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1 **Connectivity of larval cod in the transition area between North Sea and Baltic Sea and**
2 **potential implications for fisheries management**

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12 Running title: Connectivity of larval cod in the Baltic/North Sea transition area

14 **Abstract:**

17 Connectivity of pelagic, early life stages via transport by ocean currents may affect survival
18 chances of offspring, recruitment success and mixing of stocks across management units.
19 Based on drift model studies, transport patterns of particles representing exogenously feeding
20 cod larvae in the transition area between North Sea and Baltic were investigated in order to i)
21 determine long-term trends and variability in advective transport of larvae from spawning
22 grounds to juvenile nursery areas, ii) estimate the degree of exchange between different
23 management areas and iii) compare the results with spatial distributions of juvenile cod. The
24 transport of particles showed considerable intra- and inter-annual variability, but also some
25 general patterns of retention within and dispersion to different management areas. Good
26 spatial overlap of particle end positions, representing potential juvenile settlement areas, with
27 observed distributions of juveniles in bottom trawl surveys suggests that the drift simulations
28 provide reasonable estimates of early life stage connectivity between cod populations in the
29 investigated areas. High exchange rates of particles between management areas of up to ca.
30 70% suggest that cod populations in the investigated areas are demographically correlated.
31 Results are discussed in relation to their relevance for stock structure, fish stock assessment
32 and management.

34 Keywords: connectivity, early life stages, fisheries management, juvenile nursery areas,
35 spatial management, stock structure

37 **Introduction**

39 The exchange of individuals among populations and habitats is an important process from an
40 ecological perspective, affecting e.g. species distribution ranges, the demographic and genetic
41 structure of populations, population dynamics, density-dependent processes and species
42 interactions (Roughgarden *et al.*, 1988; Gaines and Lafferty, 1995; Gaylord and Gaines,
43 2000; Grosberg and Cunningham, 2001; Hixon *et al.*, 2002). In the marine world,
44 connectivity of pelagic early life stages via ocean currents is of particular interest (e.g. Cowen
45 and Sponaugle, 2009), as retention in or transport to favorable or unfavorable habitats may
46 lead to variability in survival chances and eventually in recruitment success (Sinclair, 1988;
47 Baumann *et al.*, 2006; Huwer *et al.*, 2014). In commercially important marine fish stocks
48 which are annually assessed to estimate stock size and status and to inform about resulting
49 fishing opportunities, the exchange of individuals between different management units is
50 particularly important (Selkoe *et al.*, 2008; Reiss *et al.*, 2009; Eero *et al.*, 2014).

51 According to Gulland (1983) a ‘stock’ is assumed to be a discrete group of fish which show
52 little mixing with adjacent groups and which have the same growth and mortality parameters
53 across a particular geographical area. If large numbers of individuals are moving across
54 boundaries of management units, either by active migration or by passive transport, this may
55 lead to erroneous assumptions about stock-recruitment relationships, growth and mortality
56 parameters needed in stock assessment and, due to variable fishing effort between
57 management units, to overexploitation of certain stocks or stock units (Heath *et al.*, 2013;
58 Eero *et al.*, 2014). Thus, management strategies will benefit from increased understanding of
59 movement patterns in space and time and linkages among populations by exchange of eggs,
60 larvae, juveniles or adults, i.e. population connectivity (Palumbi, 2004).

61
62 Many marine fish stocks are managed in large areas, which often have limited connection to
63 management areas of neighboring stocks, e.g. the Arcto-Norwegian cod north of Norway and
64 the Northern cod in the Southern Labrador and eastern Newfoundland area (ICES, 2005), or
65 Baltic sprat which is managed as a single unit in ICES subdivisions 22-32 (ICES, 2015a) with
66 only a very small border to one adjacent management unit in the area of the Belt Sea (see Fig.
67 1).

68 In contrast, in the transition area between North Sea and Baltic Sea there are four cod stocks
69 which are managed in separate, relatively small management units, which are in close
70 vicinity to each other (Fig. 1): i) Skagerrak (together with North Sea), ii) Kattegat in ICES
71 SD 21, iii) western Baltic cod in SDs 22-24 and iv) eastern Baltic cod in SDs 25-32. (see fig.
72 1; ICES, 2015a,b).

73 The spawning grounds of cod in these areas are generally well described and their spatial
74 distribution seems to be rather stable over the years (see Hüssy, 2011; Hüssy *et al.*, 2012 and
75 references therein). Although a number of relevant processes for recruitment success of cod
76 in the western Baltic and the Kattegat have been identified, recruitment dynamics and
77 potential exchange of recruits between the different spawning and management areas are
78 poorly known (Hüssy, 2011) and it is generally recognized that the cod stock structure and
79 the borders of distribution areas of populations inhabiting the transition area from the North
80 Sea to the Baltic are unclear (Nielsen *et al.*, 2005; Svedäng and Svensson, 2006). Cod
81 populations in this region apparently consist of a mixture of resident and migratory stocks
82 (Svedäng and Svensson, 2006; Svedäng *et al.*, 2007; Svedäng *et al.*, 2010a; Hüssy, 2011).
83 Consequently, considerable mixing of stocks in this region may be anticipated as a result of
84 both migrations of adult fish as well as drift of early life stages (Hüssy, 2011).

85 Despite this evidence for connectivity between areas, the standard stock assessments for cod
86 in the Baltic and North Sea region have only recently begun to consider mixing between
87 management areas, e.g. for eastern and western Baltic cod stocks mixing in SD 24 (Hüssy *et*
88 *al.*, 2015; ICES, 2015a,c). Stock mixing in the areas from Skagerrak and Kattegat over the
89 Belt Sea to the Arkona basin (ICES SD’s 20-24, see Fig. 1) is not taken into account. From a
90 management perspective, it is important to gain a better understanding of connectivity in this
91 region at different life history stages to elucidate the resulting recruitment and stock
92 dynamics as well as the recovery potential and appropriate management measures for the cod
93 stocks.

94
95 In previous studies, we have assessed the importance of variability in environmental
96 conditions for egg survival within different spawning grounds of cod stocks in the North Sea-
97 Baltic Sea transition area (Hüssy *et al.*, 2012) as well as the advective transport and the
98 variability in environmentally-mediated survival of eggs and yolk-sac larvae along drift
99 routes in relation to both spatial and temporal dynamics (Hinrichsen *et al.*, 2012). The aim of
100 the present study was to go a step further in the life cycle by exploring the fate of offspring

101 during the exogenously feeding larval stage. We utilized a hydrodynamic model to simulate
102 the drift of exogenously feeding cod larvae which were originally released on different
103 spawning grounds in the western Baltic and the Kattegat. The objectives of the study were to
104 i) determine long-term trends and variability in advective transport of larvae from spawning
105 grounds to juvenile nursery areas, ii) estimate the degree of exchange between the
106 management areas of eastern and western Baltic, Kattegat and North Sea and iii) compare the
107 results with spatial distributions of juvenile cod. The results are discussed in the light of their
108 potential influence on genetic diversity as well as their relevance for stock assessment and
109 management in the transition area between the North Sea and the Baltic.

110

111

112 **Material and Methods**

113

114 *Identification of larval release areas*

115 In previous studies, major spawning grounds of cod in the transition area between North Sea
116 and Baltic (Fig. 1) were identified to be located in the Kattegat, the Sound, the Little and
117 Great Belt, Kiel Bay, the Fehmarn Belt, and to a limited degree in Mecklenburg Bay (Hüssy,
118 2011; Hüssy *et al.*, 2012 and references therein). Based on spatio-temporal distributions of
119 drifting particles representing yolk-sac larvae of western Baltic cod at the end of the
120 endogenous feeding period obtained from a previous modelling study (Hinrichsen *et al.*,
121 2012), spatial distributions of seeding areas for particles representing feeding larvae were
122 identified. This was done by calculation of dispersal kernels (Edwards *et al.*, 2007) from
123 Principal Component Analysis (Hinrichsen *et al.*, 2012) for particles which were initially
124 released as spawned eggs at each of the specific spawning grounds (Fig. 1). Based on the
125 duration of the spawning season from December to May, particles were seeded at the centre
126 of the grid cells every 10 days from December 11 to June 10, resulting in 19 different release
127 dates throughout the spawning season. In order to account for seasonal variations, we chose
128 different release areas of feeding larvae for the early (December-January), mid (February-
129 March) and late (April-June) spawning season. As a second step we used results from
130 hydrodynamic model runs, combined with a drift model approach considering feeding larval
131 cod as drifting particles, in order to hindcast long-term spatio-temporal distributions of these
132 late larval stages.

133

134

135 *Hydrodynamic model*

136 The hydrodynamic model is based on the free surface Bryan-Cox-Semtner model (Killworth
137 *et al.*, 1991) which is a special version of the Cox numerical ocean general circulation model
138 (Bryan, 1969; Semtner, 1974; Cox, 1984). A detailed description of the equations and
139 modifications made, necessary to adapt the model to the Baltic Sea can be found in Lehmann
140 (1995) and Lehmann and Hinrichsen (2000). The model domain comprises the entire Baltic
141 Sea. The horizontal resolution is 5 km, with 60 vertical levels specified. The Baltic Sea model
142 is driven by atmospheric data provided by the Swedish Meteorological and Hydrological
143 Institute (SMHI: Norrköping, Sweden) and river runoff taken from a monthly mean runoff
144 database (Bergström and Carlsson, 1994). Physical properties simulated by the hydrodynamic
145 model agree well with known circulation features and observed physical conditions in the
146 Baltic (for further description see Lehmann, 1995; Hinrichsen *et al.*, 1997; Lehmann and
147 Hinrichsen, 2000).

148

149

150 *Drift Model*

151 The drift model tracks individual feeding larvae through space and time. In order to consider
152 the seasonal variability of the environmental conditions in relation to its spatial and temporal
153 variability, locations were extracted at the hydrodynamic model 5 x 5 km grid within the
154 estimated hatching areas. In the vertical domain particles were released between 1.5 and 28.5
155 m depths at a 3 m depth interval (Hinrichsen *et al.*, 2001). This range was chosen based on
156 the only study of larval cod vertical distribution in the western Baltic Sea, where larvae were
157 found in the depth range 0 – 30 m, with spatio-temporal differences in depths of highest
158 densities (Westerberg, 1994). To estimate potential effects of vertical migration behaviour a
159 sensitivity analysis was performed by analysing the drift of particles for three different depth
160 layers (0-10 m, 10-20 m, 20-30 m) separately. The spatio-temporal variability of habitat size
161 of larval release areas is given in Table 1. A total of 494 (26 years x 19 release dates) drift
162 model runs were performed. The larval particles were tracked for a duration of 90 days. The
163 seeding positions were located in the four sub-regions representing the above defined larval
164 release areas. Finally, to obtain some simple indications for the connectivity of the early life
165 stages of the western Baltic cod stock, we calculated the spatial overlap between their
166 spawning and hatching grounds in terms of sizes for commonly utilized areas.
167
168

169 *Model run*

170 Simulated three-dimensional velocity fields were extracted (at 1 hour intervals) from the
171 hydrodynamic model in order to develop a database for particle tracking. This data set offers
172 the possibility to derive Lagrangian drift routes by calculating the advection of “marked”
173 water particles. Simulated drift routes were obtained from Eulerian flow fields using a
174 Lagrangian particle-tracking technique. The three-dimensional trajectories of the simulated
175 particles were computed using a 4th order Runge-Kutta scheme (Hinrichsen *et al.*, 1997). The
176 distribution of particles at the end of the 90 days drift duration, representing relative
177 abundances of late larval/early juvenile stages, were recorded. The model runs addressed the
178 question how many particles originating from the different release areas were retained and
179 how many were transported into adjacent areas. To quantify retention within and dispersal to
180 adjacent areas, we produced time series of average proportions of particle end positions for
181 the four spawning areas for the entire season as well as seasonally resolved for early, mid and
182 late season for each year from 1979-2004. Area-specific averages and standard deviations of
183 proportions of final drift destinations for all years from 1979-2004 were determined for the
184 four release areas in early, mid, late and total spawning season.
185
186

187 Comparison of particle end positions with spatial distribution of juvenile cod

188 In order to test the results from the drift modelling, we compared maps of average particle
189 end positions per ICES quarter square, representing potential juvenile settlement areas, with
190 the observed spatial distribution of juvenile cod. To that end, catch per unit effort (cpue) data
191 of 0-group cod from regularly conducted standard bottom trawl surveys in the area were
192 downloaded from the ICES trawl database (ICES Database of Trawl Surveys (DATRAS),
193 2015. International Bottom Trawl Survey (IBTS) and Baltic International Trawl Survey
194 (BITS, Copenhagen). For more details see Supplementary Material.
195
196

197 **Results**

198
199 In the following sections results concerning the extent of larval release areas and particle end
200 positions are mainly described for the entire spawning season, while their seasonal variations
201 are presented in detail in the Supplementary Material.

202
203 *Release areas of feeding larvae*
204 Seeding areas for particles representing feeding larvae of western Baltic cod (Fig. 2 &
205 Supplement S1) were generally only partly located within their original spawning grounds
206 but showed a high degree of spatial overlap between areas of origin (Table 1, Fig. 2). For the
207 Kattegat spawners, larval release areas were generally also located in the south-central
208 Kattegat, as well as north of the initial spawning area along the Swedish west coast (Fig. 2).
209 Offspring originating from the Sound were generally not found in the Sound at the end of the
210 yolk-sac stage, but in the southern and central Kattegat, resulting in a high degree of overlap
211 with the Kattegat release area (Fig. 2). A large part of offspring originating in the Great Belt
212 was also found to be located in the original spawning ground at the end of the endogenously
213 feeding period, but there was also a relatively high degree of spatial overlap with the larval
214 release areas of offspring of Kattegat and Sound origin in the south-central Kattegat (Fig. 2).
215 Compared to the three other spawning areas, offspring originally spawned in the Kiel Bight
216 and Mecklenburg Bay were found to be closer connected to their initial spawning area,
217 covering the eastern part of Kiel Bay and parts of the Mecklenburg Bay, however, there was
218 also a certain degree of spatial overlap with the larval release area of Great Belt offspring
219 (Fig. 2).
220
221 *Particle end positions*
222 The model runs conducted in the present study addressed the question how many particles,
223 representing different larval cohorts originating from the different western Baltic cod
224 spawning grounds (Fig. 1) ended up within the different ICES Subdivisions of the western
225 and the central Baltic Sea. A sensitivity analysis of particle depth on drift patterns showed
226 that depth of occurrence has an impact on drift direction and distance. The deeper the
227 particles, the further were they transported towards the east (Supplementary Figure S2). At
228 present, no information exists on the vertical migration patterns of larvae in the
229 Kattegat/western Baltic Sea, and drift patterns of larvae are therefore integrated over the
230 entire depth range where they have been observed in the field (Westerberg, 1994). Time
231 series of yearly averages of retention within release areas and dispersal to adjacent areas for
232 the entire spawning season (Fig. 3a-d) and seasonally resolved for the early, mid and late
233 spawning season (Figs. Supplement S3-S6) are presented, as well as averages and standard
234 deviations of proportions of final drift destinations in the different areas for all years from
235 1979-2004 in early, mid, late and total spawning season (Table 2).
236 Particles initially released in the Kattegat did mainly end up in the Kattegat and Skagerrak,
237 with high inter-annual variability (Fig. 3a, Table 2). In the 1980s, a particularly strong
238 northward drift occurred, with a very large share of particles transported into Skagerrak,
239 reaching values between 50-60%, while fewer particles stayed in Kattegat. Since the 1990s,
240 relatively stable shares of 40-50% and 10-15% were transported to Skagerrak and Kattegat
241 and south into SD22, respectively, whereas only very few particles were transported to the
242 more eastern subdivisions 24-28. On average, 46% of particles were transported to
243 Skagerrak, 12% to SD 22, 2% to SD 24, 1% to SD 25 and <1% to SDs 23, 26 and 28, while
244 38% stayed in Kattegat (Table 2).
245 The particles released in the Sound show a very similar pattern as the particles released in
246 Kattegat (Fig. 3b), with almost identical average shares of particles ending in the different
247 areas (Table 2). This means that there was basically no retention of particles in the Sound (0.6
248 + 0.2%). Instead, all offspring originating from this area were transported into adjacent
249 areas, with on average >80% in northern direction (45% to SD20 and 38% to SD 21), a
250 smaller share of 12% towards south in SD 22 and very few further east. Another interesting
251 fact about the Sound is that this area did basically not receive any particles from adjacent

252 areas either, with total average values of particles ending in SD 23 ranging between 0.4 and
253 0.6%.

254 Particles released in the Great Belt in the northern part of SD 22 also showed similar general
255 drift patterns as Kattegat and Sound, with high inter-annual variability and a generally high
256 transport towards north (Table 2, Fig. 3c). Also for this release area, northward drift was
257 particularly pronounced during the 1980s when a higher fraction was transported to
258 Skagerrak than to Kattegat, while during the early 1990s more particles ended in Kattegat
259 than in Skagerrak. Since the mid 1990s more or less equal shares ended in Skagerrak and
260 Kattegat. However, the overall share of particles transported to Skagerrak and Kattegat was
261 around 35% and thus smaller than for particles released in Kattegat and the Sound, while
262 there was a higher share of retention within SD 22 (on average ca. 20%). Also, a higher
263 average share of 4% and 3% were drifted eastward to SD 24 and SD 25, respectively, with
264 some years (e.g. 1979, 1983-1985, 1995) ranging between 5-10%.

265 Particles released in Kiel Bay and Mecklenburg Bay in the southern part of SD 22 showed the
266 highest retention (41%) of all 4 investigated release areas (Table 2, Fig. 3d). However, also
267 from this area considerable shares of on average 15% and 20% were transported to Skagerrak
268 and Kattegat. Furthermore, this area also showed a high variability with respect to drift into
269 other areas, with some years characterized by high shares of northward drift and others by
270 high shares of eastward drift. This variability becomes particularly evident when comparing
271 the time series for SD 21 and SD 25, which were showing alternating patterns, with low
272 transport to SD 25 and high transport to SD 21 in 1980-1982, 1988-1994 and 1996-1999 and
273 an opposite pattern in 1979, 1983-1985, 1995 and 2000. In these latter years up to 26% were
274 transport to SD 25 and up to 7% reached as far east as SD 26. The high inter-annual
275 variability of transport to SD 25 is also witnessed by the high standard deviation of 7.6 at an
276 average of 9.7% (Table 2). In contrast to the alternating pattern between SD 21 and SD 25,
277 northward transport to Skagerrak and eastward transport to SD 24 were rather stable at values
278 of ca. 10-20% and 10-15%, respectively. It should also be noted that SD 24 belongs to the
279 same management unit as SD 22, which means if particles ending in SD 22 and SD 24 are
280 combined, more than half of the particles released in Kiel and Mecklenburg Bay were
281 retained within that management unit.

282
283 To further illustrate the potential for variability in transport between areas, we have mapped
284 two extreme examples of eastward and northward transport for particles released in the Kiel
285 and Mecklenburg Bay area (see Supplementary Material, Fig. S7a,b).

286
287

288 *Comparison of particle end positions with spatial distribution of juvenile cod*

289 For particles initially released in the Kattegat, there is a good match between high numbers of
290 particle end positions (Fig. 4a) and abundance of juvenile cod (Fig. 4d) at the border between
291 Kattegat and Skagerrak, as well as in the eastern Skagerrak along the coast of Sweden. A
292 large number of particles ended also in the central Skagerrak, but for this area no trawl data
293 were available for comparison with juvenile occurrence.

294 Within the Kattegat, there is a good spatial match, with high abundance of particle end
295 positions and juveniles in the southeastern Kattegat, while lower values of particles in the
296 western part of the Kattegat correspond to low or zero catches of juveniles. However, when
297 considering the overall picture of all particles and juvenile abundance in the entire
298 investigation area, the proportions do not match well, as there is a low juvenile abundance in
299 the southeastern Kattegat compared to the high numbers of particles in this area.

300 Particles initially released in the Sound show an almost identical pattern as particles released
301 in the Kattegat, and therefore no separate map is shown for this release area.

302 Particles initially released in the Great Belt also show a similar pattern as particles released in
303 the Kattegat and the Sound (Fig. 4b), with centers of aggregations along the Swedish
304 Skagerrak coast, at the border between Skagerrak and Kattegat and in the southeastern
305 Kattegat. However, there are also areas of increased accumulations of particles in the
306 southwestern Kiel Bay as well as in the central Mecklenburg Bay, which matches high
307 juvenile abundances in these areas.

308 Finally, for the release area Kiel Bay and Mecklenburg Bay, there is a good match between
309 particle end positions and juvenile CPUEs in the southern part of the study area, with high
310 accumulations in the western and southern Kiel Bay as well as in central parts of
311 Mecklenburg Bay (Figs. 4c and d).

312

313

314 Discussion

315

316 *Larval drift, hydrography, juvenile nursery areas and connectivity*

317 Connectivity, or the exchange of individuals among populations, is an important process from
318 an ecological perspective, but also for conservation and management of harvested species
319 (e.g. Selkoe *et al.*, 2008; Cowen and Sponaugle, 2009; Reiss *et al.*, 2009). The connectivity
320 of Atlantic cod (*Gadus morhua*) populations in the transition area between the North Sea and
321 the Baltic has been the topic of a number of studies (Pihl and Ulmestrand, 1993; Nielsen *et*
322 *al.*, 2003, 2005; Svedäng and Svenson, 2006; Svedäng *et al.*, 2007, 2010a, 2010b). However,
323 these investigations were focused on migrations and genetic structure of adults and larger
324 juveniles, while transport of early life stages has not been considered, despite the fact that
325 pelagic eggs and larvae can be transported over large distances via ocean currents. In
326 previous studies Hüssy *et al.* (2012), Hinrichsen *et al.* (2012) and Pacariz *et al.* (2014a,
327 2014b) have analyzed the fate of cod eggs and yolk-sac larvae in this transition area. These
328 studies showed that environmentally mediated mortality and survival success were
329 predominantly affected by egg buoyancy, ambient temperatures and transport into suitable or
330 unsuitable habitats, and that transport patterns are highly variable within and between years,
331 with average transport directions towards the north.

332 As for the egg stage, the transport patterns during the exogenously feeding larval stage
333 investigated in the present study were generally also very dynamic and showed high intra-
334 and inter-annual variability of particle end positions. However, recurring patterns of larval
335 transport were found, e.g. the general drift in northward direction for the three northern
336 spawning areas and the high retention for the spawning area in Kiel Bay and Mecklenburg
337 Bay. Furthermore, a striking feature of our modelling study was the high overlap of larval
338 release areas in the middle (February-March) and partly also the early (December-January)
339 spawning season, while late in the spawning period April-June) the larval release areas were
340 more distinct with only little overlap. This can be related to lower ambient temperatures in
341 mid and partly also early season and the correspondingly longer temperature-dependent egg
342 and yolk-sac larval developmental times associated with longer drift durations resulting in
343 larger drift distances. In contrast, higher ambient temperatures associated with shorter
344 development times and shorter drift durations at the end of the spawning season (Hinrichsen
345 *et al.* 2012) resulted in smaller release areas for feeding larvae, which were more
346 concentrated in the vicinity of the initial spawning areas. Another interesting result was that
347 the Sound showed basically no retention but transport of >80% of particles towards the north,
348 and generally an identical drift pattern as the Kattegat. This is caused by the fact that eggs
349 spawned in the Sound are more or less immediately flushed northward into the Kattegat
350 (Hinrichsen *et al.*, 2012) and the release area of larvae initially originating from the Sound is
351 therefore very similar to the release area of larvae from the Kattegat spawning ground.

The comparison of particle end positions with catches of juvenile cod from bottom trawl surveys showed a high degree of concurrence, with centers of nursery areas around Skagen at the northern tip of Denmark and along the Swedish coast, as well as in Kiel and Mecklenburg Bay. However, there were also some discrepancies with high numbers of particles but no concurrent juvenile occurrence in the central Skagerrak, which can be explained by the local topography. Even though not sampled in the IBTS, juvenile cod are likely not able to find a suitable settling habitat in this area due to the large depths in the eastern part of the Norwegian Trench. Considering Kattegat alone, there is actually a good spatial match, with a juvenile nursery area in the southeast and no juvenile occurrence in the western part. However, the proportions of particles and juvenile catches did not agree well, with relatively low juvenile catches compared to the high numbers of particles ending in this area. This may be related to the fact that the exchange rates between areas and the associated particle end positions represent relative, general patterns rather than actual abundances, as no information on spawning intensity and estimates of actual numbers of eggs and larvae released in the different spawning areas were available. Furthermore, there is an important difference between “total connectivity”, i.e. the number of transported particles and “realized connectivity”, i.e. the number of transported particles which actually survive and contribute to successful recruitment and eventually reproduction (Selkoe *et al.*, 2008). This issue has at least partly been considered in our previous studies on cod eggs, which estimated egg mortality due to unfavourable environmental conditions in the spawning areas and along the drift routes (Hüssy *et al.*, 2012; Hinrichsen *et al.*, 2012). However, analyses of realized connectivity during the larval stage would require estimates of larval mortality by linking the drift model with a bioenergetics growth model and realistic prey fields as well as absolute measures of initially released eggs and their attributes (i.e. size, buoyancy) based on spawning stock size, stock composition and fecundity. As these necessary data and tools for estimation of absolute numbers are not available, drift patterns can at present only be captured as probability distributions. Nevertheless, the overall good agreement between spatial patterns of particle end positions and juvenile catches suggests that our modelling study provides reasonable estimates of larval drift and juvenile settling areas, and thus of general patterns of early life stage connectivity between cod populations in the investigated areas, while the actually realized connectivity between areas awaits further quantification.

The strong differences of retention and dispersal patterns of larval cod in space and time are a consequence of the specific, spatially and temporally highly variable physical environmental conditions in our study area, which in turn lead to a highly dynamic ocean circulation (for details see e.g. Stigebrandt, 1983; Schinke and Matthäus, 1998; Lehmann *et al.*, 2002). The combination of these highly variable environmental conditions with the small size and close vicinity of the cod management units in the transition area between North Sea and Baltic lead to a high potential for exchange of individuals between management units via advective transport during the pelagic stages of the life cycle.

Evidence for stock structure in the transition area between North Sea and Baltic

In the transition area between the North Sea and the Baltic Sea there is ample evidence for complex stock structuring from area-specific stock indices (Svedäng and Svenson, 2006; Svedäng *et al.*, 2010a), tagging experiments (Pihl and Ulmestrand, 1993; Svedäng *et al.*, 2007), chemical signatures in otoliths (Svedäng *et al.*, 2010b) and genetics (Nielsen *et al.*, 2003). Cod in the Kattegat (SD 21) consist of a mixture of resident and migratory stocks undertaking migrations as far as the North Sea (Svedäng *et al.*, 2007). Throughout the area from the Belt Sea (SD 22) to the Arkona Basin (SD 24) spawning migrations occur towards the southern Kattegat and Great Belt respectively with return migrations to their respective

402 feeding grounds (Hüssy, 2011 and references therein). In the Sound however, cod seem to be
403 exclusively resident (Svedäng *et al.*, 2007).

404 Despite this apparent stock structuring driven by individual fish's behaviour, there seems to
405 be limited genetic differentiation. While North Sea, Kattegat, Sound and Belt Sea cod are
406 genetically similar (Nielsen *et al.*, 2003; Svedäng *et al.*, 2010b), they differ significantly from
407 cod in the Baltic Sea east of Bornholm (Nielsen *et al.*, 2003). In order to explore the
408 connectivity between stocks from different areas, Nielsen *et al.* (2005) examined the genetic
409 linkage between adults and juveniles within each area. Juvenile cod in the North Sea,
410 Kattegat/Skagerrak, Belt Sea and Eastern Baltic are genetically related to adults in the same
411 areas indicative of limited exchange with other areas. Juveniles from the Western Baltic Sea
412 on the other hand were closer related to adults from the Belt Sea (Nielsen *et al.*, 2005). This
413 suggests early life stage dispersal from the Belt Sea towards the east. Additionally, a number
414 of genetically distinct local populations occur along the Skagerrak coast, with no apparent
415 trend of isolation by distance. This suggests that the primary driver for genetic stock
416 structuring is not migration of adults but drift of early life stages without subsequent return
417 migration as juveniles or adults(Knutsen *et al.*, 2003).

418 Extensive and temporally variable drift of North Sea cod larvae into coastal waters in the
419 Skagerrak are known to occur, and between 1-10% of juveniles in the Skagerrak were
420 estimated to be of North Sea origin (Knutsen *et al.*, 2004; Stenseth *et al.*, 2006). In
421 combination with results from the present study, this suggests that the Skagerrak/Kattegat
422 may be an area where cod originating from the North Sea, the Skagerrak, the Kattegat and the
423 western Baltic are mixing via larval drift, while the eastern Baltic is isolated through limited
424 exchange of both early life stages and adults.

425 Although there is evidence for a certain degree of natal homing in cod in the area of
426 investigation, the lack of genetic differentiation documents that extensive gene flow occurs
427 between stocks in the transition area between the North Sea and the western Baltic. The high
428 dispersal rates between areas observed in the present study suggest that dispersal of early life
429 stages may be the driving force for this lack in genetic differentiation.

430

431

432 *Implications for fisheries management*

433 Hinrichsen *et al.* (2011) documented the usefulness of hydrodynamic and coupled
434 biophysical models for fisheries management, owing to their ability to estimate the transport
435 and survival chances of early life stages, the settlement probability of juvenile fish and the
436 spatio-temporal scales of connectivity between stocks.

437 Stock identity and geographical boundaries used to define fish stocks are of particular
438 concern for fisheries management as a failure to recognize biological populations could result
439 in non-optimal or unsustainable management of the resources (Heath *et al.*, 2013; Eero *et al.*,
440 2014). Development of various stock separation techniques can potentially allow accounting
441 for mixing of biological populations in stock assessment, as demonstrated by a recent
442 example for Eastern and Western Baltic cod. (Hüssy *et al.*, 2015; ICES 2015a,c). Our
443 analyses in the present paper demonstrate that the stock structure in the transition area
444 between North Sea and Baltic may be even more complex when considering early life stages
445 and involve four different cod management units: Skagerrak/North Sea, Kattegat, Western
446 Baltic and Eastern Baltic.

447

448 Evaluations of fishing opportunities based on stock assessments are mostly focused on the
449 adult components of the stocks. The exchange of offspring between different stock
450 assessment or management units may not be an issue for assessing the adult biomass levels or
451 fishing pressure, given that homing takes place (Robichaud and Rose, 2001; Svedäng *et al.*,

452 2007). However, the relationship between parent stock biomass and resulting recruitment is
453 an important basis for defining biological reference points used for fisheries management.
454 Stock recruitment relationships may be blurred extensively if large parts of the eggs and
455 larvae spawned in a given management unit do not remain as recruits in the same area, but
456 instead contribute as recruits to adjacent stock units. Exchange of recruits needs to be
457 considered for small adjacent assessment units with extensive water movement as
458 demonstrated in this study for the transition area from the North Sea to the Baltic. Drift of
459 early life stages can thus be one of the reasons for the lack of well-defined relationships
460 between recruitment and the size of parent stock within the assessment units, in addition to
461 drivers affecting recruitment survival.

462
463 The “realized connectivity” (Selkoe *et al.*, 2008), i.e. the numbers of transported particles
464 which actually survive and contribute to recruitment in the investigated cod stock areas, is
465 presently not quantified. Therefore, it is difficult to evaluate the magnitude of the potential
466 problem that the apparently substantial drift of early life stages causes for stock assessment
467 and management. However, given the high probability of substantial exchange of recruits
468 between the defined assessment units, stock recruitment relationships within a given unit
469 should be treated with caution. Quantitative analyses of the origin of recruitment in different
470 areas are recommended as a next step, for example using otolith chemistry (Svedäng *et al.*,
471 2010b). Furthermore, studies on larval vertical migration behaviour and regular
472 ichthyoplankton surveys are advocated to improve the input for drift modelling and to further
473 quantify connectivity between areas.

474 From a management point of view, one could consider combining the smaller units into one
475 single assessment covering a larger geographical area in order to avoid violating the closed
476 population assumption that is the basis for stock assessment. However, a shortcoming of this
477 approach is that weaker subpopulations may not get sufficiently protected as the most
478 abundant sub-stock will mask the developments in smaller populations (e.g. Eero *et al.* 2014).
479 In fact, a number of recent studies have argued for a finer spatial resolution in fisheries
480 management to account for subpopulations structure, e.g. for cod in the North Sea (Heath *et*
481 *al.* 2013). Ideally, spatial processes should be modelled as part of stock assessment, which
482 however increases the complexity of stock assessments and data demands (Goethel *et al.*
483 2011). Thus, there is a need for both better understanding of connectivity to quantify the
484 exchange of recruits between areas as well as further development of stock assessment
485 modelling tools to identify most appropriate solutions for stock assessment and fisheries
486 management purposes taking into account spatial processes.

487 Hydrodynamic and coupled biophysical models such as the one used in this study are
488 considered valuable tools to estimate spatio-temporal scales of connectivity within and
489 between stocks, to identify potential issues with stock area definitions and thereby to
490 contribute to conservation, management, and recovery of fish stocks.

491

492

493 **Supplementary material**

494 Supplementary material is available at the ICESJMS online version of the paper. It contains
495 results on the seasonal variations concerning the extension of larval release areas and particle
496 end positions, as well as additional information about the data sources used for the mapping
497 of juvenile cod abundances from IBTS and BITS bottom trawl surveys.

498

499

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507

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702 **Tables**

703 Table 1: Sizes of spawning grounds, larval hatching grounds and spatial overlap of hatching
 704 grounds with spawning grounds for early, middle and late western Baltic cod spawners (all
 705 values are in km²)

Area	Spawning ground size	Hatching ground size			Spatial overlap between hatching grounds and spawning grounds											
					Kattegat			Øresund			Great Belt			Western Baltic		
		early	mid	late	early	mid	late	early	mid	late	early	mid	late	early	mid	late
Kattegat	2825	6675	6675	5700	450	100	900	1125	300	1500	0	0	0	0	0	0
Øresund	850	6475	6825	3775	0	0	0	25	0	75	0	0	0	0	0	0
Great Belt	1440	8225	9225	5125	0	0	0	0	0	0	900	885	900	300	830	325
Western Baltic	3085	6325	7750	5425	0	0	0	0	0	0	80	0	55	1125	1290	950

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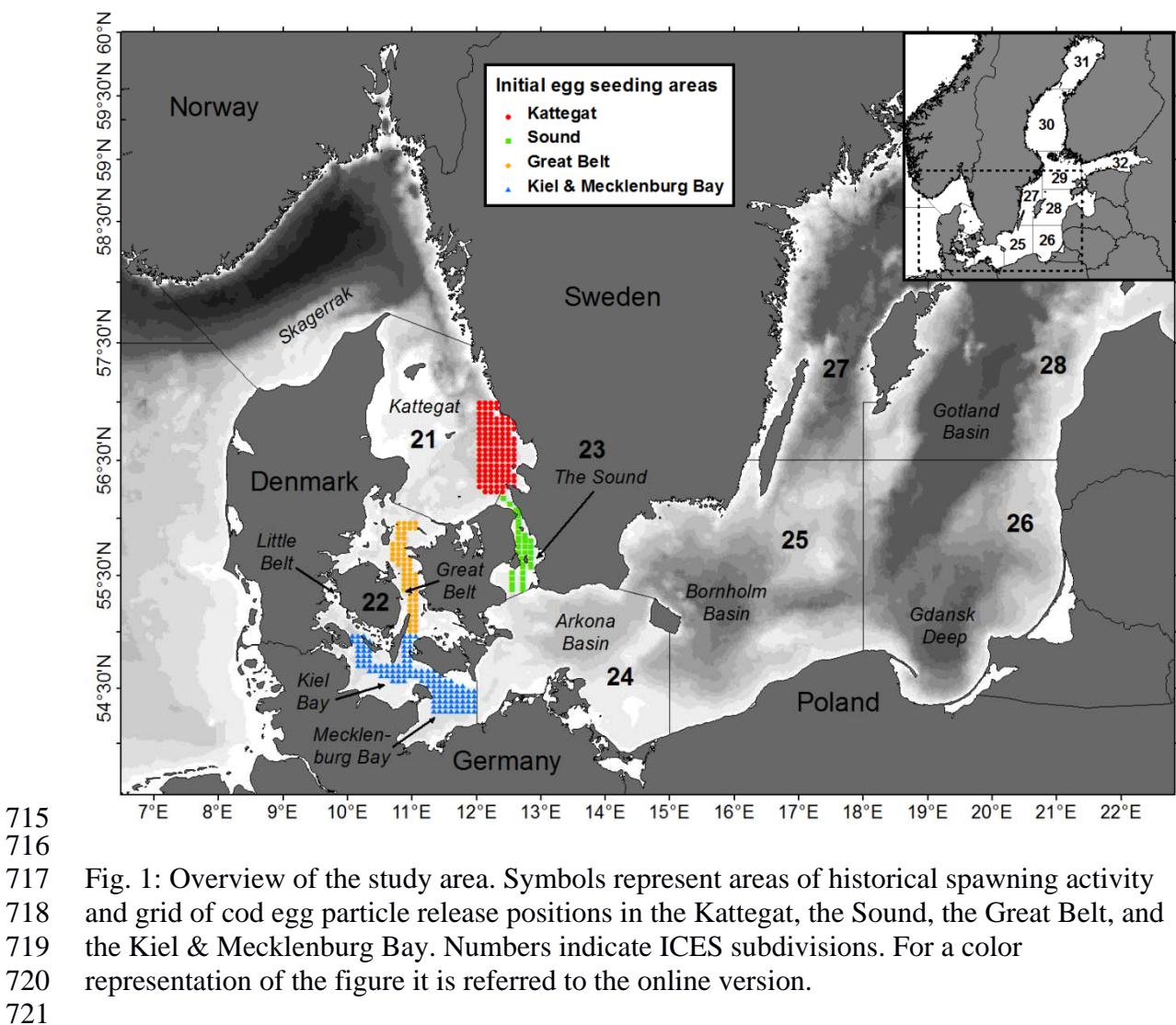
708 Table 2: Averages and standard deviations (1979-2004) of proportions [%] of particle end
 709 positions by initial spawning areas and destination areas for early (December-January), mid
 710 (February-March), late (April-June) and total (December-June) spawning season

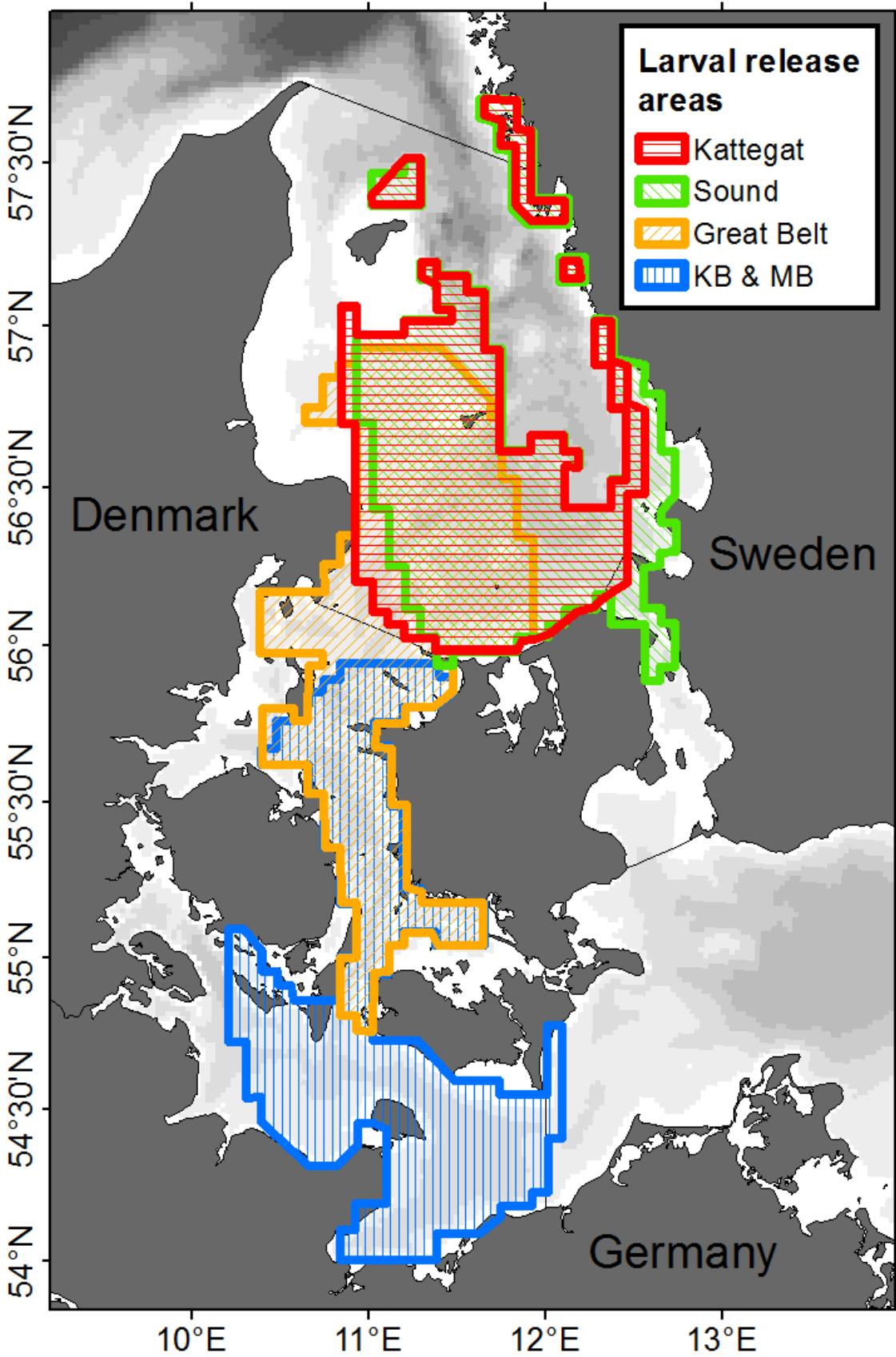
Release area	Release period	Destination area							
		Skagerrak	SD21	SD22	SD23	SD24	SD25	SD26	SD28
Kattegat (SD 21)	early	45.6 ± 12.0	35.2 ± 9.2	13.4 ± 4.8	0.8 ± 0.3	2.9 ± 1.9	2.0 ± 2.1	0.2 ± 0.5	0.0 ± 0.0
	middle	51.5 ± 10.8	37.4 ± 10.0	8.2 ± 3.6	0.4 ± 0.4	1.4 ± 1.3	1.1 ± 1.4	0.1 ± 0.1	0.0 ± 0.0
	late	39.2 ± 9.2	42.3 ± 7.3	15.3 ± 6.1	0.6 ± 0.4	2.2 ± 1.3	0.6 ± 1.0	0.0 ± 0.0	0.0 ± 0.0
	total	45.8 ± 6.8	38.1 ± 6.8	12.1 ± 3.4	0.6 ± 0.2	2.2 ± 0.9	1.2 ± 1.0	0.1 ± 0.2	0.0 ± 0.0
Sound (SD 23)	early	45.1 ± 12.2	34.7 ± 9.0	13.5 ± 4.6	0.6 ± 0.3	3.3 ± 2.0	2.6 ± 2.6	0.3 ± 0.7	0.0 ± 0.0
	middle	50.0 ± 10.6	37.5 ± 9.6	9.0 ± 3.5	0.4 ± 0.4	1.7 ± 1.3	1.4 ± 1.6	0.2 ± 0.3	0.0 ± 0.0
	late	37.0 ± 8.9	42.0 ± 7.1	15.7 ± 4.9	0.9 ± 0.6	3.2 ± 1.4	1.4 ± 1.8	0.0 ± 0.0	0.0 ± 0.0
	total	45.3 ± 7.2	37.5 ± 6.8	12.1 ± 2.8	0.6 ± 0.2	2.6 ± 0.9	1.8 ± 1.2	0.2 ± 0.3	0.0 ± 0.0
Great Belt (SD 22 N)	early	31.5 ± 10.2	31.6 ± 8.1	27.4 ± 6.6	0.6 ± 0.4	4.8 ± 2.9	3.7 ± 4.4	0.4 ± 0.8	0.0 ± 0.0
	middle	42.6 ± 10.6	36.3 ± 8.5	14.3 ± 4.3	0.3 ± 0.3	3.4 ± 2.1	3.0 ± 3.7	0.2 ± 0.4	0.0 ± 0.0
	late	33.4 ± 11.0	36.9 ± 6.8	21.6 ± 6.9	0.4 ± 0.3	5.2 ± 2.8	2.7 ± 3.6	0.0 ± 0.1	0.0 ± 0.0
	total	35.8 ± 5.5	33.7 ± 6.1	19.7 ± 3.9	0.4 ± 0.2	4.2 ± 1.8	3.1 ± 3.1	0.3 ± 0.4	0.0 ± 0.0
KB & MB (SD 22 S)	early	8.2 ± 4.2	16.4 ± 6.1	50.4 ± 11.8	0.6 ± 0.5	11.4 ± 5.3	11.3 ± 10.7	1.9 ± 3.9	0.0 ± 0.1
	middle	19.2 ± 9.4	26.3 ± 7.9	35.9 ± 6.9	0.2 ± 0.1	8.2 ± 3.9	9.0 ± 8.8	1.3 ± 2.3	0.1 ± 0.4
	late	15.0 ± 7.0	25.7 ± 4.5	38.7 ± 7.5	0.4 ± 0.4	11.1 ± 4.0	9.0 ± 6.9	0.3 ± 0.5	0.0 ± 0.0
	total	14.7 ± 4.3	23.1 ± 5.3	41.2 ± 5.9	0.4 ± 0.2	10.0 ± 2.7	9.7 ± 7.6	1.2 ± 1.9	0.0 ± 0.2

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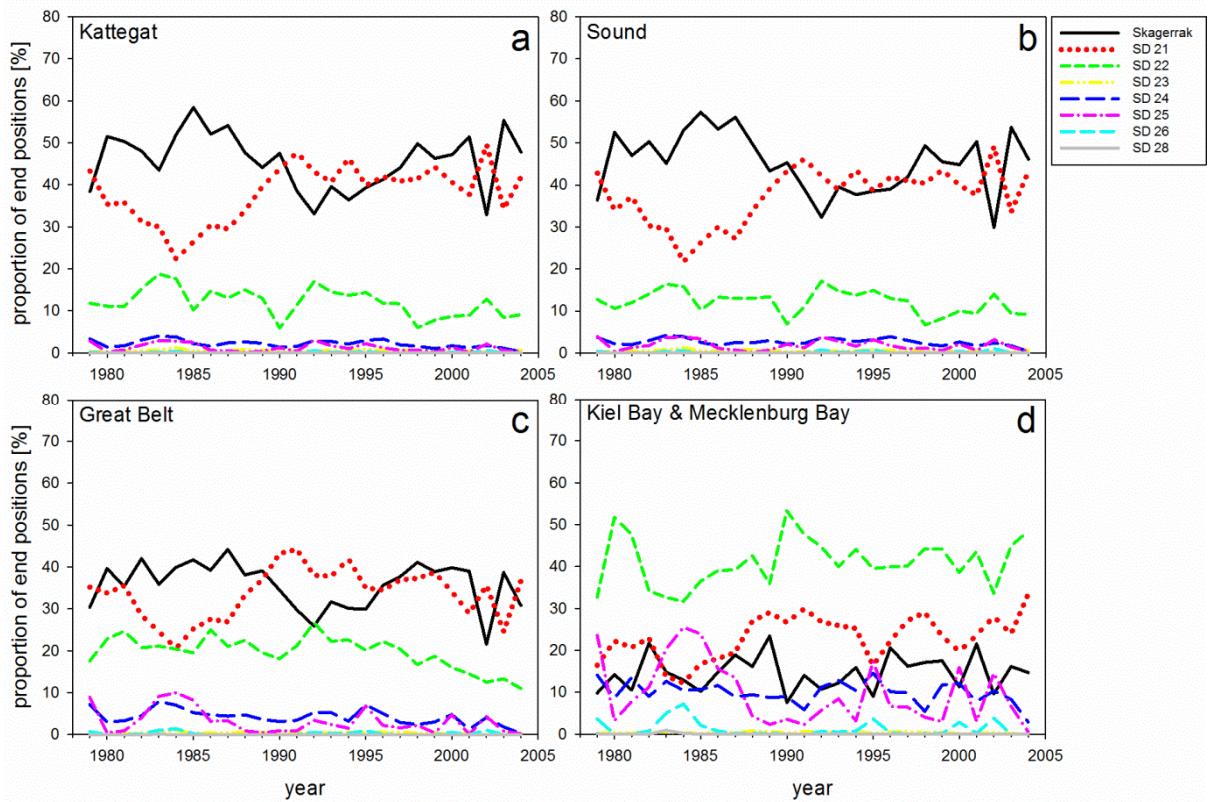
713 **Figures**

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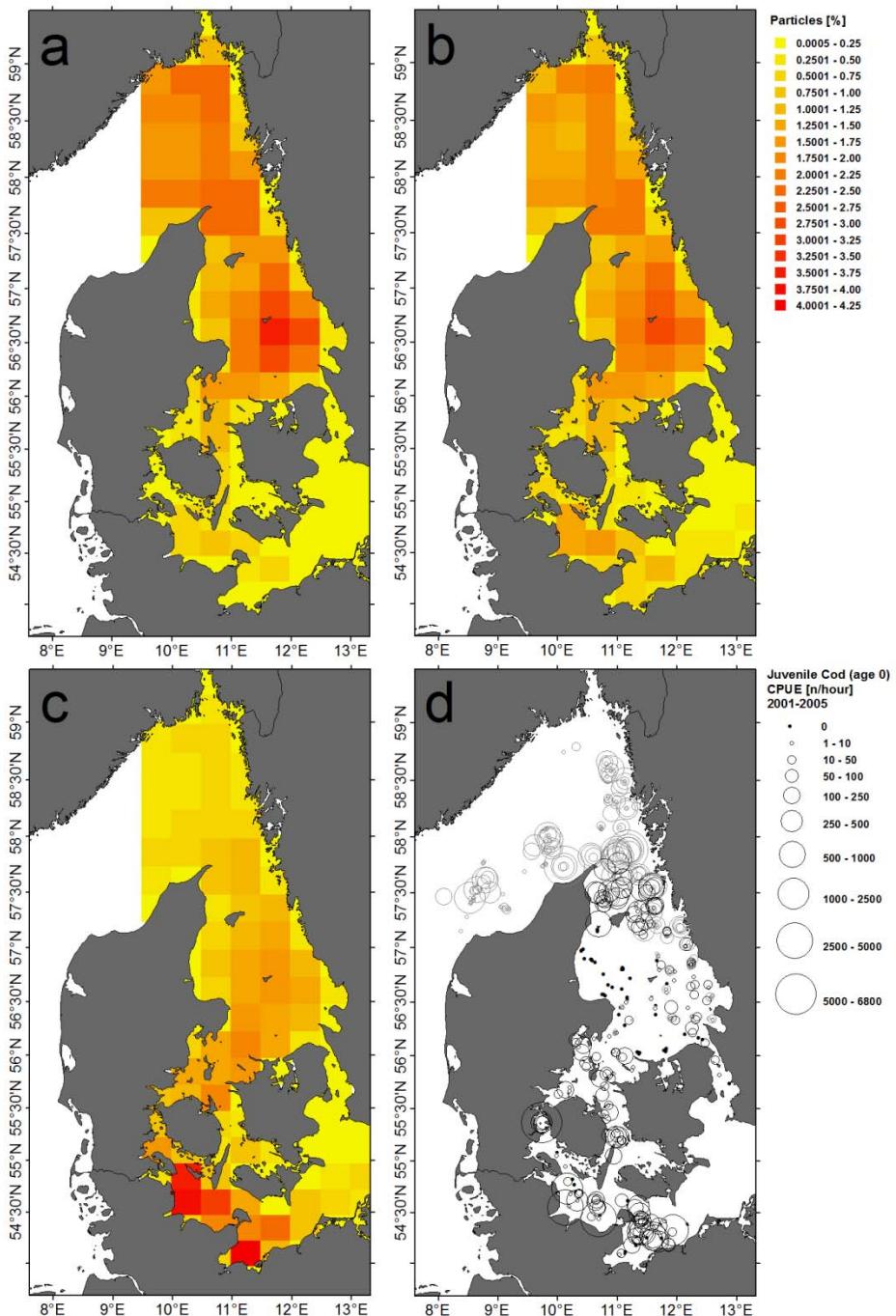




722
723 Fig. 2: Extent and overlap of release areas of larvae originating from the four spawning
724 grounds in Kattegat, Sound, Great Belt and Kiel & Mecklenburg Bay. For a color
725 representation of the figure it is referred to the online version.
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730 Fig. 3: Time series of proportions of particles ending in Skagerrak and ICES SD's 21-28 for
731 particles originating in (a) Kattegat, (b) Sound, (c) Great Belt and (d) Kiel & Mecklenburg
732 Bay. For a color representation of the figure it is referred to the online version.
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737 Fig. 4: Comparison of average (1979-2004) particle end positions (%) for particles released
738 in (a) Kattegat, (b) Great Belt and (c) Kiel & Mecklenburg Bay with (d) catch per unit effort
739 (cpue, n/hour) of juvenile cod from bottom trawl surveys (grey circles: IBTS - International
740 Bottom Trawl Survey, black circles: BITS - Baltic International Trawl Survey) in the period
741 2001-2005. For a color representation of the figure it is referred to the online version.