
Northward range expansion of Bay of Biscay anchovy into the English Channel

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Abstract :

European anchovy *Engraulis encrasicolus* is a widely distributed, warm-water species which has been postulated to be a climate change 'winner'. For decades, the northern-most stock resided in the Bay of Biscay, where it typically spawned during late spring, mostly in the south. An apparent regime shift in the mid-1990s saw the sudden appearance and subsequent increase of anchovy further north. This northward range expansion was found to be driven by remnant spawning populations in the North Sea. During the autumn of 2019 and 2020, for the first time, post-larval anchovy were found in the English Channel, far from their nearest known spawning grounds. Identifying the origin of these anchovy is important for management purposes and to understand the mechanisms driving populations at the limits of their distribution. Microsatellite- and mtDNA-based analyses confirmed that the observed post-larval anchovy originated from the Bay of Biscay and were genetically distinct from English Channel and southern North Sea specimens. By combining acoustic and egg data from local surveys with larval drift modelling, we examined the processes underpinning this northward expansion. Our analysis suggests that due to population increase, spawning activity in the Bay of Biscay has expanded in space and time, increasing larval transport and survival into the Channel area. This newly recorded process underpinning an observed poleward shift is different from the one driving the anchovy expansion that started in the mid-1990s. However, both caused range expansion at the species' northern distribution limit, demonstrating the potentially complex impacts of climate change.

Keywords : *Engraulis encrasicolus*, Climate change, Connectivity, Acoustics, Population genetics, Larval drift modelling, Spatial density-dependent effects

37 1. Introduction

38 Understanding species distribution is important for management and conservation purposes.
39 Species distribution is expected to change substantially due to climate change, with shifts of the
40 limits of the species distribution range (Pinsky et al. 2020), even more rapidly in the oceans than on
41 land (Lenoir et al. 2020). Investigating the mechanisms underpinning observed contractions and
42 expansions and changes in phenology will aid in predicting any future changes as a result of
43 ecological or anthropogenic drivers (Pörtner & Peck, 2010). Climate change affects lower trophic
44 levels such as phytoplankton (Boyce et al. 2010) and zooplankton (Ratnarajah et al. 2023 and
45 references therein) with cascading impacts on higher trophic levels. Small pelagic fish exhibit large
46 changes in abundance and distribution. This is because they respond rapidly to changing
47 environmental conditions as they are short lived, exhibit rapid growth and high fecundity and
48 because they depend directly on zooplankton prey. Although statistical projections of small pelagic
49 fish distribution in Europe predict significant expansion to the north (Schickele et al. 2021), the
50 mechanisms driving these changes vary by species and are often poorly understood (Peck et al.
51 2021).

52 European anchovy, *Engraulis encrasicolus*, is a widely distributed warm water species which
53 is found from South Africa northwards along the shelf seas of west Africa into the Mediterranean-
54 and Black Sea and in northwestern European waters (FAO 2022). Here, it is generally considered a
55 climate change winner (Townhill et al. 2023) and the Bay of Biscay (Fig. 1) has traditionally
56 represented its most consistent northern-most spawning area. The Bay of Biscay stock is of
57 significant commercial importance and as part of its management the fishery was closed between
58 2005-2009, following a succession of poor recruitments. Since 2010, when the fishery reopened, the
59 stock has continued to rebuild with the highest historical biomass observed in recent years (ICES
60 2023). The reasons for this increase seem to be a combination of good recruitments linked to

61 favourable environmental conditions and a reduction in fishing mortality (Bueno-Pardo et al. 2020,
62 Uriarte et al. 2023).

63 Historically, spawning did occur further north in de Zuiderzee (Fig. 1), a shallow inland sea
64 off the southern North Sea. Anchovy were reportedly found in significant numbers (Aurich 1953),
65 until in 1932 the Zuiderzee was sealed off from the North Sea following the introduction of a dam
66 (the Afsluitdijk, Fig. 1) and anchovy all but disappeared from the area for decades (Beare et al.
67 2004a). From the mid-1990s, increasing numbers of anchovy were reported from the northern
68 fringes of its traditional distribution: from opportunistic commercial landings in the English Channel,
69 and from catches in fisheries-independent surveys in the Irish Sea (Armstrong et al. 1999) and
70 particularly the North Sea (Boddeke & Vingerhoed 1996, Beare et al. 2004a, b, Alheit et al. 2012
71 Montero-Serra et al. 2015). In the absence of dedicated anchovy surveys in key areas, a collaborative
72 multi-disciplinary approach aimed to determine the origin of these anchovy in the North Sea and the
73 possible mechanisms underpinning their increase (Petitgas et al. 2012). North Sea anchovy were
74 found to be genetically distinct from those in the Bay of Biscay. Further evidence of a lack of
75 connectivity with the Bay of Biscay was provided by the results of a particle drift modelling
76 experiment, which confirmed that eggs released from the main spring spawning locations situated in
77 the southern part of the Bay of Biscay were unlikely to reach the North Sea nor the English Channel
78 (Petitgas et al. 2012). While limited spawning did occur in the north of the Bay of Biscay, it occurred
79 later in the season, when prevailing hydrographic circulation was more southward, which would also
80 have prevented anchovy from reaching the English Channel and the North Sea. The study therefore
81 provided strong evidence that the observed increase of anchovy in the north of its range was due to
82 improved recruitment of a local remnant population rather than a colonisation of the North Sea by
83 Bay of Biscay anchovy as egg/larvae or as adults (Petitgas et al. 2012).

84 From 2013, a new pelagic survey provided the first fisheries-independent information on
85 anchovy in the western English Channel, directly north of the Bay of Biscay (PELTIC, Doray et al.
86 2021). The survey took place during the autumn when North Sea-spawned anchovy migrate to the
87 western English Channel (Huret et al. 2020) and when they appeared as opportunistic bycatch in
88 some of the local sardine and sprat fisheries. Anchovy were found in the English Channel from the
89 start of the survey series (2013), first in small numbers but annually increasing in both range and
90 biomass (ICES 2021). Biological data confirmed that anchovy of different ages, including age 0,
91 migrate from the North Sea to overwinter in the English Channel, as previously confirmed (Petitgas
92 et al. 2012, Huret et al. 2020). In the early years of the survey anchovy was only found in mixed
93 aggregations with other small pelagic species. More recently, as anchovy biomass increased, mono-

94 specific schools became more common and were typically found in the lower half of the water
95 column.

96 During the 2019 and 2020 PELTIC surveys, a new observation suggested potentially further
97 changes to anchovy dynamics. For the first time, post-larval anchovy were observed as surface
98 schools along the transects off the north coast of Brittany (France). The unusual shape and
99 behaviour of the surface schools (Fig. 2), resembling post-larval or juvenile anchovy from Bay of
100 Biscay (Boyra et al. 2016) and their geographic position, seemingly emerging from the southwest of
101 the English Channel and extending east along the Brittany coast, suggested that these anchovy were
102 different from those typically encountered in the area. Given that the English Channel appears to be
103 a natural boundary between two spawning populations, Bay of Biscay anchovy in the south and the
104 North Sea population further northeast (Petitgas et al. 2012, Huret et al. 2020), it is important to
105 identify the origin of these anchovy and the possible reason for this change.

106 We used three different approaches to investigate the possible causes behind these
107 observations. Firstly, the origin of the anchovy juveniles was investigated using genetics, through
108 individual assignment tests. Specifically, adults collected throughout the Bay of Biscay, English
109 Channel and North Sea regions were genotyped at microsatellite loci to establish the genetic
110 characteristics of the southern (Bay of Biscay) and Northern (Channel/North Sea) populations. This
111 differentiation then permitted individual post-larvae to be assigned to their respective source
112 population. Secondly, any recent changes in annual anchovy juvenile and egg distribution were
113 investigated by comparing them with historic distribution maps from fisheries-independent surveys
114 in the broader area. Thirdly, the potential role of regional oceanographic processes underpinning
115 these observations were explored. A particle tracking model was used to investigate any recent
116 changes in the connectivity patterns from the observed spawning locations, which may be able to
117 explain the observations in 2019 and 2020. Also, the potential role of the Ushant Front, an important
118 seasonal hydrographic feature located between the Bay of Biscay and the English Channel (Pingree
119 1975), was investigated. Fronts may act as a barrier to cross-frontal mixing of planktonic organisms
120 (Woodson et al. 2012) and interannual variation in the autumn position of this front was explored
121 using temperature profiles recorded during the PELTIC surveys.

122 2. Material and Methods

123 2.1. Surveys

124 Data on anchovy eggs, juveniles and adults formed the basis of this study and were collected on
125 several annual pelagic surveys in the Bay of Biscay and the western English Channel. All surveys

126 considered in this study were annually coordinated which includes standardisation of methodologies
127 (Doray et al. 2021). A detailed description of the surveys is provided elsewhere (Doray et al. 2021)
128 and a short summary is included here (Table 1). These data were included to explore the wider
129 distribution and connectivity of anchovy juveniles in the Bay of Biscay and western English Channel
130 during the autumn and the associated spawning location the preceding spring.

131 2.2. Genetics

132 *Sample collection and molecular analyses*

133 Samples of adult anchovy were collected from a number of sites across multiple years by demersal
134 and pelagic trawls (Table 2, Fig. 1). All samples contained multiple age classes apart from the 2019
135 sample, which consisted solely of juvenile anchovy. Individual (dorsal) finclip samples were preserved
136 in absolute ethanol. Genomic DNA was extracted using a standard cetyltrimethyl ammonium bromide
137 (CTAB)-chloroform/isoamylalcohol method (Winnepeninckx et al. 1993). Nuclear variation was
138 assessed at 6 microsatellite loci: Ee2, Ee10 (Landi et al. 2005), Ee2-91b, Ee2-135, Ee2-507, Ee2-508
139 (Pakaki et al. 2009). The various loci were individually amplified by Polymerase Chain Reaction (PCR)
140 in 10 ul reactions containing ~50 ng of DNA, 3 pmol of each primer (forward primer labelled with a
141 Cy5 fluorescent dye group), 0.1 U of Taq DNA polymerase (Bioline, UK), 1X supplied PCR Buffer, 2.0
142 mM MgCl₂, and 0.2 mM deoxynucleotide triphosphate (dNTP) and using the originally described
143 thermoprofiles for each locus. PCR amplicons were separated on an Applied Biosystems 3,500
144 sequencer with alleles inferred using GENEMAPPER (Applied Biosystems). mtDNA sequence variation
145 was assessed by PCR amplification of the control region using primers described by Pappalardo et al.
146 (2015) and sequencing using the internal primer (5'-CCCTTAGGCAGTTCAAGCAC-3') with Big Dye
147 technology on an Applied Biosystems 3500. Sequence alignment was performed in BIOEDIT (Hall 1999)
148 using default settings.

149 *Statistical analysis of genetic variation*

150 Microsatellite variation within samples was characterised using numbers of alleles (N_A), allelic richness
151 (A_R), observed heterozygosity (H_O), and expected heterozygosity (H_E), calculated using FSTAT 2.9.3
152 (Goudet, 1995). Deviations from Hardy-Weinberg equilibrium (HWE) were measured using F_{IS} and
153 tested for significance by 10,000 permutations in FSTAT 2.9.3, while genotypic linkage equilibrium
154 between pairs of loci were tested using exact tests (10,000 batches, 5,000 iterations) in GENEPOP 3.3
155 (Raymond & Rousset 1995). Genetic differentiation among samples was quantified by global and
156 pairwise F_{ST} values, with associated significance evaluated by 10,000 permutations (exact F_{ST} estimator
157 test, Goudet et al. 1996). Pairwise F_{ST} values among samples were visualised using principal
158 coordinates analysis (PCoA), performed in genetic analysis in Excel (GenAlEx). mtDNA variation was

159 described by haplotype number and haplotype diversity (h) (Nei 1978) calculated in Arlequin software
160 (Excoffier & Lischer 2010). Phylogenetic relationships among haplotypes were inferred using
161 maximum likelihood trees constructed in MEGA v 6.06 (Tamura et al. 2013). Partitioning of variation
162 was analysed using analysis of molecular variance (AMOVA, Excoffier et al. 1992) derived estimates of
163 various Φ -statistics, as well as pairwise Φ_{ST} with significance of the various indices assessed by 10,000
164 permutations.

165 *Assignment of post-larval anchovy individuals*

166 The individual clustering method in STRUCTURE 2.3.4 (Pritchard et al. 2000) was used to estimate the
167 most probable number of genetic groups within the data and the membership of individuals to these
168 groups. Optimal models were assessed following Pritchard et al. (2000) and where there was support
169 for $K > 1$, ΔK (Evanno et al. 2005) was also assessed. To complement the individual-based STRUCTURE
170 analysis, classical individual assignment (IA) tests were also performed in GenAIEx. Specifically, the
171 adult samples were pooled into Southern and Northern groups identified by F_{ST} and STRUCTURE
172 analysis. These were then used as baseline samples in IA tests. The post-larval samples were treated
173 as 'unknown' and each individual was assigned to either the Northern or Southern group.

174 2.3. Anchovy Egg and Juvenile distribution

175 Dedicated anchovy data were available for the western English Channel from an acoustic autumn
176 survey from 2017 (PELTIC survey, Table 1, Doray et al. 2021) and the distinct acoustic backscatter
177 data attributed to juvenile anchovy were combined with those from the Bay of Biscay (JUVENA
178 survey, Table 1, Boyra et al. 2013) to provide broad-scale distribution maps to explore any continuity
179 in distribution of juvenile anchovy between the two areas. Acoustic backscatter collected during
180 both acoustic surveys was partitioned by species and size using ratios obtained from nearby trawl
181 hauls, although acoustic features such as school morphology also contributed (more details provided
182 in Doray et al. 2021). As mentioned previously, the juvenile anchovy schools focused on in this study
183 were different from the anchovy typically encountered during the PELTIC survey, and the species
184 and size composition obtained from targeted trawls confirmed this.

185 We compared recent juvenile anchovy distribution maps in 2017-2021 with those from
186 2008-2010 as representative of a period of typical historical conditions. Data from before 2008 were
187 not considered as the Bay of Biscay anchovy stock was recovering from a collapse following years of
188 poor recruitment, which may not have been representative for historical observations.
189 Unfortunately, no concurrent survey data were available for the English Channel for 2008-2010 but
190 particle tracking modelling showed that eggs or larvae were unlikely to have made it to the English
191 Channel in that period (Petitgas et al. 2012).

192 As changes in the juvenile anchovy autumn distribution may have been related to spawning
193 location, we mapped anchovy egg density distribution for these same periods, 2008-2010 and 2017-
194 2021. Anchovy egg data were available from two spring surveys, including PELGAS, which collects
195 information on egg densities using the Continuous Underway Fish Egg Sampler (CUFES, Checkley et
196 al. 1997) whilst running acoustic transect lines, and the BIOMAN survey (Santos et al. 2018, 2023)
197 which collects information on egg densities using different methods including CUFES to sample eggs.
198 Ichthyoplankton samples, including eggs and larvae, were also collected in the English Channel
199 during the autumn, using a vertical ringnet deployment at up to 100 stations per year (Doray et al.
200 2021).

201 Due to differences in sampling gears, survey design and data units (primarily acoustic and
202 ichthyoplankton data), the spatial data were standardised by gridding the backscatter and egg
203 density data (*sensu* Doray et al. 2018a) by 0.25° longitude and latitude cells.

204 2.4. Early Life Stage dispersal model

205 We used the Lagrangian particle tracking module detailed in Huret et al. (2010) to simulate the
206 transport of early life stages of anchovy over the years 2008 to 2010, and 2017 to 2021 from known
207 spawning grounds in the Bay of Biscay. The objective of simulating the early years was to test the
208 hypothesis that no, or negligible, drift from the Bay of Biscay to the English Channel occurred
209 compared to more recent years. We also simulated five recent years to check whether the simulated
210 interannual variability in connectivity between the two eco-regions is consistent with our (field)
211 observations of post-larvae abundance in the western Channel. The particle tracking module was
212 coupled online to the hydrodynamic model MARS (Lazure et al. 2009). We used the MARS3D V11.1
213 with a configuration at 2.5 km spanning an area from Northern Portugal to the southern North Sea,
214 as further detailed in Petton et al. (2023; see their Figure 5). The model used 40 depth layers in the
215 vertical domain. Atmospheric forcing was provided by the Météo-France model ARPEGE. Daily run-
216 off data from the main rivers were included. Boundary conditions for temperature and salinity were
217 provided by the Mercator PSY2V4 and PSY4v3 re-analysis, for the early and late years simulated,
218 respectively. The Lagrangian module has the same time step as the hydrodynamic model, i.e.
219 approximately 2 min, and a few seconds on the vertical, to resolve vertical mixing based on a non-
220 naive random walk (Ross & Sharples 2004). On the horizontal, a diffusion coefficient of 5 m².s⁻¹ was
221 set for the random walk.

222 For each simulated year, we initiated the particle distribution based on egg distribution as
223 sampled in May during the PELGAS survey (Doray et al. 2018b) with CUFES (Checkley Jr et al. 1997,
224 Huret et al. 2018). Since the survey could not be conducted in 2020, we used BIOMAN CUFES data

225 for that year. For each of the selected years, 25,000 particles were released on the 15th of every
226 spawning month from April to August (Huret et al. 2018), proportional to the observed horizontal
227 egg distributions derived from each annual survey, and randomly from surface to 20 m depth. Egg
228 specific gravity was specified based on its relationship with surface water density (Huret et al. 2016)
229 and varied throughout egg development following (Ospina-Álvarez et al. 2012). Yolk sack larvae had
230 a similar buoyancy as the last egg developmental stage. When total larval length reached 6 mm, they
231 started migrating in the vertical domain between the surface and 25 m depth, following
232 observations in the Bay of Biscay (M. Huret unpubl. data). The Lagrangian module was coupled to a
233 bioenergetic Dynamic Energy Budget (DEB) module to simulate the development and growth of
234 anchovy larvae (Gatti et al. 2017). Temperature data used to force the bioenergetics were provided
235 by the hydrodynamic model, while f of the DEB Holling Type II functional response was set to 0.8,
236 which generated an average growth rate that only depended on temperature without considering
237 food limitation. Since zooplankton concentrations and interannual variability remain poorly
238 validated in biogeochemical models, we made that choice to avoid spurious growth or mortality
239 effects. Hence, interannual and seasonal variability considered with our dispersal model arose solely
240 from circulation and temperature and not food availability.

241 Larval drift and bioenergetics were influenced by many processes, many of which were
242 associated with significant uncertainties. In addition, fecundity is variable throughout the spawning
243 season but could not be quantified here. Therefore, we included a set of constraints, with the aim of
244 providing a more complete understanding of the biophysical factors driving the connectivity
245 between the Bay of Biscay and the English Channel, and eventually to be able to draw more robust
246 and realistic conclusions. First, we calculated the number of particles ending in the English Channel
247 (north of 48.5° N and east of 5.7° W) after a drift period of 60 days. Since all simulations started with
248 the same number of particles, changes in this result highlighted the effects of seasonal variability in
249 the circulation, and interannual variability in both the circulation and the spatial distribution of
250 spawning. The drift duration of 60 days corresponded to the maximum age at which larvae reached
251 40 mm Standard Length in the Bay of Biscay (Aldanondo et al. 2016), estimated to be the length at
252 which European anchovy metamorphose (Ré 1996, La Mesa et al. 2009). Second, the numbers of
253 particles were weighted by the total numbers of eggs, as the sum of densities over the sampled area,
254 observed during the annual surveys in May. Little information was available about the egg densities
255 outside the May survey period, although these were known to vary. For that reason, the third
256 constraint was the application of a spawning curve as derived from Huret et al. (2018, their Figure 8)
257 to correct the contribution of each month to spawning, with highest contribution in June, and lowest
258 in April and August. Finally, we only considered the larvae ending in the Channel that reached

259 metamorphosis at age 60 days. Metamorphosis was based on the requirement to reach a specific
260 maturity level provided by the bioenergetic model, which itself depended on each individual's life
261 history (see Gatti et al. 2017). This final constraint was expected to adversely impact larvae with low
262 growth rates due to low temperatures either as a result of having spawned during early months or in
263 colder years. This was included to represent the feature that slow growing larvae have higher
264 mortality rates.

265 2.5. Ushant Front position

266 One of the main oceanographic features of the area is the Ushant Front which separates stratified
267 waters to the west and mixed waters in the east (Pingree 1975) and runs from the Isle of Ushant
268 (Ouessant) off Brittany across the "mouth" of the English Channel to the south coast of England. The
269 front forms a potential boundary for planktonic organisms and although it was considered in the
270 hydrographic model used for the particle tracking, its exact location during the annual autumn
271 survey was explored using the temperature profiles from the approximately 100 evenly-spaced CTD
272 stations annually sampled during the PELTIC survey (Doray et al. 2021). Stations where the
273 difference between surface and bottom temperature (ΔT) was above 0.5 °C were considered
274 stratified and those with a smaller or no temperature difference were considered vertically mixed
275 (Monterey & Levitus 1997). The front was drawn by interpolating between stations which separated
276 the mixed and stratified waters. Between 2013-2016 only data from the northern waters of the
277 English Channel were available due to restricted survey coverage. From 2017 coverage included the
278 whole of the English Channel.

279 3. Results

280 3.1. Genetic analysis of population structure (adults)

281 The total number of alleles per locus ranged from 12 to 40 (mean 25). Summary statistics are
282 presented in Table 2. Multilocus F_{IS} values were significant for all samples except the Irish Sea-1
283 sample. However, these values were largely due to locus Ee2-508 and Ee2, which reported significant
284 heterozygote deficits in 9 and 10 samples (out of 12), respectively. In the case of Ee2-508 it did
285 conform to HWE in the two Biscay offshore samples as well as in Irish Sea-1. No other locus exhibited
286 a heterozygote deficit in more than two samples. Linkage disequilibrium tests provided no evidence
287 of linkage between any pair of loci (i.e. a pair of loci yielding significant tests results for a number of
288 samples). Global genetic structure as measured by F_{ST} was highly significant ($F_{ST} = 0.017$; $P < 0.0001$).
289 Pairwise F_{ST} values supported a clear separation between the Northern (Irish Sea, English Channel,
290 North Sea) and Southern (Biscay and North France) adult samples with the post-larval sample

291 clustering with the Southern group (Fig. 3). Differentiation between the North/Biscay adult groups
292 was also supported by AMOVA (F_{CT} (among groups) = 0.02, $P < 0.001$; F_{SC} (among samples within
293 groups) = 0.005 $P < 0.0001$). Global genetic structure as measured by F_{ST} was highly significant ($F_{ST} =$
294 0.017; $P < 0.0001$). The final mtDNA alignment comprised 449 bp and revealed 108 haplotypes.
295 Phylogenetic reconstruction partitioned these haplotypes into two highly supported clades (labelled
296 A and B to fit with Zarraonaindia et al. 2012 and Silva et al. 2014) with 76 and 32 haplotypes in clade
297 A and B, respectively (Fig. 4). Overall haplotype diversity was high ($h = 0.95$) and similar among samples
298 (Table 2). However, the mtDNA reported the same North-South partitioning as the microsatellite data
299 (Fig. 3) with clade A being almost absent from the northern samples (3%) compared to 50.4% among
300 the southern samples. This translated into highly significant pairwise Φ_{ST} values in all comparisons
301 between regions while only one pairwise value was significant within regions (Table 2). In line with the
302 nuclear patterns the post-larval sample also exhibited a much higher frequency of mtDNA clade A than
303 found among northern samples (Table 2).

304 The various Bayesian clustering analyses unanimously identified $K=2$ (Fig. 5) as the optimal model (P
305 = 0.99 and nearly zero for all other K - values tested). The pattern of individuals clustering followed the
306 F_{ST} based analyses in revealing the adults from the four Biscay and N. France sites clustered into one
307 group (hereafter southern group) while the adults sampled in the Irish Sea/Bristol Channel, English
308 Channel and North Sea sites clustered into the other group (hereafter northern group). The post-larval
309 individuals exhibited a strong membership the southern group. Similarly, when the post-larval
310 individuals were treated as 'unknown' the vast majority (42 of 48 individuals) were assigned to the
311 southern group by IA tests (adults were pooled into a northern and southern reference populations
312 as supported by the other analyses).

313 3.2. Survey-derived anchovy juvenile and egg distribution

314 Autumn juvenile anchovy showed a variable distribution for the years included in this study. During
315 the historical period (2008-2010), juvenile anchovy showed coastal (2008) as well as offshore (2009
316 and particularly 2010) distribution (Fig. 6). More recently, juvenile anchovy distribution was
317 generally higher on the shelf with a hotspot off the Gironde estuary in most years. In 2017 and 2018,
318 the northern-most distribution of juvenile anchovy seemed to be restricted to a narrow coastal strip
319 off Brittany with no juveniles observed in the western English Channel. In 2019, small numbers of
320 juvenile anchovy were found in the SW of the English Channel, along the north coast of Brittany. It
321 was unclear from the map whether these were connected to the northern Bay of Biscay due to a
322 significant gap in survey coverage (detailed in caption of Fig. 6). Apart from typical shelf sea
323 distribution in 2020, juvenile anchovy were found further offshore in the north of the Bay of Biscay

324 with significant numbers also in the western English Channel, extending at least 120 n.mi. east into
325 the Channel. Anchovy were reported at the easternmost transects of the survey and may therefore
326 have extended further east in the English Channel (ICES 2021). Juvenile anchovy densities were
327 lower in 2021 and while found at the northern perimeter of the Bay of Biscay (48° N), none were
328 found in the western English Channel. Both the length range (4.0-9.5 cm v 5.0-10 cm) and weighted
329 mean length (4.5 cm v 6.5 cm) of juvenile anchovy in the English Channel were smaller in 2019
330 compared to 2020 (Fig. 7). In both 2019 and 2020 the juvenile anchovy from the surface schools
331 were distinctly smaller than the anchovy typically encountered during the survey and which included
332 ages 0 to 2 year old (Fig. 7).

333 In the early period (2008-2010), spring egg densities (May) were relatively low and were
334 confined to the southern Bay of Biscay (Fig. 8 Fig. 8). From 2017, densities were generally higher with
335 some evidence of spawning activity occurring further north in some years. In 2020 a distinct band of
336 high egg densities suggested peak spawning in May occurred further offshore, whereas in 2021 two
337 parallel bands of spawning were observed, one inshore along the coast and one off the shelf edge (
338 Fig. 8). In 2019, 2020 and 2021, spawning occurred further north than previously observed. In 2010
339 and 2017, spring coverage included the southwestern English Channel and no anchovy eggs were
340 found. To date no anchovy eggs or recently hatched larvae were recorded in ichthyoplankton
341 samples collected during the PELTIC survey in the western English Channel during October.

342 3.3. Early Life Stage dispersal model

343 The larval drift modelling revealed intra- and inter-annual variability in the connectivity patterns
344 between the yearly egg distribution, as observed during the surveys, and the larval distribution at
345 age 60 days (Fig. 9 a). The number of larvae reaching the English Channel at the end of the larval
346 stage generally decreased as the spawning season progressed (Fig. 9 a), from 1.6 % in April, ~0.6 % in
347 May and June, and fewer than 0.2% in July and August (monthly averages across the years). The
348 annual proportion (averaged across spawning months) was lower during the early period (less than
349 0.02% in 2009-2010) compared to the recent period (1.8 % and 1.6 % in 2020 and 2021 respectively),
350 although 2008 (0.6%) saw an intermediate proportion. The largest contribution of larvae reaching
351 the Channel were predicted to originate from April and May 2020 spawning times (5.4 % and 2.1%,
352 respectively) and from April and June 2021 (3.0 % and 2.8 %, respectively). All particles reaching the
353 English Channel originated from the northern Bay of Biscay (north of 46° N, Fig. A1).

354 After applying the total annual egg production, based on estimates obtained from the
355 surveys, the year 2020 was predicted to contribute about 2 to 4 times more individuals to the
356 Channel compared to 2021 and 2019, respectively (Fig. 9 b). When considering the known spawning

357 curve, with a peak in June, then the annual contributions remained almost similar, with 2021
358 increasing slightly relative to 2020. Contributions in years 2009 and 2010 were reduced to null since
359 their monthly contribution came from April and May when spawning is low compared to June (Fig.
360 9c). When considering the larval bioenergetics, with the constraint of reaching the juvenile stage at
361 age 60 days, most larvae made it to the English Channel in 2021. Particularly June-spawned eggs
362 contributed (Fig. 9 d) when temperature was more favourable (warmer) for rapid growth compared
363 to earlier in the year. None of the larvae born in April reached the Channel at day 60 of the juvenile
364 stage (all simulated years). When all constraints were combined, the years 2020 and 2021, and
365 particularly the month June contributed the highest number of larvae to the Channel, followed by
366 2018 and 2019. The early years (2008-2010) contributed none or only negligible numbers of larvae.

367 3.4. Variability in Ushant Front position

368 Annual October frontal maps derived from temperature profiles collected during the PELTIC surveys
369 showed a consistent position of the Ushant front in the south of the survey for most of the years
370 (when data were collected at the southern end of the Channel: 2017-2019 and 2021, Fig. 10). The
371 only exception was 2020 when the southern end of the front was positioned much further west. In
372 2012 the front was extended further west but this was due to that survey taking place significantly
373 later compared to the rest of the time series (late October to mid-November) and exhibited winter
374 conditions.

375 4. Discussion

376 4.1. Juvenile anchovy surface schools in English Channel 377 originate from the Bay of Biscay

378 This study aimed to identify the origin of large numbers of juvenile anchovy surface schools
379 observed, for the first time, in the southwestern and southern English Channel in 2019 and 2020,
380 and to investigate the mechanisms through which they got there. The absence of anchovy eggs in
381 ichthyoplankton monitoring in the English Channel, the continuity in distribution of anchovy
382 juveniles from the Bay of Biscay into the Channel, as well as the results from particle tracking
383 modelling and from genetic studies all strongly suggest that they originated from the Bay of Biscay.
384 This was the first time this was observed and appeared to present a new scenario in anchovy
385 dynamics in the area, following the finding that previously recorded range expansion was caused by
386 improved survival of remnant spawning populations (Petitgas et al. 2012).

387 The microsatellite and mtDNA results for adults presented in this study clustered Northeast
388 Atlantic anchovy into two spatial coherent groups: a southern group containing specimens from the

389 Bay of Biscay and Brittany, and a northern group containing those from the Irish Sea, Bristol Channel,
390 English Channel and North Sea. This separation readily aligned with results from other genetic
391 studies (Zarraonaindia et al. 2012, Huret et al. 2020). The high level of genetic divergence between
392 the northern and southern groups permitted individuals to be robustly assigned. Both STRUCTURE
393 and IA analysis assigned the majority of post larval samples to the southern group. This detection of
394 larvae of Biscay origin in the Channel suggested that connectivity between the Bay of Biscay and the
395 English Channel had become possible in recent years through larval drift.

396 This was confirmed by particle tracking modelling conducted during the current study, which
397 suggested that the potential for connectivity has increased between the end of the 2000's and the
398 most recent years (2018-2021). It confirmed that previous conditions, represented by 2008 - 2010,
399 were not conducive to eggs/juveniles reaching the English Channel due to prevailing spawning taking
400 place in the south of the Bay of Biscay. Some northern spawning activity was observed in 2008, and
401 some eggs were predicted to reach the Channel. However, total spawning activity that year was very
402 low and in addition, most of those larvae reaching the Channel originated in April. This matched
403 previous findings (Petitgas et al. 2012). In contrast, particle tracking modelling based on spawning
404 conditions during recent years (2017 to 2021), predicted that anchovy larvae were able to reach the
405 Channel, specifically off northern Brittany. Initially, predicted numbers were negligible (2017) and
406 moderate (2018 and 2019) which in part matched the survey observations with first post-larval
407 anchovy reported in 2019. In 2020, very high numbers were predicted to arrive in the Channel,
408 which also matched survey observations. Spawning has increased everywhere in the Bay of Biscay as
409 a result of a growing anchovy Spawning Stock Biomass since the early 2010's (ICES 2023). In the
410 most recent years, spawning has also increased substantially in the northern part of the Bay of
411 Biscay in May, the only part that our study suggests connects with the English Channel through larval
412 drift. This northward expansion of the spawning distribution was previously described and related to
413 density-dependent processes under increasing Spawning Stock Biomass (Petitgas et al. 2014,
414 Erauskin-Extramiana et al. 2019). Temperature may have contributed as well although this is not
415 proven explicitly in this study: 2019 and 2020 were particularly mild, which may have facilitated a
416 temporal (earlier) and spatial (northerly) expansion of the spawning habitat. Forecasted increases in
417 temperature are anticipated to improve conditions for anchovy egg production, and to expand its
418 spawning habitat. Both factors would induce higher egg densities and, under density-dependent
419 processes, will further increase the potential for spawning north in the Bay (Erauskin-Extramiana et
420 al. 2019) and hence connectivity with the English Channel.

421 Not all model predictions matched survey observations as moderate and high numbers were
422 predicted to reach the Channel in 2018 and 2021, respectively, yet no juveniles were encountered

423 during the survey in the English Channel. As in 2020, juveniles were found in 2021 towards the
424 northern boundary of the Bay of Biscay but in much lower densities than in 2020. The discrepancies
425 between modelled and observed juvenile distributions could be due to several reasons. The
426 dispersal model assumed annual spawning location throughout the season were as observed during
427 May surveys of that year. While the total spatial range is likely not to change within a year, seasonal
428 shifts in dominant spawning activity may occur and could have influenced the connectivity. Also, the
429 two acoustic surveys monitoring juvenile anchovy only provide a snapshot of a few weeks and a
430 slight alteration in survey timing or hydrography may result in any anchovy influx being missed. This
431 may be exacerbated by the fact that some post-larvae may have developed swimming ability which
432 was not considered by the drift model. Another possibility is that the juveniles continued to drift
433 north rather than entering the channel. This could be caused by subtle oceanographic features that
434 were not captured (accurately) in the hydrographic model which underpinned the dispersal model.
435 The Ushant front, situated across the mouth of English Channel may act as a barrier, limiting
436 planktonic (surface) organisms, including post-larval anchovy, to pass. This could explain the
437 observation that most larvae were observed in the Channel in 2020 when the Ushant front was
438 extended much further west than in other years. Also, the presence of Bay of Biscay genetic features
439 in the Bristol Channel sample suggested that some anchovy may have previously drifted north past
440 the frontal barrier at the entrance of the English Channel. The Ushant Front, which, like other fronts
441 is itself likely to be affected by climate change (Ferrari 2011), and its potential role in the
442 connectivity of anchovy between the two areas, requires further examination.

443 4.2. When were these anchovy juveniles born?

444 The particle tracking model results suggested it was primarily spawning in June and to a lesser extent
445 May and July, which contributed eggs that reached the English Channel. This could not be confirmed
446 by survey data, as no detailed age information was available for the juvenile anchovy sampled.
447 However, the mean size of the juvenile anchovy of 4.5 cm (2019) and 6.5 cm (2020) suggested that
448 fish were between 40 and 70 and between 60 and 80 days old, respectively (Aldanondo et al. 2016).
449 Given their capture date (between 9th and 18th of October in both years) and local conditions, this
450 would suggest these fish were born between late July and late August. Within the Bay of Biscay,
451 Aldanondo et al. (2016) estimated the hatch-date of autumn juveniles to range from mid-June to
452 mid-August with a peak in mid-July. This was at least one month later than the spawning peak
453 previously reported to be in May-June (Motos et al. 1996, Huret et al. 2018). The length distribution
454 of the juvenile anchovy in the current study also suggested that their birth date was later than June
455 as estimated by the larval drift experiment. This apparent inconsistency across several studies could

456 be explained if late (post-June) spawned individuals have improved survivability, compared to those
457 originating from the peak spawning period in June.

458 4.3. What does the future hold for these Biscay juveniles in the 459 Channel?

460 It is at this stage not known whether the juvenile anchovy that reach the English Channel settle there
461 or return to the Bay of Biscay. Their survival is likely dependent on the genomic properties which will
462 influence the ability to adapt to northern conditions. The transcriptome study by Montes et al.
463 (2016) reported evidence of adaptive divergence between offshore spawning ecotypes from Bay of
464 Biscay and northern inshore spawning ecotypes.. This points to selection differences between the
465 regional groups and could suggest Bay of Biscay specimens are not able to survive or mix with those
466 from the North Sea. If they do stay and integrate in the northern population, it would alter what has
467 been a prolonged localised restriction on dispersal and gene flow between both regions, and could
468 be observed in future adult genetic samples. The current distinct genetic signatures of the two
469 populations (this study, Petitgas et al. 2012, Huret et al. 2020) suggests that this has not happened
470 yet, although the reference samples in this study were collected several years prior to the post-larval
471 samples. In addition to the genetic differences between Bay of Biscay and northern anchovy, there is
472 some evidence that the growth rates of the two populations is different (Menu et al. 2023).

473 4.4. What are the possible implications?

474 Changes in species distribution can have significant implications for the management of the stock,
475 for example through misalignment with monitoring survey coverage and fishing effort. For anchovy
476 in the Bay of Biscay a survey-derived recruitment index was a key contributor to improved
477 assessment of this short-lived species after its crash in the early 2000s (Boyra et al. 2013, Uriarte et
478 al. 2023). The presence of significant juvenile anchovy biomass outside the original survey area
479 (11.4% *sensu* ICES 2021), as observed in 2020, could therefore adversely impact the accuracy of the
480 index with risks to the stock and the fishery. Also, while catches in the English Channel and southern
481 North Sea have thus far been opportunistic and relatively low, a continued increase of anchovy
482 biomass in the region may attract new, more targeted fisheries. Any possible integration of the Bay
483 of Biscay stock with northern anchovy, as discussed above, would further challenge the
484 management of the spawning populations.

485 There are also potential ecological implications of distributional shifts. Several other small
486 pelagic fish species reside in this area and the introduction of significant biomass of a generalist
487 planktivorous species like anchovy (Raab et al. 2011, Patel et al. 2023), may alter the
488 trophodynamics through competition or predation on eggs and larvae (Plirú et al. 2012). Juveniles

489 can have particularly large impacts on prey due to their high densities and high mass-specific rates of
490 feeding (Peck et al. 2021 and references therein). Influx of anchovy juveniles such as reported in this
491 study could therefore cause local food limitation. This would adversely affect local autumn spawning
492 planktivorous fish such as sardine (Coombs et al. 2010) which rely on productivity towards the end
493 of the plankton growing season for larval stage winter survival (Capuzzo et al. 2022). Changes in the
494 community can alter predator-prey relationships and ultimately modify entire food webs (Edwards &
495 Richardson, 2004). Like other small pelagic fish, anchovy plays a pivotal ecological role as a mid-
496 trophic species in the marine environment, channelling energy from lower trophic levels to top
497 predators. While not necessarily linked to anchovy, changes in some predator distributions have
498 been reported in the area in recent years. Bluefin tuna *Thunnus thynnus* reappeared in the English
499 Channel in 2014 after decades of absence, and increases in prey abundance are likely to have
500 contributed (Horton et al. 2021). Anchovy is also a favoured prey of the Critically Endangered
501 Balearic shearwaters *Puffinus mauretanicus*. The species has seen a northwards postbreeding range
502 expansion into the Celtic Sea although no directly link was found with prey distribution (Philips et al.
503 2021).

504 Changes in biogeography and abundance are just some of the potential impacts of climate
505 change on biota which also includes changes in phenology and body size (Edwards & Richardson
506 2004, Perry et al. 2005, Dulvy et al. 2008, Simpson et al. 2011, Cheung et al. 2013). Understanding
507 the mechanisms underlying these dynamics is essential to predict future human influences on
508 biodiversity, and guide conservation responses. For anchovy in the Northeast Atlantic Ocean, after
509 more than half a century of limited change in distribution at the northern boundary, two such
510 processes, both causing poleward movement, have now been described. First, Petitgas et al. (2012)
511 demonstrated that observed northward anchovy range expansion from the mid-1990s was a results
512 of climate-driven improved survival of northern remnant spawning populations. Second, in this study
513 we report a new scenario, observed just over two decades later, and have provided evidence that a
514 density-dependent driven change in spatio-temporal spawning patterns has enabled early life stages
515 to expand their normal distribution by more than 100 nautical miles. The current study has
516 highlighted that a taxa's range dynamics at the edge of its distribution is complex and may be due to
517 environmental factors, biotic interactions, human impact and species' life histories.

518

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530

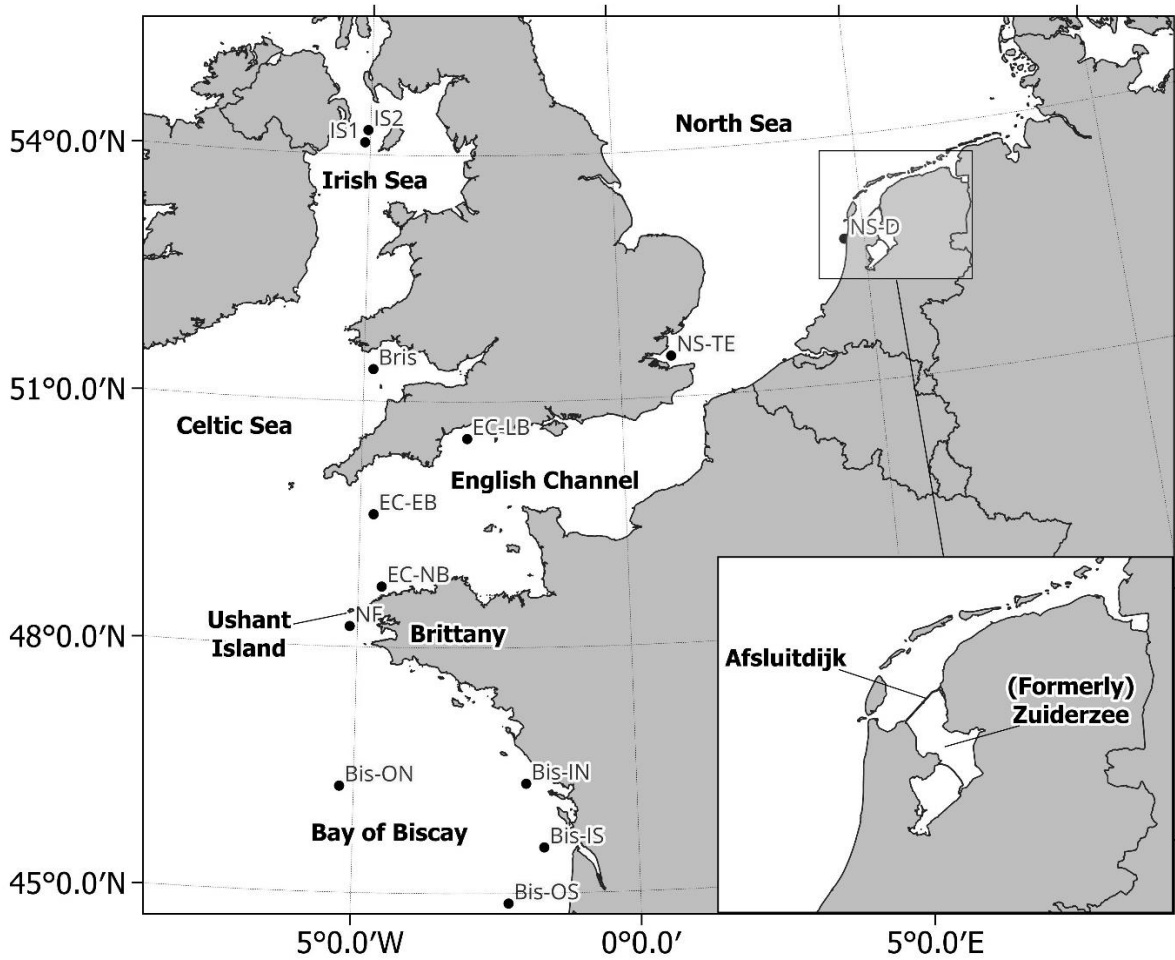
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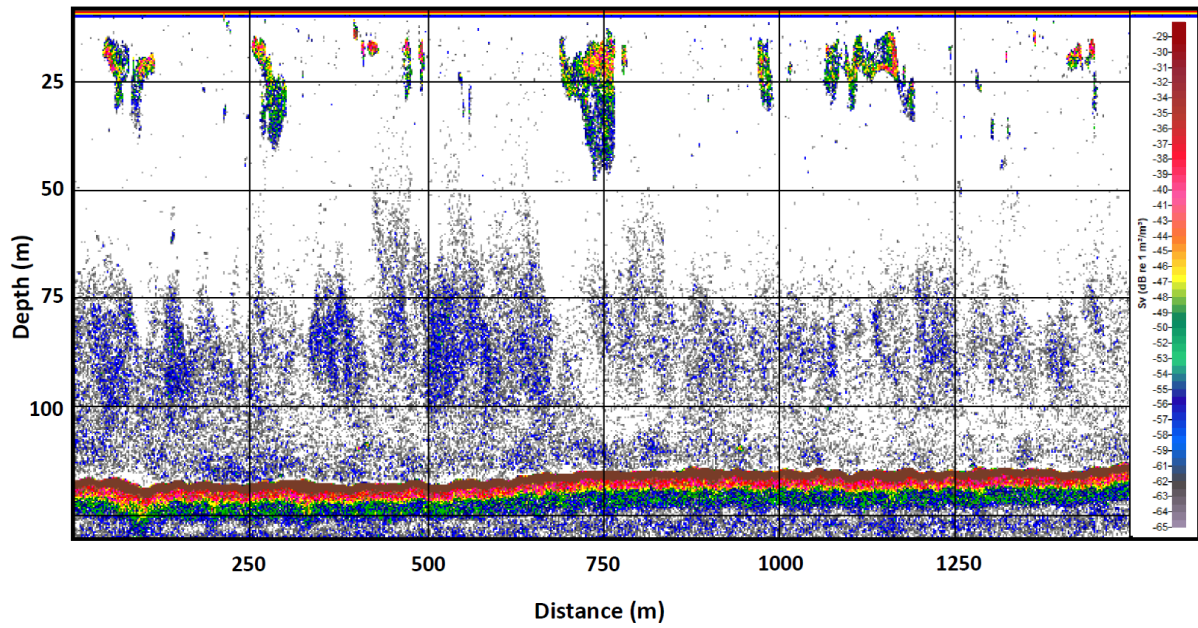
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Fig. 1. Map of study area in the Northeast Atlantic Ocean, including North Sea, English Channel and Bay of Biscay and other relevant geographic areas as referenced in the text, including the historic Zuiderzee (inset). Genetic sampling stations denoted by black points (•), with associated details included in Table 2. Abbreviations of sample locations: Irish Sea-1 (IS1), Irish Sea-2 (IS2), Bristol Channel (Bris), English Channel- Eddystone Bay (EC-EB), English Channel-Lyme Bay (EC-LB), North Sea – Thames Estuary (NS-TE), North Sea – Dutch (NS-D), North France (NF), Biscay Inshore North (Bis-IN), Biscay offshore (Bis-ON), Biscay Inshore South (Bis-IS), Biscay offshore South (Bis-OS), English Channel-post larvae (EC-NB).

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Fig. 2. Echogram (visualised using Echoview Software®) displaying an example of post-larval/juvenile anchovy surface schools observed during the PELTIC survey in French waters of the western English Channel. This example was observed 18/10/2020 at 10:41 GMT and was representative of post-larval observations in 2019 and 2020. Echogram represents backscatter at 38 kHz (density scale on right) and -65 dB threshold. Depth (m) on y-axis (top to bottom), and distance (m) on x-axis. Seabed is represented by dense (red/brown) layer at bottom.

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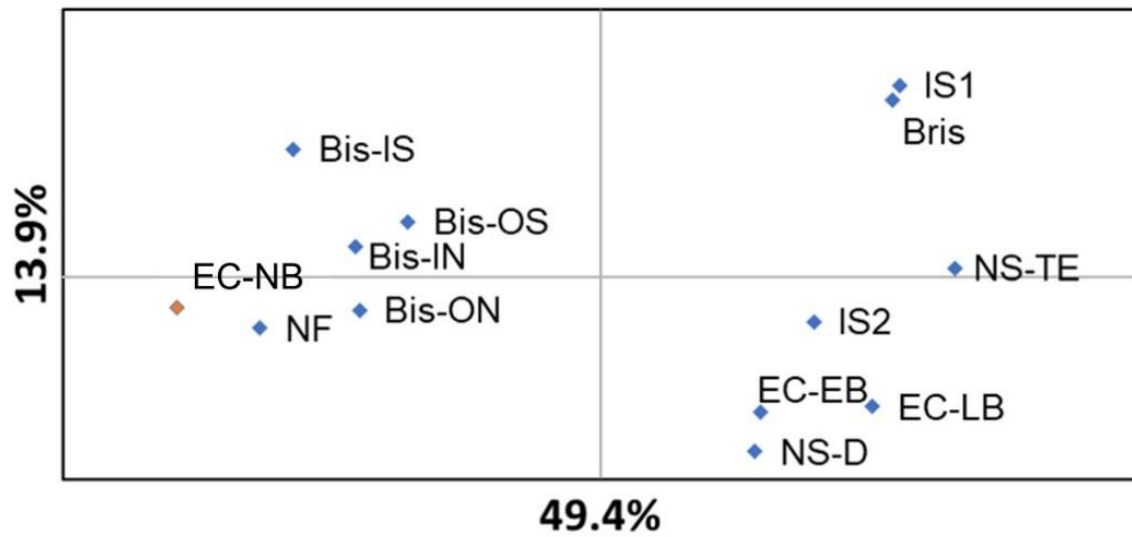
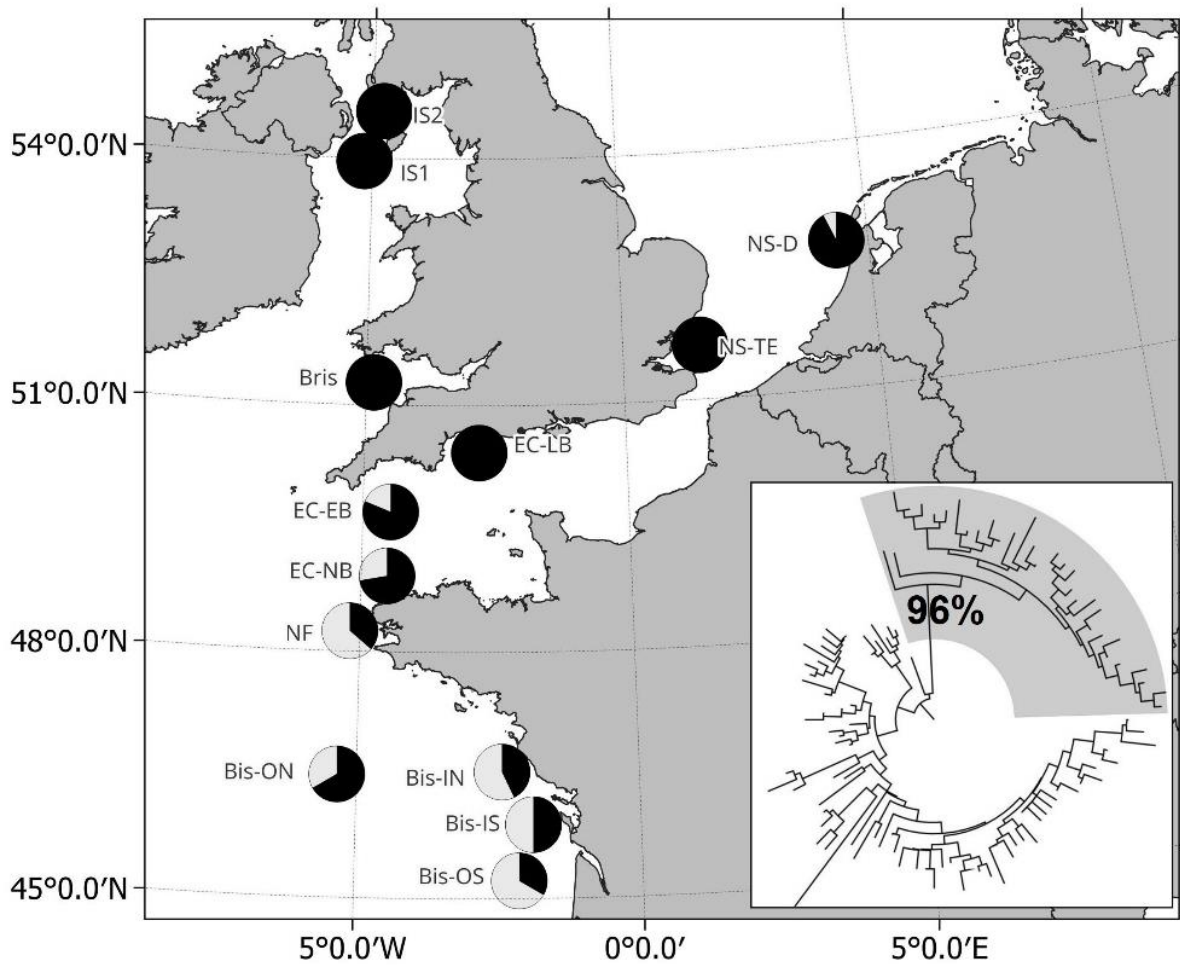


Fig. 3. Principal coordinates analysis (PcoA) of genetic distance between anchovy individuals demonstrating the clear difference between the northern (right) and Biscay (left) groups based on microsatellite analysis. Abbreviations of samples locations: Irish Sea-1 (IS1), Irish Sea-2 (IS2), Bristol Channel (Bris), English Channel- Eddystone Bay (EC-EB), English Channel- Lyme Bay (EC-LB), North Sea – Thames Estuary (NS-TE), North Sea – Dutch (NS-D), North France (NF), Biscay Inshore North (Bis-IN), Biscay offshore (Bis-ON), Biscay Inshore South (Bis-IS), Biscay offshore South (Bis-OS), English Channel-post larvae (EC-NB). Note that the juvenile anchovy larvae (EC-NB) are demarcated with an orange diamond.



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Fig. 4. Map of Northeast Atlantic Ocean showing genetic sample locations with pie charts denoting relative proportion of the two major mtDNA clades (clade A in grey, clade B in black). Inset shows Maximum Likelihood phylogenetic tree with high bootstrap support (96%) for separation of these clades (clade B sequences shaded). Post-larval sample represented by EC-NB. Further details of genetic sampling locations and associated genetic results in Table 2. Abbreviations of samples locations: Irish Sea-1 (IS1), Irish Sea-2 (IS2), Bristol Channel (Bris), English Channel- Eddystone Bay (EC-EB), English Channel-Lyme Bay (EC-LB), North Sea – Thames Estuary (NS-TE), North Sea – Dutch (NS-D), North France (NF), Biscay Inshore North (Bis-IN), Biscay offshore (Bis-ON), Biscay Inshore South (Bis-IS), Biscay offshore South (Bis-OS), English Channel-post larvae (EC-NB).

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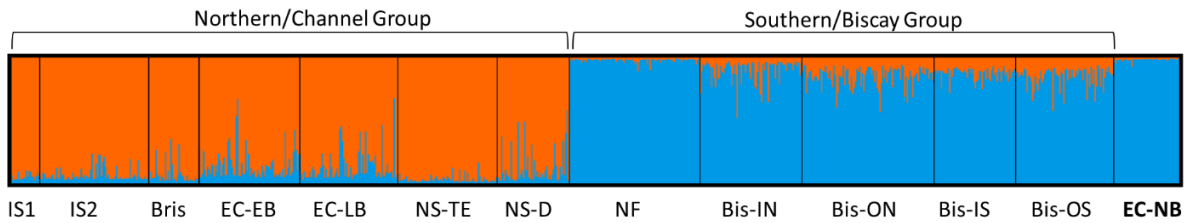
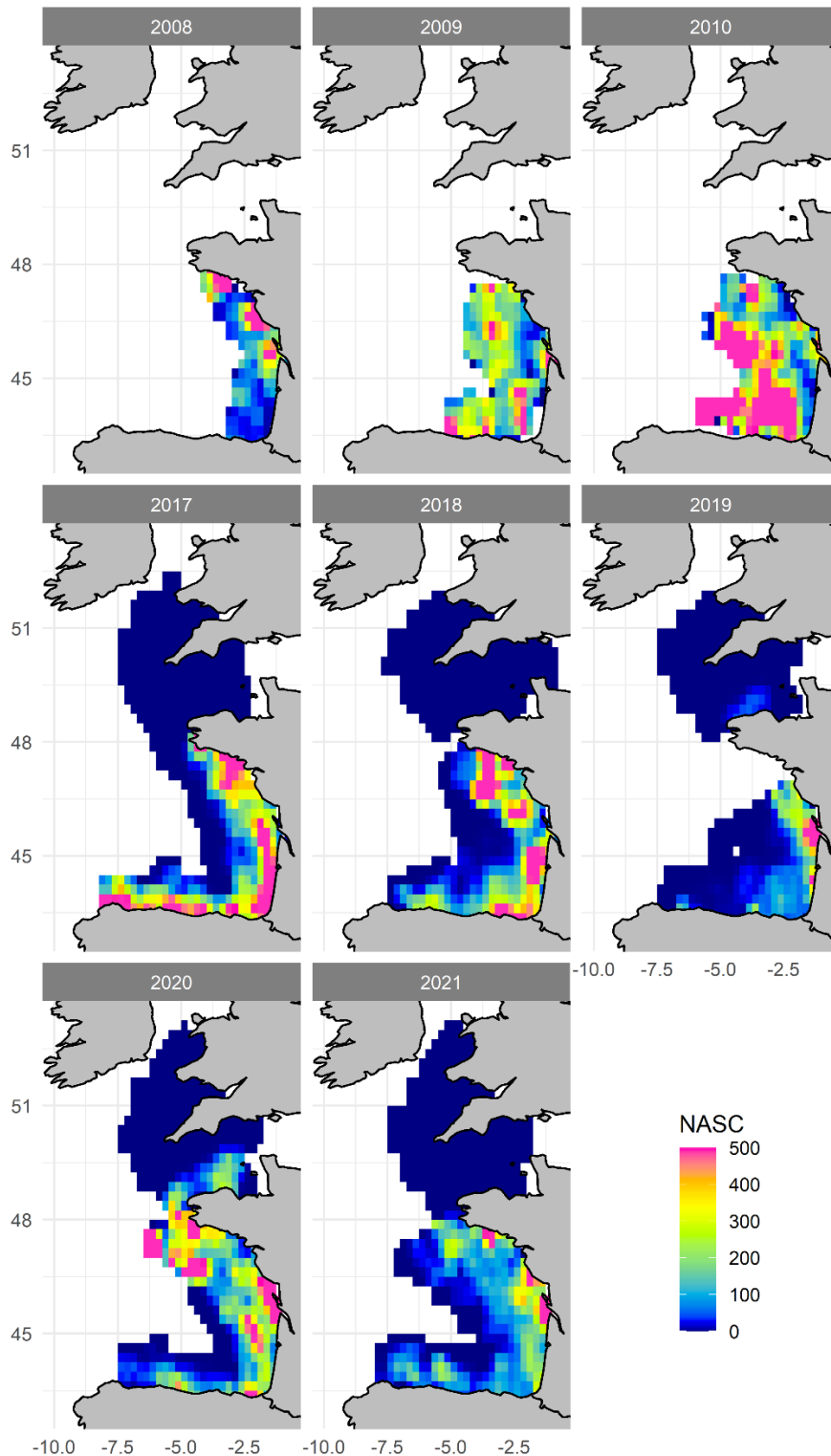


Fig. 5. STRUCTURE barplot (Pritchard et al. 2000) reporting the assignment of individual anchovy specimens (x-axis) from different sample location (abbreviations refer to sampling locations, see below), delineated by black lines, under the optimal clustering mode of $K=2$ based on microsatellite results of anchovy collected during this study in the Northeast Atlantic. Two distinct groups termed Northern and Biscay. Emboldened sample EC-NB represents the juvenile anchovy from the surface schools. y-axis denotes relative contribution of microsatellite to either of two clusters, represented by orange and blue colours. Abbreviations of samples locations: Irish Sea-1 (IS1), Irish Sea-2 (IS2), Bristol Channel (Bris), English Channel- Eddystone Bay (EC-EB), English Channel-Lyme Bay (EC-LB), North Sea – Thames Estuary (NS-TE), North Sea – Dutch (NS-D), North France (NF), Biscay Inshore North (Bis-IN), Biscay offshore (Bis-ON), Biscay Inshore South (Bis-IS), Biscay offshore South (Bis-OS), English Channel-post larvae (EC-NB).



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Figure 6 Maps of Northeast Atlantic Ocean showing Grid maps ($0.25^\circ \times 0.25^\circ$) of annual autumn juvenile anchovy backscatter (NASC: Nautical Area Scattering Coefficient in m^2nmi^{-2}) distribution as a proxy for abundance from Bay of Biscay (JUVENA) to western Channel and Celtic Sea (from 2017, PELTIC). Please note juvenile anchovy backscatter present in the English Channel in 2019 and 2020. Also note the gap in survey coverage in 2019, between latitudes of $\sim 46.5^\circ$ and 48° .

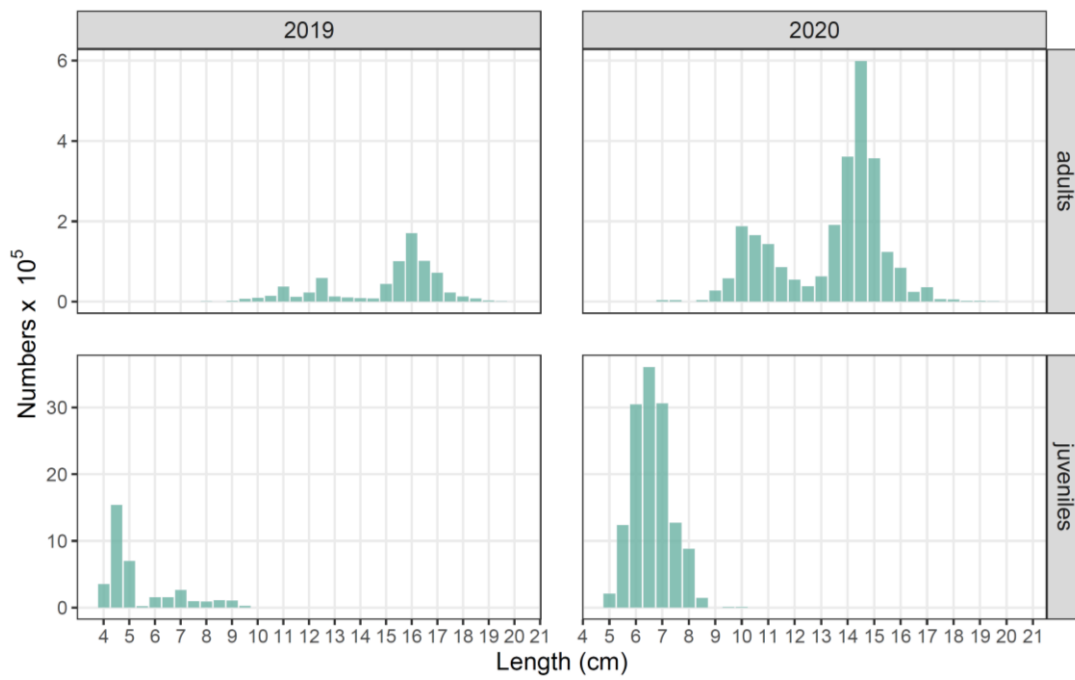


Fig. 7. Length frequency distribution of anchovy observed during the PELTIC 2019 (left) and 2020 (right) surveys in the western English Channel. Juvenile fish from the distinct surface schools (bottom) compared to those typically encountered in the survey and consisted of anchovy ages 0-2 (top).

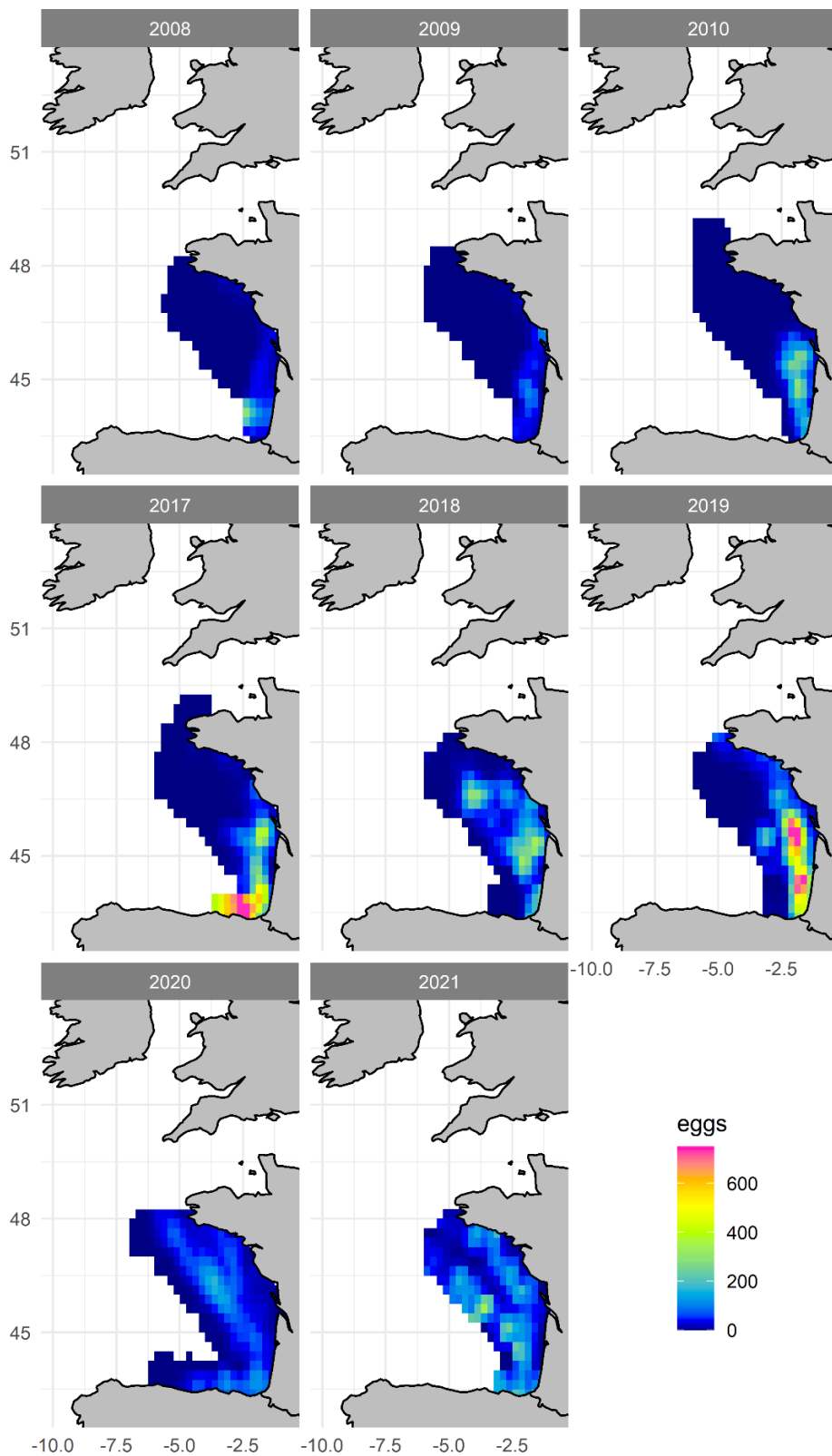
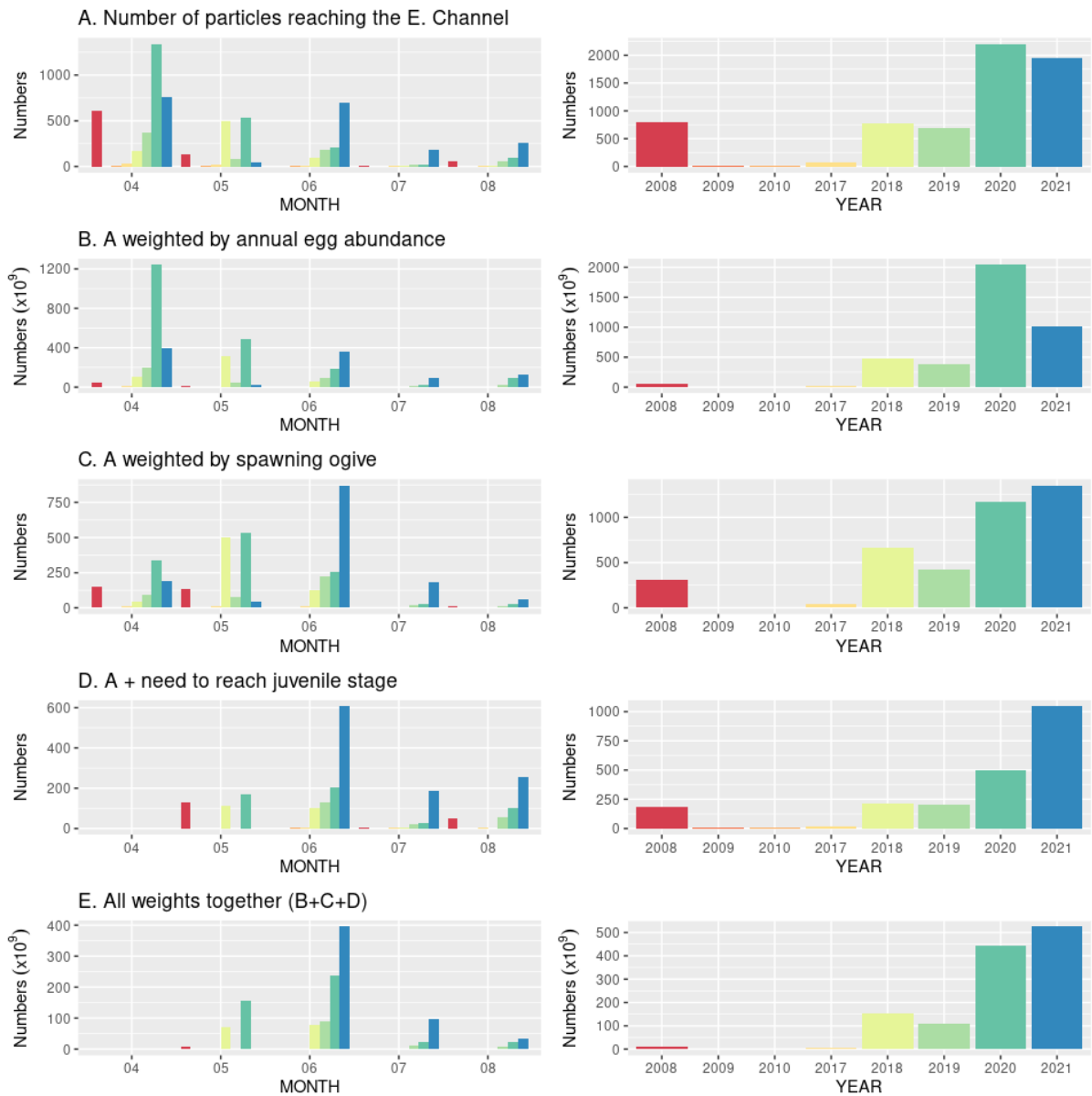
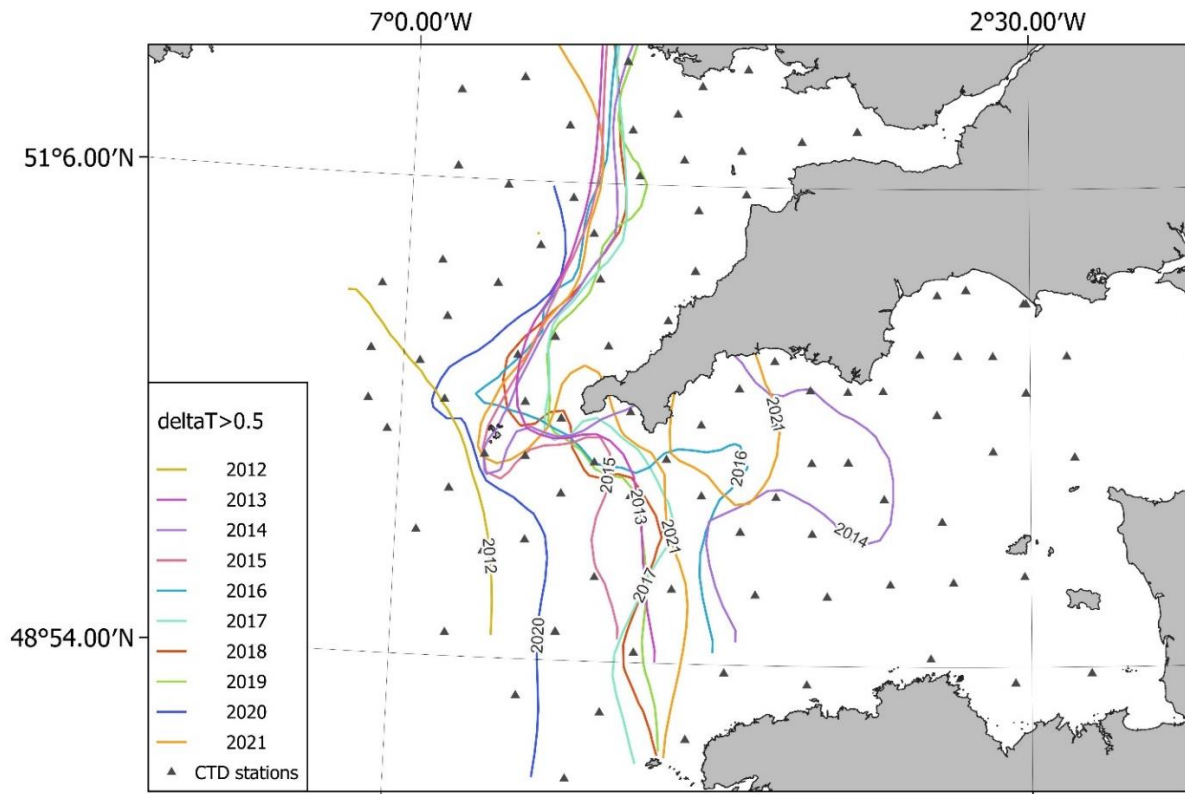


Fig. 8. Maps of the Northeast Atlantic Ocean showing Grid maps ($0.25^\circ \times 0.25^\circ$) of anchovy egg densities (per 10 m^{-3}) as obtained from the Continuous Underwater Fish Egg Sampler (CUFES) during the annual spring survey PELGAS for the periods 2008-2010 and from 2017, 2019 and 2021 and from BIOMAN in 2020. No PELGAS survey was conducted in 2020 due to covid.



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Fig. 9. Monthly (left) and annual (right) numbers of particles reaching the English Channel (north of 48.5°N and east of 5.7°W) after a drift period of 60 days following release in each month of the spawning period. Raw model output (A) sensu Fig. A1 and with the number of particles weighted by the total number of eggs estimated during the survey in May (B), by the proportion of spawning among months (C), only considering particles that reached metamorphosis based on the bioenergetic model (D), and with all previous weighting and constraints combined (E). Note that numbers are much higher in B and E because of the weighting by the total egg abundance. Colours on the monthly panels (left) correspond to the years as coloured on the yearly panels (right).



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Fig. 10. Map of northeast Atlantic showing main Ushant frontal position, colour-coded by year, as derived by interpolating between stations that delineated stratified waters, where the CTD profile exhibited a thermocline, and mixed waters. The water column was considered stratified when the difference between surface and bottom temperature (ΔT) was above 0.5 °C (Monterey & Levitus 1997). Note that survey coverage between 2012-2016 was restricted to the northern waters of the western English Channel and therefore did not represent the whole front. Triangles represent position of CTD stations.

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Table 1. Summary details of relevant fisheries-independent surveys in the Northeast Atlantic Ocean, which collect data on anchovy. CUFES= Continuous Underway Fish Egg Sampler. Where available, data from years 2008-2010 and 2017-2021 were used in this study. More details are provided in the survey manual (Doray et al. 2021).

Survey	Geographic area	Season	Timeseries start	Data used in this study
PELGAS	Bay of Biscay	April-May	2000	Anchovy eggs (CUFES)
BIOMAN	Bay of Biscay	May	1987	Anchovy eggs (CUFES:)
JUVENA	Bay of Biscay	September	2003	Anchovy juveniles (acoustics)
PELTIC	Celtic Sea/ English Channel	October	2013	Anchovy adults, juveniles (acoustics) and fish eggs (ringnet)

*Table 2. Sample information including sample sizes for both mtDNA and nuclear microsatellite analysis. For mtDNA the number of haplotypes (nHap) and haplotype diversity (h) per sample, and the abundances of the two clades (A and B) are reported. For microsatellites, the mean number of alleles (N_A), allelic richness (A_R), observed (H_O) and expected heterozygosities (H_E) and F_{IS} values (significant values at $p < 0.05$ denoted by *) are reported.*

Sample site	Code	Coordinates	Date	Sample size mtDNA/nuclear	nHap/h	Clade frequency (A:B)	Mean N_A/A_R	$H_O/H_E/F_{IS}$
Irish Sea-1	IS1	54.15° N, 5.11° W	March 2010	21/21	19/1	21:0	10/9.8	0.79/0.79/0.005
Irish Sea-2	IS2	54.30° N, 5.05° W	March 2011	13/80	13/1	13:0	14.8/10.5	0.75/0.84/0.115*
Bristol Channel	Bris	51.39° N, 4.82° W	Nov 2010	14/37	12/0.98	14:0	12.5/10.9	0.70/0.82/0.153*
English Channel- Eddystone Bay	EC-EB	49.62° N, 4.7° W 5	Nov 2010	16/74	14/0.98	13:3	15/10.1	0.73/0.80/0.089*
English Channel-Lyme Bay	EC-LB	50.55° N, 2.99° W	Nov 2010	14/72	11/0.96	14:0	14.5/10.4	0.69/0.82/0.166*
North Sea – Thames Estuary	NS-TE	51.5° N, 1° E	June 2011	10/73	10/1	10:0	14.8/10.4	0.71/0.83/0.140*
North Sea – Dutch	NS-D	52.75° N, 4.6° E	April 2011	13/53	10/0.92	12:1	11.7/9.3	0.70/0.82/0.150*
North France	NF	48.25° N, 5.14° W	Nov 2015	22/96	20/0.99	8:14	19.5/12.0	0.75/0.82/0.087*
Biscay Inshore North	Bis-IN	46.34° N, 1.95° W	May 2011	14/75	12/0.98	6:8	17.8/11.3	0.76/0.81/0.063*
Biscay offshore North	Bis-ON	46.30° N, 5.25° W	May 2011	36/97	22/0.95	24:12	18.3/11.3	0.75/0.82/0.080*
Biscay Inshore South	Bis-IS	45.56° N, 1.65° W	May 2010	16/60	14/0.98	8:8	13.5/10.1	0.73/0.78/0.065*
Biscay offshore South	Bis-OS	44.88° N, 2.28° W	April 2010	15/72	15/1	5:10	16./10.5	0.74/0.790.070*
English Channel-post larvae	EC-NB	48.74° N, 4.57° W	Oct 2019	47/48	38/0.98	34:13	16/11.2	0.74/0.79/0.070*

Appendix 1

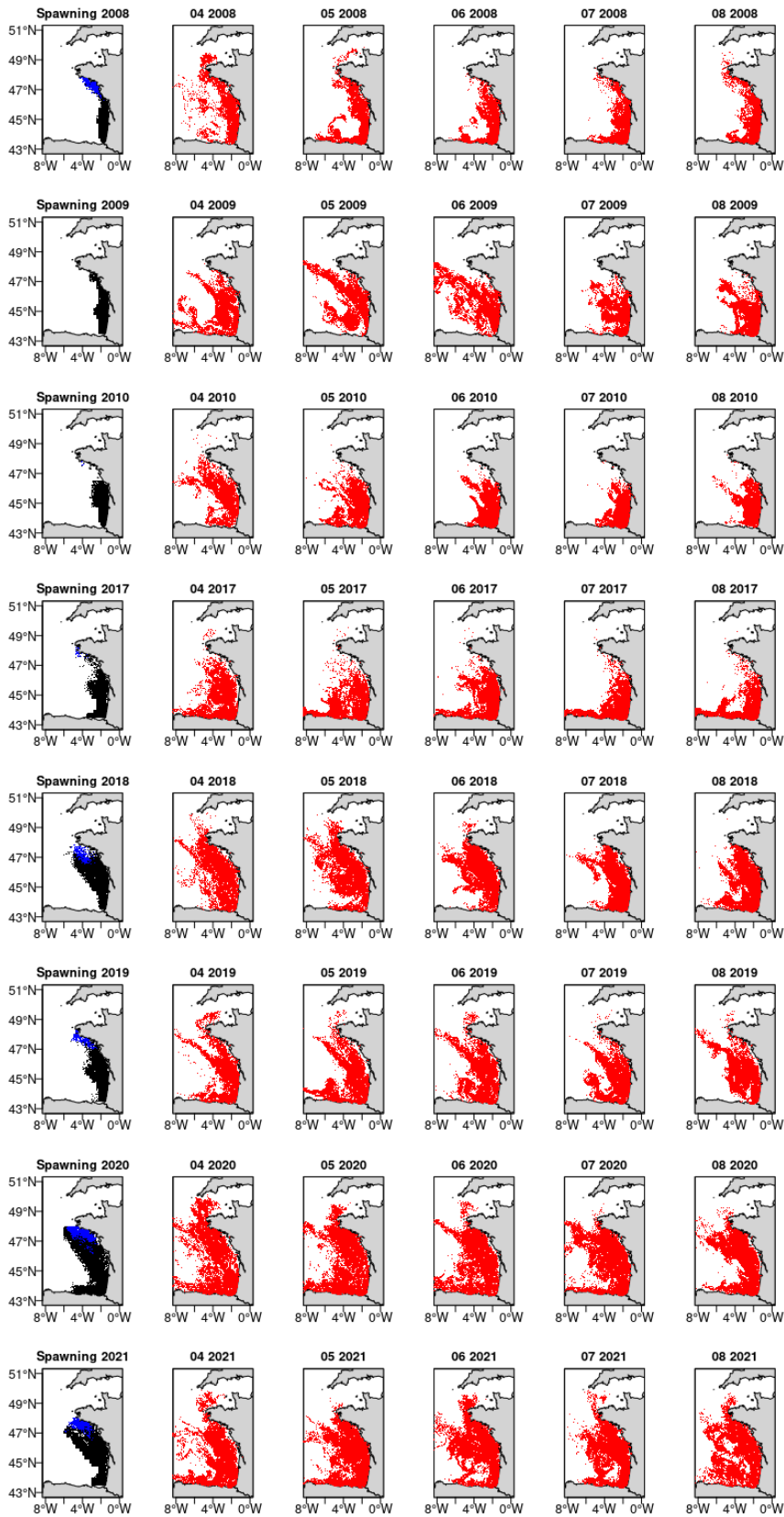


Fig. A1. Particle Tracking result: distribution of 25,000 particles on release (left column) based on spring egg distributions observed by year (top to bottom), during Pelgas (2008-2010, 2017-2019, 2021) and Bioman (2020) surveys. Columns 2-6 represent modelled end positions of these particles after a 60-day drift period when released at the position indicated in column 1, for each month of the spawning season (April to August) in the Bay of Biscay and each simulated year (2008-2010 and 2017-2021). Blue dots in the first column are starting locations of particles reaching the English Channel in the next columns.