD_{rl}$ , KDEs were estimated separately for the EBC spawning and feeding recapture seasons.

202 Due to possible mixing of stocks (EBC and WBC) in SD 24 and the fact that some cod released in SD

203 24 might belong to the WBC stock, a sensitivity analysis was conducted to estimate KDEs for the WBC

spawning (i.e. December to April which includes the main spawning season and a period of migration

- to and from the spawning ground; Hüssy 2011) and feeding seasons (defined as May to November).
- 206 This analysis showed that the estimated KDEs from the WBC feeding and spawning seasons were sim-

ilar to the estimated KDEs from the EBC feeding and spawning seasons, both for historical and con-

- 208 temporary datasets (Fig. S3). In addition, for the contemporary data, genetic and otolith shape analyses
- 209 revealed that  $\sim 80$  % of the recaptured cod released in SD 24 belonged to the EBC stock, highlighting

210 a higher presence of EBC in the recaptures (Hüssy et al. 2020).

211 The size  $(km^2)$  of the home ranges and core areas for each  $SD_{rl}$  and season were calculated in ArcMAP

212 (v.10.4.1). In addition, in the southern Baltic Sea, the area of home range overlap (%) and core area

overlap (%) between historical and contemporary datasets were also calculated for each  $SD_{rl}$ .

214 2.3.2 Generalized additive models (GAMs)

215 For the KDE analyses, records were grouped into seasons without taking into account the effects of

216 DAL on d (e.g., cod that were at liberty for two months were considered alongside cod that were at

217 liberty for two years). Previous studies on North Atlantic cod stocks described a linear relationship

218 between *d* and *DAL* for some groups, while for other groups a non-linear relationship linked to season-

ality was found (Rogers et al. 2014, Espeland et al. 2008). Therefore, to further explore the seasonal

220 movement patterns of EBC, generalized additive models (GAMs), with a restricted maximum likeli-

- hood approach (Wood 2006), were applied to the relationship between *d* and *DAL*. Our prior expectation
- was that the relationship between *d* and *DAL* would be affected by cod release location. Thus, *d* would
- change according to the proximity of  $SD_{rl}$  to spawning and feeding areas (e.g., with shorter d for cod
- recaptured during the spawning period and released in an area closer to the spawning ground).  $Length_{rl}$
- was included as an additional explanatory variable to assess possible effects of fish size and ontogenyon *d*.
- 227 The GAM model was formulated as follows:

$$d = \alpha + s(DAL:SD_{rl}) + Length_{rl} + \varepsilon$$
<sup>(2)</sup>

230

228

where  $\alpha$  is the intercept, *s* is the thin plate smoothing spline function (Wood, 2003) and  $\varepsilon$  an error term. An interaction was used between the continuous variable *DAL* and the factor *SD<sub>rl</sub>* to assess possible seasonal differences in *d* between *SD<sub>rl</sub>*.

234 Due to the low number of recaptures for the contemporary dataset, the GAM was performed only with 235 the historical dataset. To analyse the shape of the relationship between d and DAL, two separate models 236 were fitted to data with release dates from quarter 2 (April – June: spawning period) and from quarter 237 4 (October – December; feeding period). Preselection of the quarter of release and treatment of DAL as 238 a continuous variable allowed us to capture possible effects of seasonality (movements between spawn-239 ing and feeding grounds) on d. A gamma distribution with a logarithmic link function was used for the 240 GAMs because it best represented the distribution of d. 241 To improve consistency and representation of the datasets, the GAMs were fitted to restricted data. 242 Only cod with a *DAL* between 30 and 550 days and a *Length*<sub>*rl*</sub> between 25 and 70 cm (n = 1,202 for cod

- released in quarter 2; n = 1,981 for cod released in quarter 4) were considered. To avoid taking the log
- of zero, all zero distances were given the value of the lowest observed distance (~1 km). All GAMs
- 245 were implemented using the "mgcv" library in R (Wood 2006). Model fit was assessed by visual in-
- spection of the residuals (see Fig. S4).

# 247 **3.** Results

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

254 5; Table S2).

3.1 Movement patterns in the spawning season with Kernel Density Estimation

256

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

263 In the contemporary dataset, recaptures during the spawning season mostly occurred in the same SD of 264 release (Fig. 7; Table 1). These findings are consistent with the historical dataset from the southern Baltic areas with high home range overlaps of  $\sim 50$  % (Fig. 8; Table 2). However, some differences 265 266 between the datasets occurred in the southern Baltic area. In the contemporary dataset, core areas and 267 home ranges in SD 24 and 25 occurred in close proximity to Bornholm Island on the boundary between 268 the two SDs (Fig. 8), while in the historical dataset the home range extended towards the western or 269 eastern direction depending on if cod were released in SD 24 or 25, respectively. In addition, cod re-270 leased in SD 26 had two core spawning areas in the historical period, (SD 25 and 26) while in the 271 contemporary dataset cod were mainly recaptured in SD 26 (Fig. 8). In the historical dataset, recaptures 272 during the spawning season of cod released in the northern and central areas (SDs 27-32) were mainly 273 found in SD 25 and to some extent in SD 26, or in the SD of release (Fig. 6; Table 1). One exception to 274 this pattern occurred in SD 32, where cod were found to have core area and home range within SD 32.

#### 3.2 Movement patterns in the feeding season with Kernel Density Estimation

276 In general, both home ranges and core areas during the feeding season were similar to the home ranges 277 and core areas detected during the spawning season, irrespective of the dataset (Fig. 6 and 7; Table 2). 278 In the historical dataset, there was a general trend of recapture close to the area of release, albeit some 279 notable exceptions were observed. For example, cod released in SD 29 had core feeding areas that were 280 limited to the northern Baltic, while in the spawning season a core area was also detected in the southern 281 Baltic. Cod released in SD 26 had a core feeding area in SD 26, and an extended home range, which 282 spanned SD 25, SD 26 and SD 28.2. During the feeding season of cod released in the southern Baltic 283 areas, the overlap in core areas and home ranges between historical and contemporary datasets was 284 higher than in the spawning season (Fig. 8; Table 2). This high overlap was especially true for cod 285 released in SD 24 (home range overlap ~91 %) but less so in SDs 25 and 26 (home range overlap ~55 286 % and 78 %, respectively; Table 2). Visually, foraging areas appeared to be constricted in the contem-287 porary period (Fig. 8).

- 288 3.3 Movement patterns with Generalised Additive Models
- GAM models applied to the historical dataset for cod released in quarter 2 and 4 explained 15.5 % and
- 290 15.7 % of the deviance of the overall model, respectively (see Tables S3 and S4 for model summaries).
- For cod released in quarter 2 (spawning period) in SD 24, 26, 29 and 32, *DAL* had no significant effect
- on the distance between release and recapture positions, while for cod released in SD 25, 27 and 28.2
- 293 the effect was significant showing that *d* slightly increased over time and reached an asymptote (Table
- 294 S3, Fig. S5). For cod released in quarter 4 (feeding period) for most of the  $SD_{rl}$  the DAL had a significant
- effect on *d* (Table S4, Fig. S6). In particular, a positive, almost linear effect of *DAL* on *d* was found for
- cod released in SD 25 and 29. In comparison, cod released in SD 24, 26, 27 and 28.2 displayed a positive
- 297 nonlinear relationship between DAL and d, whereby d increased to a point but then declined to a mini-
- mum at around 300 to 350 *DAL*, and then increased thereafter (Table S4, Fig. S6). There was no signif-
- icant effect of *DAL* on *d* for cod released in SD 32 (Table S4, Fig. S6).
- 300 A significant positive nearly linear effect of  $Length_{rl}$  on d was found for cod released both in quarter 2
- and 4, with cod displaying an increase in *d* with increasing body size (Tables S3 and S4, Fig. S5 and
- 302 S6). Therefore, larger cod tended to be recaptured at more distant locations, whereas smaller cod tended
- 303 to be recaptured closer to the point of release.

## 304 4. Discussion

305 The re-analysis of historical tagging data combined with contemporary data enabled the description of 306 movement patterns and area utilisation of EBC for both time periods. In agreement with our expecta-307 tions, this study has shown that in the historical period, cod released in the central and northern area of 308 the Baltic generally travelled greater distances than cod released in the southern Baltic. Furthermore, 309 data from the recent tagging experiment indicated that the historical movement patterns in the southern 310 Baltic have been generally maintained over time. The results from the kernel density dstimation analysis 311 confirmed the patterns described in previous research (Aro 1989, 2002, Bagge & Steffensen 1989, Ro-312 bichaud & Rose 2004), highlighting two types of movement behaviours for EBC: sedentary (i.e. cod 313 recaptured year-round within the area of release) and migratory (i.e. cod covering larger distances, 314 probably linked to spawning in areas separated from the feeding grounds).

The data show that management boundaries between SD 24 and 25 are crossed all year round, both in the historical and in the contemporary period. However, this study also suggests that the percentage of cod released in SD 25 and recaptured in SD 24 has increased in the recent period. In the historical period, 6 % and 7 % of cod released in SD 25 were recaptured in SD 24 during the spawning and feeding seasons, respectively. On the other hand, in the recent period 30 % and 41 % of cod released in SD 25 were recaptured in SD 24 during the spawning and feeding seasons, respectively. These findings suggest 321 that the use of SD 24 by EBC has increased in the recent period, an observation that supports our ex-322 pectations on higher utilisation of southern areas and could result in an increased likelihood of mixing 323 between EBC and WBC in SD 24. There can be limitations to the use of tagging data to quantify the 324 degree of mixing in different areas and these need to be acknowledged. For instance, differences in 325 tagging location might influence the likelihood of recapture in a different area from that of release. In 326 fact, in the recent tagging experiment, cod in SD 25 were mainly tagged in proximity to the border with 327 SD 24, thus potentially increasing the possibility of cod released in SD 25 being recaptured in SD 24. 328 However, these results are in line with recent increases in the occurrence of EBC in SD 24, as estimated 329 by shape analysis of archived otoliths (Hüssy et al. 2016). The KDE analysis results also support this 330 finding. In the historical period, during the spawning season, core areas suggested that cod released in 331 SDs 24 and 25 were mainly recaptured in the Arkona Basin (i.e. spawning area of WBC), and in the 332 Bornholm Basin (i.e. main spawning area for the EBC), respectively. The bimodal core areas observed 333 for cod released in SD 26 indicate utilisation of both the Bornholm Basin and Gdansk Deep as the main 334 spawning areas, with cod likely moving between the two. In the contemporary period, the home ranges 335 were similar to the historical period, although core areas of cod released in SDs 24 and 25 were con-336 centrated around Bornholm Island (SDs 24 and 25) during the spawning season, whilst in the past, core 337 areas concentrated mainly in the respective area of release. Since EBC currently inhabit also SD 24 338 (Hüssy et al. 2016), these results could add evidence that, contrary to historical assumptions (Bagge et 339 al. 1994), EBC spawn in the Arkona Sea as shown by Hüssy et al. 2016 and Hemmer-Hansen et al. 340 2019.

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

348 One interesting finding during the historical period is the presence of sedentary groups in the northern 349 and central Baltic. A year-round resident population in the northern Baltic could be explained by the 350 presence of juveniles (i.e. individuals that have not reached sexual maturity) that do not participate in a 351 spawning migration. In fact, GAM results suggested that smaller fish tended to be recovered at locations 352 closer to their release positions than larger cod. However, 56 % of cod that stayed in this area had a 353 length at release that exceeded the average length at maturation (i.e. 40 cm), indicating that individuals 354 with sedentary behaviour also included adults. In addition, fish species are thought to skip spawning 355 when in low body condition as they may lack the necessary energetic reserves to successfully migrate 356 or spawn (Jørgensen et al. 2006). Due to the low salinity, fertilisation of the eggs was deemed impossi-357 ble in the Åland Sea and further north. Previously, it was assumed that recruitment to these northern

areas took place mostly through larval drift and the passive transport of young cod at times of strong
influxes of water from the south (Otterlind 1983, 1984), rather than recruitment from a local population
(Hinrichsen et al. 2017). However, spawning events have previously been observed in the Åland Sea

361 (Otterlind 1976, Vallin et al. 1999), suggesting the presence of a locally reproducing population.

362 Some active migration northward of young cod can probably take place, although migration of cod from 363 the central and southern parts of the Baltic proper to the Åland Sea was negligible according to the historical tagging results. Due to biological problems (i.e., high tagging mortality of smaller fish), it 364 was not possible to effectively tag cod smaller than 20 cm in total length, therefore, northern active 365 366 migration of young cod could have been missed in the historical period. More information is needed on 367 oceanographic processes, larval drift and possible active adult migration towards the Åland Sea to un-368 derstand the possible connectivity between these areas. Preliminary results indicate that some individ-369 uals from the Åland Sea have higher successful fertilisation at lower salinities compared to cod from 370 the Gotland and Bornholm areas (Bergström et al. unpublished). Thus, although the results of our study 371 for the northern Baltic area are restricted to the historical period, they could contribute evidence to the 372 presence of a sub-population of cod that remain and spawn in the Åland Sea. Preliminary genetic studies 373 showed some level of separation, although not very distinct, of cod in this area (Bergström et al. un-374 published). Further genetic studies are needed to confirm the possible presence of a resident population 375 in the area of the Åland Sea.

376 For cod released in SD 32 (Gulf of Finland), home range analyses indicate a year-round spatial distinc-377 tion from the home ranges of cod released in other Baltic areas. These cod are found to exhibit a sed-378 entary behaviour and are recaptured mainly in SD 32 during both feeding and spawning seasons. How-379 ever, in other studies the migration of adult cod southwards was evident and linked to spawning (Aro 380 & Sjöblom 1983, Otterlind, 1985). These differences are likely due to the fact that in the present study 381 tagging experiments in SD 32 were limited compared to previous evaluations. This is because the pre-382 sent study does not include transportation experiments of marked cod to other locations (Aro & Sjöblom 383 1983, Otterlind 1985). Further work to digitise additional historical records from this area would be 384 required to examine this discrepancy.

385 Generalized additive models were used to account for the effect of DAL on the movement patterns of 386 cod during the historical period. Different patterns were found for cod released during the spawning or 387 feeding periods, probably linked to the proximity to spawning grounds and presence of differing be-388 havioural strategies (i.e. sedentary and migratory). Cod released during the spawning period (quarter 2) 389 in SDs 25, 26 and 28.2 were potentially already in proximity to EBC spawning grounds, while cod 390 released in SD 24 were in proximity to one of the WBC spawning grounds (Bleil & Oeberst 2002). The 391 results indicate that cod released during the spawning period in SDs 24, 26, 29 and 32 were recaptured 392 closer to positions of release all year round. These findings suggest that these cod were sedentary, prob-393 ably spawning in the area of release or not participating in a spawning migration (e.g. cod released

- during spawning period in SD 29). For cod released during the spawning period in SDs 25, 27 and 28.2,
- 395 the distance between release and recapture positions increased through time, suggesting that cod moved
- away from the area of release but did not necessarily return.
- Cod released during the feeding period (quarter 4) in SDs 24, 26, 27 and 28.2 showed approximately
- an annual pattern in the distance moved from the release. The presence of this relationship between d
- and *DAL* indicates that cod moved away from the area of release, probably to reach spawning grounds,
- 400 and then returned a year later, suggesting homing behaviour to both feeding and spawning areas. Cod
- 401 released in SDs 25 and 29 during the feeding period moved away from the area of release but did not
- 402 appear to return.
- In a true migratory population, a clear cyclical signal would be expected as individuals move away and return. This is lacking in some areas, and this could be due to the presence of different movement behaviours, as indicated by the KDE analysis of the historical dataset. Since conventional tagging data consist of only two positions, release and recapture, GAM may have low power when describing temporal cyclic patterns of migration, especially when a mix of behaviours is present (Espeland et al. 2008). Individuals that alternate between spawning and feeding seasons, as well as those that display sedentary behaviour, would obscure this pattern (Espeland et al. 2008).
- 409 behaviour, would obscure this pattern (Espeland et al. 2008).
  410 Our findings, using quantitative methods to re-analyse historical tagging data combined with contem-
- 411 porary data, provide additional information on general movement patterns between different areas of 412 the Baltic Sea. However, caution is advised regarding some limitations of our analysis. Unfortunately, 413 as is the case for many historical tagging studies, there is a lack of spatially-resolved fisheries effort 414 data. Historical catch data does show lower catches in the northern Baltic Sea compared to the south. 415 This could have prevented a full detection of a northward migration of cod due to a lower probability 416 of recapture in the northern Baltic Sea. In addition, if fishing effort is higher in one area (e.g. SD 24) 417 compared to others, it might explain any lack of change in the movements of tagged cod. Further work 418 is needed to account for spatio-temporal patterns in fishing effort within our analysis, which might result 419 in an overrepresentation of some recapture locations (Wright et al. 2006). In addition, conventional 420 mark-recapture data are restricted to information on release and recapture but nothing is known about 421 movement between these two points. Application of dynamic migration models may enhance our 422 knowledge of movements on a smaller time scale. Data-storage tags also offer an advanced method for 423 gathering high-resolution data on demersal fish movements in both the horizontal and vertical dimen-424 sion (Griffiths et al. 2018) and allow behaviour to be related to the physical environment (Patterson et 425 al. 2009). Combining results from conventional tagging data with fine-scale movement patterns of in-426 dividual cod would facilitate further study on migration and how it might be related to changes in the
- 427 environment.
- Failure to incorporate information on the meta-population dynamics of marine fishes in fishery management risks the depletion of local sub-populations that may eventually contribute to stock collapse
  (Hilborn et al. 2003; Kritzer & Sale 2004; Heath et al. 2008, Neat et al. 2014). Our study suggests that

- 431 possible meta-populations in the Baltic Sea (e.g. northern and southern Baltic cod) may have existed in
- the historical period with individuals experiencing different patterns of movement. This means that cod
- 433 from different areas of the Baltic may have experienced different salinity, oxygen and temperature con-
- 434 ditions (Mion et al., 2021). The applied implications of this are that the removal of individuals in one
- area could be more costly than in other areas, therefore a spatial adjustment of exploitation strategies,
- 436 such as the setting of a maximum sustainable yield for each spatial unit, may be required to ensure
- 437 sustainable harvesting (Holmes et al. 2014). Future management of fisheries, especially where meta-
- 438 populations exist or where mixing between different stocks occur, should implement the use of tagging
- data in area-based assessment models (e.g. Stock Synthesis; Methot & Wetzel, 2013) to provide a more
   reliable estimation of stock status.
- 441 Our results show that re-analysing historical conventional tagging data can still provide important in-
- sights on movement patterns and area utilisation that can be readily compared with contemporary data.
- 443 In doing so, the biological knowledge of a stock, or multiple stocks, is increased, which could inform
- 444 future management actions.

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# 451 6. References

- Andersen Ø, Wetten OF, De Rosa MC, Andre C, Carelli Alinovi C, Colafranceschi M, Brix O,
  Colosimo A (2009) Haemoglobin polymorphisms affect the oxygen-binding properties in Atlantic
  cod populations. Proc Royal Soc B 276:833–841, <a href="https://doi.org/10.1098/rspb.2008.1529">https://doi.org/10.1098/rspb.2008.1529</a>.
- Aro E (1989) A review of fish migration patterns in the Baltic. Rapports et Procès-verbaux des Réunions
   du Conseil International pour l'Exploration de la Mer 190:72–96
- Aro E (2002) Fish migration studies in the Baltic Sea a historical review. ICES J Mar Sci 215:361 370
- 459 Aro E & Sjöblom V (1983) Cod off the coast of Finland in 1974-82. ICES CM 1983/J: 25, 17 pp.
- Bagge O & Steffensen E (1989) Stock identification of demersal fish in the Baltic. Rapports et Procès verbaux des Réunions du Conseil International pour l'Exploration de la Mer 190: 3–16
- 462 Bagge O, Thurow F, Steffensen E, Bay J (1994) The Baltic cod. Dana 10:1–28
- Bartolino V, Tian H, Bergström U, Jounela P, Aro E, Dieterich C, et al. (2017) Spatio-temporal dynamics of a fish predator: Density-dependent and hydrographic effects on Baltic Sea cod population.
  PLoS ONE 12(2):e0172004, https://doi.org/10.1371/journal.pone.0172004

- Bleil M & Oeberst R (2002) Spawning areas of the cod stock in the western Baltic Sea and minimum
   length at maturity. Arch fish mar res 49:243-258
- Bolle LJ, Hunter E, Rijnsdorp AD et al. (2005) Do tagging experiments tell the truth? Using electronic
   tags to evaluate conventional tagging data. ICES J Mar Sci 62:236–246
- 470 Burt WH (1943) Territoriality and home range concepts as applied to mammals. J Mammal 24:346–352
- 471 Calenge C (2015). Home Range Estimation in R: The adehabitatHR Package. R Package Version 0.3.23
- 472 Cardinale M & Modin J (1999) Changes in size-at-maturity of Baltic cod (*Gadus morhua*) during a
   473 period of large variations in stock size and environmental conditions. Fish Res 41:285–295
- 474 Cardinale M & Svedäng H (2011) The beauty of simplicity in science: Baltic cod stock improves rapidly
  475 in a 'cod hostile' ecosystem state. MEPS 425:297-301. https://doi.org/10.3354/meps09098
- 476 Carstensen J, Andersen JH, Gustafsson BG, Conley DJ (2014) Deoxygenation of the Baltic Sea during
   477 the last century. Proc Natl Acad Sci U S A 111:5628–5633
- Casini M, Hjelm J, Molinero JC, Lövgren J, Cardinale M, Bartolino V, Belgrano A, Kornilovs G (2009)
   Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. Proc Natl Acad Sci USA 106:197–202
- 481 Dean MJ, Hoffman WS, Zemeckis DR, Armstrong MP (2014) Fine-scale diel and gender-based patterns
  482 in behaviour of Atlantic cod (*Gadus morhua*) on a spawning ground in the Western Gulf of Maine.
  483 ICES. J. Mar. Sci. 71(6): 1474–1489.
- 484 Drinkwater K (2005) The response of Atlantic cod (*Gadus morhua*) to future climate change. ICES J
   485 Mar Sci 62:1327–1337
- 486 Drinkwater K (2015) Comparison of the response of Atlantic cod (*Gadus morhua*) in the high-latitude
  487 regions of the North Atlantic during the warm periods of the 1920s–1960s and the 1990s–2000s.
  488 Deep Sea Res Part II Top Stud Oceanogr 56:2087–2096
- 489 Eero M, Hjelm J, Behrens J, Buchmann K, Cardinale M, Casini M, Gasyukov P, Holmgren N, Horbowy
  490 J, Hüssy K, Kirkegaard E (2015) Eastern Baltic cod in distress: biological changes and challenges
  491 for stock assessment. ICES J Mar Sci 72(8):2180–2186
- 492 Eero M, Vinther M, Haslob H, Huwer B, Casini M, Storr-Poulsen M, Köster FW (2012) Spatial man493 agement of marine resources can enhance the recovery of predators and avoid local depletion of
  494 forage fish. Conserv Lett 5:486–492
- Engelhard GH, Righton DA, Pinnegar JK (2014) Climate change and fishing: a century of shifting
   distribution in North Sea cod. Glob Chang Biol 20:2473–2483
- Engelhardt J, Frisell O, Gustavsson H, Hansson T, Sjöberg R, Collier TK, Balk L (2020) Severe thia mine deficiency in eastern Baltic cod (*Gadus morhua*). PLoS One 15(1):e0227201,
   <a href="https://doi.org/10.1371/journal.pone.0227201">https://doi.org/10.1371/journal.pone.0227201</a>
- Espeland SH, Olsen EM, Knutsen H. et al. (2008) New perspectives on fish movement: kernel and
   GAM smoothers applied to a century of tagging data on coastal Atlantic cod. MEPS 372:231–241.
- Griffiths CA (2019) Using electronic tagging data to investigate the individual-, population-and community-level consequences of movement in free-roaming marine fish. Doctoral dissertation, University of Sheffield and University of Tasmania.
- Griffiths CA, Patterson T, Blanchard J, Righton D, Wright S, Pitchford J, Blackwell P (2018) Scaling
   marine fish movement behaviour from individuals to populations. Ecol Evol 8:10.1002/ece3.4223

- Heath MR, Kunzlik PA, Gallego A, Holmes SJ, Wright PJ (2008) A model of meta-population dynam ics for North Sea and West of Scotland cod—the dynamic consequences of natal fidelity. Fish Res
   93:92–116
- Hemmer-Hansen J, Hüssy K, Baktoft H, Huwer B, Bekkevold D, Haslob H, et al. (2019) Genetic anal yses reveal complex dynamics within a marine fish management area. Evol Appl 12:830–844
- Hilborn R., Quinn TP, Schindler DE, Rogers DE (2003) Biocomplexity and fisheries sustainability.
   PNAS 100:6564–6568.
- Hinrichsen HH, von Dewitz B, Lehmann A, Bergstrom U, Hussy K (2017) Spatio-temporal dynamics 514 515 155:28-40, cod nursery areas in the Baltic Sea. Prog Oceanogr of https://doi.org/10.1016/j.pocean.2017.05.007 516
- Horbowy J, Podolska M, Nadolna-Altyn K (2016) Increasing occurrence of anisakid nematodes in the
  liver of cod (*Gadus morhua*) from the Baltic Sea: Does infection affect the condition and mortality
  of fish? Fish Res 179:98–103
- Hüssy K (2011). Review of western Baltic cod (*Gadus morhua*) recruitment dynamics. ICES J Mar Sci
   68:1459–1471
- 522 Hüssy K, Hinrichsen HH, Eero M, Mosegaard H, Hemmer-Hansen J, Lehmann A, Lundgaard LS (2016) 523 Spatio-temporal trends in stock mixing of eastern and western Baltic cod in the Arkona Basin and 524 the implications for recruitment. ICES J Mar Sci 73(2):293-303, https://doi.org/10.1093/icesjms/fsv227 525
- Hüssy K, Casini M, Haase S, Hilvarsson A, Horbowy J, Krüger-Johnsen M, Krumme U, Limburg K,
  McQueen K, Mion M, Olesen HJ, Radtke K (2020) Tagging Baltic Cod TABACOD. Eastern Baltic
  cod: Solving the ageing and stock assessment problems with combined state-of-the-art tagging methods. DTU Aqua Report no. 368-2020. National Institute of Aquatic Resources, Technical University
  of Denmark. 64 pp. + appendices
- ICES (2014) Report of the Baltic Fisheries Assessment Working Group (WGBFAS), 310 April 2014,
   ICES HQ, Copenhagen, Denmark. ICES CM 2014/ACOM:10. 919 pp
- ICES (2020) Baltic Fisheries Assessment Working Group (WGBFAS). ICES Scientific Reports. 2:45.
   632 pp. https://doi.org/10.17895/ ices.pub.6024
- ICES (2021) Cod (*Gadus morhua*) in subdivisions 24–32, eastern Baltic stock (eastern Baltic Sea). In
   Report of the ICES Advisory Committee. ICES Advice 2021, cod.27.24-32,
   https://doi.org/10.17895/ices.advice.7745
- Jørgensen C, Dunlop ES, Opdal AF, Fiksen Ø (2008) The evolution of spawning migrations: state de pendence and fishing-induced changes. Ecology 89(12):3436–3448
- Kritzer JP & Sale PF (2004) Metapopulation ecology in the sea: from Levins' model to marine ecology
   and fisheries science. Fish Fish 5:131–140.
- Köster F, Möllmann C, Hinrichsen H, Wieland K, Tomkiewicz J, Kraus G, Voss R, Makarchouk A,
   Mackenzie B, Stjohn M (2005) Baltic cod recruitment the impact of climate variability on key
   processes. ICES J Mar Sci 62:1408–1425, https://doi.org/10.1016/j.icesjms.2005.05.004
- Köster FW, Huwer B, Hinrichsen HH, Neumann V, Makarchouk A, Eero M, Dewitz BV et al. (2017)
   Eastern Baltic cod recruitment revisited—dynamics and impacting factors. ICES J Mar Sci 74:3–19

<sup>Mackenzie BR, Gislason H, Möllmann C, Köster FW (2007) Impact of 21<sup>st</sup> century climate change on
the Baltic Sea fish community and fisheries. Glob Chang Biol 13:1348–1367,
<u>https://doi.org/10.1111/j.1365-2486.2007.01369.x</u></sup> 

- Meier HEM, Eilola K, Almroth-Rosell E, Schimanke S, Kniebusch M, Höglund A, Pemberton P, Liu
   Y, Väli G, Saraiva S (2018) Disentangling the impact of nutrient load and climate changes on Baltic
   Sea hypoxia and eutrophication since 1850. Clim Dyn 1–22
- Metcalfe JD (2006) Fish population structuring in the North Sea: understanding processes and mecha nisms from studies of the movements of adults. J Fish Biol 69:48-65
- Methot RD & Wetzel CR (2013) Stock synthesis: a biological and statistical framework for fish stock
  assessment and fishery management. Fish Res 142:86–99.
  https://doi.org/10.1016/j.fishres.2012.10.012
- Mion M, Hilvarsson A, Hüssy K, Krumme U, Krüger-Johnsen M, McQueen K, Mohamed E, Motyka
  R, Orio A, Plikshs M, Radtke K, Casini M (2020) Historical growth of Eastern Baltic cod (*Gadus morhua*): Setting a baseline with international tagging data. Fish Res 223:105442,
  https://doi.org/10.1016/j.fishres.2019.105442
- Mion M, Haase S, Hemmer-Hansen J, Hilvarsson A, Hüssy K, Krüger-Johnsen M, Krumme U,
   McQueen K, Plikshs M, Radtke K, Schade FM, Vitale F, Casini M (2021) Multidecadal changes in
   fish growth rates estimated from tagging data: A case study from the Eastern Baltic cod (*Gadus morhua*, Gadidae). Fish Fish, https://doi.org/10.1111/faf.12527
- Möllmann C, Diekmann R, Müller-Karulis B, Kornilovs G, Plikshs M, Axe P (2009) Reorganization
   of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime
   shift in the Central Baltic Sea. Glob Chang Biol 15:1377–1393
- Neat FC, Bendall V, Berx B, et al. (2014) Movement of Atlantic cod around the British Isles: implications for finer scale stock management. J Appl Ecol 51:1564–1574, doi: 10.1111/1365-2664.12343
  (2014).
- 572 Nissling A, Kryvi, Vallin L (1994) Variation in egg buoyancy of Baltic cod *Gadus morhua* and its
   573 implications for egg survival in prevailing conditions in the Baltic Sea. MEPS 110:67–74,
   574 <u>https://doi.org/10.3354/meps110067</u>
- 575 Nordeide JT (1998) Coastal cod and Northeast Arctic cod do they mingle at the spawning grounds in
   576 Lofoten? Sarsia 83:373–379
- Orio A, Bergström U, Florin AB, Lehmann A, Šics I, Casini M (2019) Spatial contraction of demersal
  fish populations in a large marine ecosystem. J Biogeogr 46:633–645,
  https://doi.org/10.1111/jbi.13510.
- Otterlind G (1976) Fish stocks and fish migration in the Baltic Sea environment. Ambio Special Report
   4:89-101.
- 582 Otterlind G (1983) Torsken och Bottenhavet. Yrkesfiskaren 7(1):10-11.
- 583 Otterlind G (1984) Cod migration and transplantation experiments. ICES CM 1984/J: 13. 6 pp.
- Otterlind G (1985) Cod migration and transplantation experiments in the Baltic. J Appl Ichthyol 1(1):3 16
- Pálsson OK & Thorsteinsson V (2003) Migration patterns, ambient temperature, and growth of Icelandic cod (*Gadus morhua*): evidence from storage tag data. Can J Fish Aquat Sci 60:1409–1423,
  doi: 10.1139/f03-117.
- Patterson TA, Basson M, Bravington MV, Gunn JS (2009) Classifying Movement Behaviour in Relation to Environmental Conditions Using Hidden Markov Models. Journal of Animal Ecology, 78(6):1113–1123. http://www.jstor.org/stable/40405875
- Powell RA (2000) Animal home ranges and territories and home range estimators. In: Research Techniques in Animal Ecology: Controversies and Consequences (Eds L. Boitani and T.H. Fuller). Columbia University, New York, USA, pp. 65–110.

- 595 R Core Team (2020) R: A language and environment for statistical computing. https://www.r-project.org/
- Reusch TBH, Dierking J, Andersson H, Bonsdorff E, Carstensen J, Casini M, Czajkowski M, Hasler B,
  Hinsby K, Hyytiäinen K, Johannesson K, Jomaa S, Jormalainen V, Kuosa H, Kurland S, Laikre L,
  MacKenzie BR, Margonski P, Melzner F, Oesterwind D, Ojaveer H, Refsgaard JC, Sandström A,
  Schwarz G, Tonderski K, Winder M & Zandersen M (2018). The Baltic Sea as a time machine for
  the future coastal ocean. Sci Adv 4(5):eaar8195, https://doi.org/10.1126/sciadv.aar8195
- Righton D & Metcalfe J (2019) Migration. In: Atlantic cod. A Bio-Ecology. John Wiley & Sons Ltd,
   pp 169–218
- Rijnsdorp AD & Pastoors MA (1995) Modelling the spatial dynamics of fisheries of North Sea plaice
   (*Pleuronectes platessa* L.) based on tagging data. ICES J Mar Sci 52:963–980
- Robichaud D & Rose GA (2004) Migratory behaviour and range in Atlantic cod: inference from a
   century of tagging. Fish Fish 5:185–214
- Rogers LA, Olsen EM, Knutsen H, Stenseth NC (2014) Habitat effects on population connectivity in a
   coastal seascape. MEPS 511:153–163
- 610 Rose GA & Rowe S (2015) Northern cod comeback. Can J Fish Aquat Sci 72:1789–1798
- 611 Seaman DE & Powell RA (1996) An evaluation of the accuracy of kernel density estimators for home
   612 range analysis. Ecology 77:2075–2085
- Sólmundsson J, Jónsdóttir IG, Björnsson B, Ragnarsson SA, Tómasson GG, Thorsteinsson V (2015)
   Home ranges and spatial segregation of cod *Gadus morhua* spawning components. MEPS 520:217–
   233
- Vallin L, Nissling A, Westin L (1999) Potential factors influencing reproductive success of Baltic cod,
   *Gadus morhua*: A review. Ambio 28:92–99
- Wieland K, Jarre-Teichmann A, Horbowa K (2000) Changes in the timing of spawning of Baltic cod:
   possible causes and implications for recruitment. ICES J Mar Sci 57:452–464
- Wood SN (2003) Thin-plate regression splines. J R Stat Soc B 65:95–114, doi:10.1111/1467 9868.00374
- Wood SN (2006) Generalized Additive Models: An Introduction with R. Journal of Statistical Software,
   16. CRC/Chapman and Hall, Boca Raton, Florida. http://www.jstat soft.org/
- Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies.
   Ecology 70:164–168
- Wright PJ, Galley E, Gibb IM, Neat FC (2006) Fidelity of adult cod to spawning grounds in Scottish
   waters. Fish Res 77:148–158
- Zemeckis DR, Martins D, Kerr LA, Cadrin SX (2014) Stock identification of Atlantic cod (*Gadus morhua*) in US waters: an interdisciplinary approach. ICES J Mar Sci 71:1490–1506
- 630

# 631 Figures



633 *Figure 1.* Map of the Baltic Sea with ICES subdivisions. The former spawning grounds of the Gotland

- 634 Deep and Gdansk Deep are shaded in blue, while the active spawning ground of the Bornholm Basin
- 635 is marked in blue (Modified after Cardinale and Svedäng, 2011).



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

640





642 *Figure 3.* Example of an historical map visualising Swedish tagging experiments carried out in 1958

643 (red) and 1959 (blue) in the Baltic Sea (nearby Bornholm Island). Arrows indicate the release and dots

the recapture locations of cod. Filled dots represent cod that were recaptured within a year of release,
while additional years (>1) from release are represented as circles surrounding a recapture location. For

example, in the bottom right of the map, a cod is recaptured after 10 years and its recapture location is

647 illustrated as a blue dot surrounded by nine circles.





649 (blue dots) positions for fish released in SD 29 (Åland Sea) during the historical tagging experiments.

650





- ods. Spawning and feeding seasons are assigned based on recapture time. Thick line: median; box:
- 655 25<sup>th</sup> and 75<sup>th</sup> percentiles; whiskers: 1.5 times the interquartile range; black dots: outliers).





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



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



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

a)		Spawning SDrc													
a)															
Dataset	SDrl	IVb	20	21	22	23	24	25	26	27	28	29	30	31	32
Historical	24	0.1 (1)	1.5 (11)		16.1 (119)	1.4 (10)	61.6 (458)	18.4 (137)	0.5(4)		0.4 (3)				
	25		0.3 (6)		1.0 (18)	0.2(4)	6.0 (111)	87.6 (1622)	4.7 (86)	0.1(1)	0.2 (3)				
	26				0.3 (2)		2.9(21)	43.6 (317)	52.4 (381)	0.1(1)	0.7 (5)				
	27		0.5(1)		0.5(1)	0.5(1)	3.6 (8)	63.4 (140)	4.1 (9)	27.2 (60)		0.5(1)			
	28					0.1(1)	1.4 (11)	52.9 (427)	27.2 (220)	0.4 (3)	18.1 (146)				
	29	1.0(1)	1.0(1)				3.03 (3)	32.3 (32)	13.11 (13)	8.1 (8)	9.1 (9)	32.4 (32)			
	30		- ( )					9.1 (2)	9.1 (2)	4.6 (1)		22.7 (5)	54.6 (12)		
	32							2.5(4)	2.47 (4)			()	()		95.1 (154)
Contemp.	24				2.1 (2)		54.3 (51)	43.7 (41)							, ()
	25					1.9(1)	29.6 (16)	66.7 (36)	1.9(1)						
	26						4(1)	20 (5)	76 (19)						
b)		Feeding	g												
		SDrc													
Dateset	SDrl	IVb	20	21	22	23	24	25	26	27	28	29	30	31	32
Historical	24	0.3 (1)	1.2 (4)		13.2 (43)	2.8 (9)	54.8 (178)	26.5 (86)	1.2 (4)						
	25		0.3 (2)		0.4 (3)	0.1(1)	7.0 (50)	85.8 (609)	5.1 (35)	0.7 (5)	0.6 (4)		0.1(1)		
	26						0.7 (2)	33.5 (90)	61.0 (164)		4.9 (18)				
	27				0.5(1)		0.5 (1)	34.6 (72)	1.4 (3)	61.1 (127)	1.0 (2)	1.0(2)			
	28							27.5 (101)	16.6 (61)	1.6 (6)	54.2 (199)				
	29							7.4 (5)	7.4 (5)	2.9 (2)	4.4 (3)	73.5 (50)	1.5(1)		2.9 (2)
	30							2.2 (1)		4.4 (2)		8.9 (4)	80.0 (36)	2.2(1)	2.2 (1)
	32								1.7 (3)		0.6(1)		· · ·		97.7 (169)
Contemp.	24			3.7 (2)	9.3 (5)		63.0 (34)	24.0 (13)	. ,		~ /				. ,
	25				4.5 (2)		40.9 (18)	54.5 (24)							
	26				3.3 (1)		. ,	30.0 (9)	66.7 (20)						

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

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

KDE 50 %					
Season	$SD_{rl}$	Historical (km <sup>2</sup> )	Contemporary (km <sup>2</sup> )	Overlap (km <sup>2</sup> )	Historical overlaps Contemporary %
Spawning	24	12.7	11.4	6.9	54.4
	25	7.8	13.1	3.8	48.5
	26	19.4	12.8	10.2	52.5
	27	31.4			
	28	29.2			
	29	93.5			
	30	78.5			
	32	12			
Feeding	24	21.7	20.9	13.8	63.5
	25	13.5	12.6	6.2	45.9
	26	18	18.3	15.9	88.0
	27	21.9			
	28	25.5			
	29	21.7			
	30	24.6			
	32	7.1			
KDE 95 %					
Season	$SD_{rl}$	Historical (km <sup>2</sup> )	Contemporary (km <sup>2</sup> )	Overlap (km <sup>2</sup> )	Historical overlaps Contemporary %
Spawning	24	61.6	35.5	34.6	56.2
1 0	25	48.4	32.8	24.6	50.7
	26	69.6	55	45.8	65.8
	27	94.9			
	28	88.7			
	29	240.3			
	30	264.9			
	32	28.2			
Feeding	24	57.8	57.8	52.4	90.6
e	25	56	40.5	30.9	55.2
	26	75.9	62.6	58.8	77.5
	27	77.7			
	28	113.2			
	29	200.1			
	30	113.8			
	32	21.1			