



HAL
open science

Derivation of a standardized index to explore spatial, seasonal and between-year variation of squid (*Loligo spp.*) abundance in the English Channel

Anna Marcout, Eric Foucher, Graham Pierce, Jean-Paul Robin

► To cite this version:

Anna Marcout, Eric Foucher, Graham Pierce, Jean-Paul Robin. Derivation of a standardized index to explore spatial, seasonal and between-year variation of squid (*Loligo spp.*) abundance in the English Channel. *Fisheries Research*, 2025, 285, pp.107333. <10.1016/j.fishres.2025.107333>. <hal-05041580>

HAL Id: hal-05041580

<https://hal.science/hal-05041580v1>

Submitted on 21 Apr 2025

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



HAL Authorization

1 **Derivation of a standardized index to explore spatial, seasonal and between-**
2 **year variation of squid (*Loligo* spp.) abundance in the English Channel**

3 Anna Marcout^a, Eric Foucher^b, Graham Pierce^c, Jean-Paul Robin^a

4 ^a Normandie Université, UNICAEN, Alliance Sorbonne Université, MNHN, UA, CNRS, IRD,
5 Biologie des Organismes et Ecosystèmes Aquatiques (BOREA), Esplanade de la Paix, 14032 Caen

6 ^b Ifremer, Laboratoire Ressources Halieutiques, Port-en-Bessin, France, France

7 ^cInstituto de Investigaciones Marinas (CSIC), Eduardo Cabello 6, 36208 Vigo, Spain

8

9 Corresponding author: +33 (0)6 84 68 68 16; anna.marcout@unicaen.fr ;

10

11 **Abstract**

12 Long-finned squids are among the valuable resources exploited by English Channel demersal fisheries.
13 This resource consists of two short-lived species (not distinguished by fishers): *Loligo forbesii* and
14 *Loligo vulgaris*, which differ in the timing of their life cycle.

15 In the present study, we investigated spatial, seasonal and long-term biomass variation of *Loligo* spp. in
16 the English Channel using 22 years (2000-2021) of commercial fishing data to compute biomass indices.
17 Results indicated that LPUE indices (computed per month for each statistical rectangle of the English
18 Channel), standardized by vector autoregressive spatio-temporal (VAST) method, provided the best
19 squid biomass estimator.

20 Two distinct geographical patterns were observed in the English Channel, with low and stable biomass
21 indices in the West and most of the fluctuations and seasonal variations in East. Seasonal patterns seem
22 likely to be related to the presence of the two species, with the beginning of increase in June in the
23 western part of the English Channel probably corresponding to the recruitment of *L. forbesii* and a

24 second increase further east in October probably corresponding to *L. vulgaris* recruitment. Over the 22-
25 year series there was an eastward shift in squid biomass since 2014, suggesting that *L. forbesii*
26 distribution has declined in the English Channel.

27

28 **KEYWORDS:** biomass trends, VAST LPUE Standardization, bottom trawl fishery data, time series
29 clustering, centre of gravity, seasonal distribution

30 **Introduction**

31 Marine ecosystems are exposed to increasing climate change and other anthropogenic pressures (e.g.,
32 overfishing, pollution) which are expected to further intensify in the future (Moullec et al., 2021).
33 Changes in biomass and distribution of marine species are taking place, influencing the entire food web
34 (Albouy et al., 2014). Such changes take place against a background of natural climate variation
35 (including cyclic variation). Understanding spatio-temporal patterns of abundance in marine species is
36 a crucial issue in ecology and conservation biology (Fletcher et al., 2019) and for defining appropriate
37 fisheries management units (Cadrin, 2020). Such information is used to adapt resource management
38 strategies and anticipate ecological consequences of environmental changes (Morrison and Termini,
39 2016). In short-lived species such as squid the phenology of the life cycle, growth rate, body size and
40 population abundance are known to be highly sensitive to climatic variation (Caddy et al., 1983; Dawe
41 et al., 2007; Fogarty 1989; Pierce et al., 2008, 2010), presenting particular challenges (Arkhipkin et al.,
42 2015).

43 Fisheries scientists have long acknowledged the importance of population spatial structure (Berkeley et
44 al., 2004). However, in conventional stock assessments, the fisheries resource is assumed to be a single
45 homogeneous population within a spatial domain, in part because of data and computational limitations
46 (Cadrin et al., 2020, Cao et al., 2020). By ignoring fine-scale spatial heterogeneity, some conservation
47 management has failed in marine ecosystems (Kerr et al., 2010). In the present study, we illustrate the
48 use of classical methods to describe spatio-temporal changes in stock structure that may have
49 consequences for population assessments with the English Channel long-finned squid stock.

50 Temporal changes in spatial distribution of demersal species are generally best described with scientific
51 trawl survey data because they use consistent sampling gear, sampling scheme and protocol (Grosselin
52 and Laurec, 1982; National Research Council, 2000). However, because they cover many boats over a
53 wide area and during the whole year, commercial fishery data can be useful for stocks that are more
54 widely distributed than the area covered by the surveys and for species that require finer temporal
55 resolution than that of the annual snapshot of an annual survey.

56 Cephalopods in general and squids in particular differ from many other fished species due to biological
57 and ecological characteristics like a short lifespan (approximately 1 year), semelparous reproduction,
58 rapid growth, high natural mortality and sensitivity to environmental conditions that can affect their
59 migration cycle. In English Channel loliginid squids such biological traits are documented since a long
60 time (Tinbergen and Verwey, 1945; Holme, 1974; Sims et al., 2001; Moreno et al., 2002) and are not
61 different from what is described in other squid fisheries (Boyle and Rodhouse., 2005; Hastie et al., 2009;
62 Arkhipkin et al., 2015; Rodhouse et al., 2014). The attempt to describe spatio-temporal variations using
63 Channel Ground Fish Surveys (CGFS) survey data was limited to the situation in October in the Eastern
64 part of the Channel (ICES subdivision 7D) (Carpentier et al., 2009). Therefore, landings and effort from
65 the French commercial trawler fishery were used in the present study for their greater coverage in space
66 (ICES subdivisions 7D and 7E) and their better temporal resolution (allowing us to track monthly
67 changes).

68 Acknowledging the potential for fishery-dependent data sources to produce misleading biomass indices,
69 such indices are frequently "standardized" to mitigate factors that could alter catchability. Cheng et al.
70 (2023) have recommended that an initial step should involve comparing catch rates derived from
71 logbooks with those obtain from survey data. As in the present study, such comparisons can enhance
72 our understanding of potential biases caused by varying observation techniques, paving the way for the
73 development of more accurate and integrated indices of biomass.

74 In the English Channel, long-finned squids support a large-scale fishery, with the highest squid landings
75 of any areas in the Northeast Atlantic (ICES, 2020). Between 2000 and 2021, annual common squid
76 landings from the English Channel averaging 3520 t were mainly caught by bottom trawlers (ICES,
77 2023) of the French and UK fleets (80% and 15% respectively) with some recent increase in catches by
78 the Netherlands (Figure 1, redrawn from ICES, 2023). In 2019-2021, loliginid landings were below both
79 the historical mean (2000-2021) and recent past values (2016-2018) suggesting that the status of
80 loliginid populations in this area may be of concern (ICES, 2023).

81 The Channel squid stock includes two species (not distinguished by fishers or in fisheries statistics),
82 *Loligo forbesii* (Steenstrup, 1856) and *Loligo vulgaris* (Lamarck, 1798), both of which have an

83 approximately one-year lifespan (Holme, 1974; Guerra and Rocha, 1994) but which differ in the timing
84 of their life cycle (Royer, 2002; Laptikhovsky et al., 2022). The recruitment to the fishery of *L. forbesii*
85 begins in June whereas *L. vulgaris* starts appearing in fishery catches in September and the fishing
86 season ends in May (Robin and Boucaud-Camou, 1995; Royer, 2002). English Channel long-finned
87 squid have been considered as a mixed resource in previous ecological and stock assessment studies
88 (Robin and Denis, 1999; Denis et al., 2002; Royer et al., 2002; ICES 2020). Although various authors,
89 including ICES WGCEPH have called for progress in species identification and recording in fisheries
90 statistics (ICES, 2020; ICES, 2023), at present the analysis of time series for temporal trends can only
91 consider the two species together.

92 In the present study, 22 years (2000-2021) of commercial fishery data were used to compute biomass
93 indices to improve our understanding of spatio-temporal dynamics of *L. vulgaris* and *L. forbesii* in the
94 English Channel. The main objectives of this study were to (1) compute the best estimator of squid
95 biomass by testing several different standardization methods, (2) provide a description of seasonal and
96 interannual variation in squid biomass in the English Channel, identifying the areas with the highest
97 squid abundance and quantifying seasonal and interannual shifts in squid distribution.

98 **Materials and methods**

99 ***1. English Channel dataset sources***

100 Commercial squid landings (kg) and effort (hours of trawling) for all French bottom otter trawls (OTB)
101 were collected from national databases managed by Ifremer (Système d'Information Halieutique-SIH)
102 by fishing sequence, year, month and ICES rectangles from 2000 to 2021 in the English Channel. A
103 fishing sequence is defined as a succession of hauls carried out during the same fishing trip, taking place
104 in the same ICES statistical rectangle and using the same fishing gear (Mahevas et al., 2011). Typically,
105 a fishing sequence is confined to a single day. Any change in gear, vessel, or fishing zone within a single
106 day result in a new fishing sequence. Using the European Vessel Registry, vessel engine power (kW)
107 has been associated with each fishing sequence. To characterize squid distribution, we have linked each
108 ICES rectangle to the geographical coordinate of its barycentre using QGIS software and the shapefile:
109 "ICES_Statistical_Rectangles_Eco.shp" downloaded from the ICES website (Figure 2). In total,
110 927 281 fishing sequences from 1011 different vessels were analyzed.

111 The computations applied to commercial data will be compared to Channel Ground Fish Surveys
112 (CGFS) conducted in October, which operates only in the Eastern part of the Channel (ICES division
113 7D). The data also available in the Database of Trawl Surveys (DATRAS) were extracted from national
114 databases maintained by Ifremer (Système d'Information Halieutique-SIH).

115

116 ***2. Computation of squid biomass indices***

117 Commercial datasets were used to compute Landings Per Unit Effort (LPUE) by ICES rectangle and by
118 month for catches in the English Channel (30 rectangles) during the period 2000-2021 (264 months),
119 using hours of trawling as effort. According to onboard observations provided by the Ifremer program
120 "OBSMER", as well as declarations by France and the UK, there is a low squid discard level in the
121 English Channel, which is always below 6% (ICES, 2011; 2017). Discards were considered as negligible
122 (Royer et al. 2002; ICES, 2020). To obtain the best estimator of squid biomass, three different LPUE

123 indices were computed: basic LPUE, LPUE standardized with vessel power, and LPUE standardized
124 using a spatio-temporal model.

125 **2.1 Basic LPUE**

126 The basic LPUE for each month m and rectangle i is the sum of landings (L) divided by the sum of effort
127 (E):

$$128 \quad \text{LPUE}_{\text{basic } m,i} = \frac{\sum L_{m,i}}{\sum E_{m,i}}$$

129 Where L is landing in kg, E is effort in hours of trawling.

130 **2.2 LPUE standardization with vessel engine power**

131 Vessel engine power has an effect on LPUE: vessels with higher engine power can use larger gear and
132 trawl more fish at higher speeds resulting in higher landings. To make the LPUE comparable between
133 vessels, LPUE values were standardized to the LPUE of a 400 kW vessel (the most common vessel
134 engine power in our fishing data) by month m for each ICES rectangle i following this equation
135 (Hammen et al., 2011; Rijnsdorp et al., 2006):

$$136 \quad \text{LPUE}_{\text{vessel } m,i} = \sum \frac{L_{m,i}}{\frac{E_{m,i} * \text{kW}_{m,i}}{400}}$$

137 Where L is landing in kg, E is effort in hours of trawling, kW is vessel engine power in kW. This formula
138 is valid under the assumption that LPUE is linearly related to the vessel engine power in kW.

139 **2.3 LPUE standardization with spatio-temporal model**

140 We applied a vector autoregressive spatio-temporal (VAST) model implemented using the R package
141 “VAST” (<https://github.com/James-Thorson-NOAA/VAST>) (Thorson, 2019) to standardize squid
142 LPUE by month from 2000 to 2021 (264 months in total) and by rectangle. This delta generalized linear
143 mixed model method includes two components, the probability of encounter and the positive catch rate:

$$144 \quad (1) \text{ Pr } [c] = \text{ Pr } [C > 0] \times \text{ Pr } [C = c | C > 0]$$

145 Where c is the catch rate (catch per fishing hours) for each fishing sequence, $\Pr [C>0]$ is the probability
 146 of a positive catch and $\Pr [C = c | C>0]$ is the probability of catch c given that the catch is positive.
 147 $\Pr[C>0]$ is modeled as a Bernoulli random variable, and $\Pr [C = c | C>0]$ as a Gamma distributed random
 148 variable:

$$149 \quad (2) \Pr [C>0] = p_{m,i}$$

$$150 \quad (3) \Pr [C = c | C>0] = \text{Gamma} (c, \sigma^{-2}, r_{m,i} \sigma^2)$$

151 Where p_i is the encounter probability and $r_{m,i}$ the positive catch rate. σ^{-2} and $r_{m,i} \sigma^2$ are the shape and scale
 152 terms of the Gamma distribution.

153 We implemented the spatio-temporal model by incorporating vessel power as a covariate which affects
 154 catchability (Thorson et al., 2019). The encounter probability (p) for month m and rectangle i was
 155 modeled using a logit linked linear predictor, and the positive catch rate (r) for month m and rectangle i
 156 was modeled using a log-linked linear predictor as suggested by Thorson et al. (2021):

$$157 \quad (4) \text{logit } p_{m,i} = \beta_m^{(p)} + L_\omega^{(p)} \omega_i + L_\varepsilon^{(p)} \varepsilon_{m,i} + L_\eta^{(p)} \eta_{m,i}$$

$$158 \quad (5) \log r_{m,i} = \beta_m^{(r)} + L_\omega^{(r)} \omega_i + L_\varepsilon^{(r)} \varepsilon_{m,i} + L_\eta^{(r)} \eta_{m,i}$$

159 where β_m are the month-specific intercepts, L_η are vessel effects included to capture differences in
 160 fishing power among vessels. L_ω and L_ε are spatial and spatio-temporal random effects approximated
 161 using Gaussian random fields, which imply correlations in spatial variation decay as a function of
 162 distance. More detailed information about this model was provided by Thorson (2019). The biomass
 163 indices ($B_{m,i}$) in month m for rectangle y were obtained as:

$$164 \quad (6) \text{LPUE}_{\text{VAST } m,i} = \text{logit}^{-1} (\beta_m^{(p)} + L_\omega^{(p)} \omega_i + L_\varepsilon^{(p)} \varepsilon_{m,i} + L_\eta^{(p)} \eta_{m,i}) \times \exp (\beta_m^{(r)} + L_\omega^{(r)} \omega_i + L_\varepsilon^{(r)} \\ 165 \quad \varepsilon_{m,i} + L_\eta^{(r)} \eta_{m,i})$$

166 The number of knots determining the spatial resolution of the VAST model was set to 30 corresponding
 167 to the number of ICES rectangle in the English Channel analyzed.

168 **2.4 CGFS index**

169 In order to look at differences between commercial LPUE and fishery-independent data, scientific CGFS
170 survey data were used to compute a CGFS index from 2000 to 2021.

171 The CGFS occurs each year during October (Coppin et al., 2002). For each rectangle i and month m :

172
$$\text{CGFS}_{m,i} = \frac{C_{m,i}}{A_{m,i}}$$

173 Where C is catch in kg and A is the trawl area swept for each ICES rectangle in km².

174

175 **3. Statistical analysis**

176 All statistical analysis were performed in R (R Development Core Team, 2023).

177 **3.1 Assessing the accuracy of standardization by comparing with indices from scientific surveys**

178 To test the accuracy of LPUE indices standardized as an estimator of biomass, we examined correlations
179 between the CGFS index (per rectangle in October) and the three different indices obtained from
180 commercial data (per rectangle in October): LPUE_{basic}, LPUE_{vessel}, LPUE_{VAST} between 2000 and 2021.

181 Normality was checked with Shapiro-Wilk normality test. If the data followed a normal distribution and
182 were homoscedastic, Pearson's correlation test were conducted otherwise Spearman's correlation test
183 were conducted.

184 Of these three different LPUE, the one most correlated with CGFS was used for further analysis as the
185 most accurate index for biomass.

186 **3.2 Seasonal decomposition of time series**

187 We investigated interannual and long-term variability of the squid biomass index using a Seasonal and
188 Trends Loess (STL) (Cleveland et al., 1990) decomposition analysis of the average time series 2000 –
189 2021 (264 months) (i.e. averaged over all ICES rectangles of the English Channel). STL use LOESS
190 (locally estimated scatterplot smoothing) to extract smooth estimates of three components from the
191 original series (Y_t): the global trend component (T_t), which represents the long-term evolution, the
192 seasonal component (S_t), which is periodic, and the remainder (R_t) component, representing irregular
193 fluctuations:

194
$$Y_t = T_t + S_t + R_t \quad 1 \leq t \leq n$$

195 Where n is the total number of months in the time series.

196 **3.3 Time series Clustering**

197 To investigate spatial variability, time series clustering was applied on the squid biomass index time
198 series of each ICES rectangle of the English Channel to identify groups of rectangles with similar
199 temporal dynamics.

200 Euclidian distance is the most commonly used distance measure for cluster analysis however it may not
201 be the most appropriate tool for time series due to its high sensitivity to small distortions in the time
202 axis. In other words, two time series that are very similar but are slightly shifted in time relative to each
203 other can be classified as very different time series. We addressed this issue by using Dynamic Time
204 Warping (DTW) methodology (Berndt and Clifford, 1994; Aghabozorgi et al., 2015), an elastic, shape-
205 based similarity measure that deals with temporal drift.

206 First, a dissimilarity matrix was calculated between time series, considering all rectangle pairs,
207 minimizing the distance and allowing comparison at different time steps using the dynamic time warping
208 (DTW) method. The resulting distance matrix was analyzed using hierarchical clustering agglomerated
209 with the “ward.D2” method, which minimizes within-cluster variance. Time series are first considered

210 as distinct clusters, then gradually merged together in a bottom-up way (Aghabozorgi et al., 2015),
211 resulting in a dendrogram.

212 DTW analysis were implemented using the dtw R package (Giorgino et al., 2009).

213 **3.4 Spatial parameters**

214 To quantify shifts in squid biomass indices distribution, we computed the centre of gravity for longitude
215 and latitude, the inertia, and the average distance from the coast, by month from 2000 to 2021. These
216 parameters are similar to those described by Cotter et al. (2009) in the case of trawl survey data.

- 217 • Centre of gravity of the biomass indices

218 For each month m , we computed a “weight” corresponding to the proportion of the biomass indices that
219 were located in each rectangle i :

$$220 \quad W_{m,i} = \frac{\text{LPUE}_{m,i}}{\sum_{i=1}^n (\text{LPUE}_{m,i})} \text{ and } \sum W_{m,i} = 1$$

221 Using ICES rectangle centroids with coordinates X_i and Y_i for longitude and latitude respectively, centres
222 of gravity $[X_{gm}, Y_{gm}]$ were obtained as:

$$223 \quad X_{gm} = \sum_{i=1}^n (X_i * W_{m,i}) \text{ and } Y_{gm} = \sum_{i=1}^n (Y_i * W_{m,i})$$

- 224 • Inertia

225 In month m , a measure of biomass index concentration is the Inertia (C_m), which is computed as follows:

226 In each rectangle i , the distance between the rectangle centroid and the centre of gravity in month m is:

$$227 \quad D_{m,i} = \sqrt{(X_i - X_{gm})^2 + (Y_i - Y_{gm})^2}$$

228

229 and the inertia of all biomass indices in month m is:
$$C_m = \frac{\sum (\text{LPUE}_{m,i} * D_{m,i}^2)}{\sum \text{LPUE}_{m,i}}$$

- 230 • Average distance from the coast of the biomass indices

231 In each rectangle i , the shortest distance between the centroid and the nearest coast (based on the
232 countries shapefile taking into account England, the Isle of Wight, and the Continent Mainland) is
233 computed with ArcGIS, and stored in variable L_i .

234 In month m the average distance from the coast of the biomass indices is given by:

235
$$L_m = \Sigma (L_i * W_{m,i})$$

236 **Results**

237 *1. Comparison of squid biomass indices*

238 To quantify variations in squid abundance using fishery-dependent data, various standardized methods
239 for calculating Landings-Per-Unit-Effort (LPUE) were analyzed and contrasted with CGFS survey-
240 derived estimates (Figure 3). The CGFS index (kg/area swept) obtained in October showed non-
241 significant positive correlations with $LPUE_{\text{basic}}$ ($r = 0.33, p = 0.13$) and $LPUE_{\text{vessel}}$ ($r = 0.32, p = 0.14$)
242 between 2000 and 2021. However, $LPUE_{\text{VAST}}$ was significantly correlated ($r = 0.63, p = 0.002$) with the
243 CGFS indices between 2000 and 2021, suggesting that $LPUE_{\text{VAST}}$ is the most realistic index for biomass.
244 For the rest of the analysis, biomass indices refer to $LPUE_{\text{VAST}}$.

245 Monthly biomass indices from 2000 to 2021 for each ICES rectangle of the English Channel were
246 represented in 264 maps, which can be found in an animation gif in the supplementary material
247 (Appendix 1). Four “example” maps were selected to provide an overview the spatio-temporal variations
248 across season and year (Figure 4). The data from 2012 and 2017 indicate that biomass indices were
249 notably higher in December than in July, with a greater concentration of squid in the eastern part of the
250 English Channel. Moreover, the biomass indices in December 2017 surpassed those of December 2012,
251 highlighting seasonal, spatial, and interannual variations in squid biomass indices. To quantify the
252 variations between all 264 maps, different quantitative methods were employed, detailed in the
253 subsequent sections.

254 2. Seasonal decomposition of time series

255 First, interannual and long-term variability of the squid biomass index were investigated by using a
256 Seasonal and Trends Loess (STL) decomposition analysis over all ICES rectangles in the English
257 Channel between 2000 and 2021 (Figure 5).

258 The general trend of the biomass index (Figure 5.b) shows a very high peak at the start and after that
259 illustrates irregular interannual variability with highs in 2004, 2010, 2015 and 2017 and lows in 2005,
260 2009, 2013, 2016, and 2020. Rather stable periods are observed in 2006-2008 and 2017-2019. Apart
261 from the initial (2000) peak, interannual variations suggest that the biomass index can be 2-3 times
262 higher or lower from one year to the next. The general trend does not reveal any cyclic pattern in
263 interannual variations.

264 Time series decomposition indicated the existence of regular seasonal patterns (Figure 5.c) in biomass
265 indices. From 2000 to 2013, the amplitude of seasonal variations seems to have been stable [-5 ; +5].
266 There was a gradual increase in the amplitude of seasonal variation from 2014 to 2021, reaching values
267 between -5 and 13 after 2017.

268 Biomass indices showed seasonal variations (Figure 6) following a very regular pattern with an increase
269 from June to December and gradually decreased from January to May (Figure 6.a). In summer months,
270 biomass indices gradually increased from an average around 3 in June to an average around 6 in
271 September. There are more marked increases later in the year, with biomass indices reaching averages
272 of 9 in October, 13 in November and 15 (the maximum) in December. From January to May, biomass
273 indices decreased from an average around 11 to a minimum average of 1.

274 Analysis over the years of monthly indices (Figure 6.b) show that the peak in biomass indices in 2000,
275 as observed in Figure 6, is due to very high values in January and February. Apart from the initial (2000)
276 peak, biomass indices seem to have been stable for each month between 2000 and 2014. Since 2014,
277 two different dynamics were observed, a decrease of the monthly average biomass indices in summer
278 months and an increase in Autumn-Winter, which together are responsible for the increase of seasonal
279 variations found in Figure 5.c.

280 **3. Common temporal patterns between rectangle biomass indices using clustering**

281 To identify homogeneous groups of ICES rectangle biomass indices for the English Channel, time series
282 clustering was used. The cluster analysis (Figure 7) shows that the groups of rectangles having similar
283 temporal trends in biomass are clearly geographically distinct with a Western cluster and an Eastern
284 cluster. Time series decomposition of each cluster shows different dynamics, with low and stable
285 biomass indices for the Western cluster (Figure 7.c) and most of the fluctuations in the Eastern cluster
286 (Figure 7.d). Seasonal fluctuations are observed in both clusters with similar rhythmicity but with a
287 slightly delayed timing in the Eastern cluster and with a much higher amplitude in this Eastern group of
288 rectangles. Most of the variations observed at the scale of the whole of the Channel (Figure 5) are thus
289 found in the East of the English Channel.

290 **4. Analysis of spatial parameters**

291 Centre of gravity, inertia, and average distance to the coast were calculated by month from 2000 to 2021
292 to quantify shifts in distribution of squid biomass indices.

293 **4.1 Seasonal variations of squid centre of biomass**

294 Analysis of monthly centre of gravity reveals that seasonal variations are more important than
295 interannual variability. Figure 8.a shows that barycentres are grouped by months. Monthly averages
296 plotted in Figure 8.b underline that changes in average biomass location occur in a cyclic sequence.
297 Between June and September, gravity centres are found in the West of the English Channel (49.5, 49.7°N
298 ; -3.1, -2.5°E), with a slight west to east movement associated with a gradual increase in mean biomass
299 indices. From September to December gravity centres move eastwards (49.7, 50°N ; -1.8, -0.8°E) and
300 mean biomass indices increases to reach maximum values in December. From January to March, mean
301 biomass indices decreases progressively while gravity centres are still located in the eastern part of the
302 English Channel (50.1, 50.2°N ; -0.6, -0.3°E). From April, gravity centres move westwards (49.7,
303 50.0°N ; -1.7, -0.49°E) and mean biomass index reaches its lowest value in May.

304 Longitude (X_g) and latitude (Y_g) of the monthly gravity centres are highly correlated ($r = 0.88$, $p <$
305 0.0001) suggesting homogeneous shift north-east and south-west. Squid biomass indices are positively

306 correlated to the gravity centres coordinates (longitude: $r = 0.31$, $p < 0.0001$; latitude: $r = 0.39$, $p <$
307 0.0001) reflecting highest squid concentration in the north-east of the English Channel. Over the course
308 of an average fishing season (between June and March, Figure 8.b) the squid resource moves more than
309 110 nautical miles.

310 Monthly analysis of the mean distance to the coast and the Inertia (measure of dispersion) confirmed
311 the centre of gravity observations. From June to August, when the centre of gravity is further west in
312 the English Channel (the widest part of the English Channel; Figure 8), the mean distances to the coast
313 were the highest (Appendix 2.a). The gradual decrease in the mean distances to the coast observed since
314 October (Appendix 2.a) corresponds to the eastward shift of squid biomass indices (the narrowest part
315 of the English Channel; Figure 8).

316 For the dispersion parameter, maximum values were found in May and October (Appendix 2.b)
317 corresponding to the shift periods between east and west (Figure 8).

318

319 ***4.2 Interannual variations of squid biomass distribution***

320 Yearly centres of gravity are much closer together than monthly averages (Figure 9). The maximum
321 distance between annual mean points is less than 32 nautical miles (2005 vs 2018). The temporal trend
322 shows a decadal shift in the English Channel with mean centres of gravity located between -1.85 and $-$
323 1.48°E during the period 2000 – 2013 and between -1.54 and -1.05°E for the period 2014-2021, this
324 eastward shift in squid concentration since 2014 is consistent with the temporal trend observed in the
325 eastern cluster of rectangles.

326 This shift is also observed in long-term trends in inertia (a measure of dispersion) and average distances
327 to the coast, which decrease sharply from 2014 (Appendix 3.a and b). Inertia is negatively correlated to
328 squid biomass indices ($r = -0.13$, $p = 0.03$) suggesting a smaller scattering of the distribution around the
329 centre of gravity when squid biomass is high.

330 **Discussion**

331 The starting point for this study was the lack of data to describe changes in the spatial distribution of
332 English Channel squid on an appropriate timescale, defined as the duration of fishing season, which runs
333 from June to May of the following year. In such short-lived migrating populations (Holme, 1974,
334 Tinbergen and Verwey, 1945, Sims et al., 2001, Royer, 2002), it is necessary to take into account
335 distribution changes during the course of a fishing season and at all stages of cohort exploitation, as well
336 as between years (i.e. between annual cohorts). The English Channel squid stock comprises two species,
337 *Loligo forbesii* and *L. vulgaris*, which are not distinguished by fishers or in fisheries statistics. These
338 species have differing life cycle timings, with *L. forbesii* recruiting to the fishery in June and *L. vulgaris*
339 appearing in the catches starting in September, which further complicates biomass estimations. In the
340 absence of scientific surveys designed at a relevant temporal scale it is rather common to derive biomass
341 indices from commercial fishery data (Rosenberg et al., 1990; Roa-Ureta, 2012). Indices derived from
342 landings per unit of effort (LPUE) of commercial trawlers are biomass estimates rather than abundance
343 estimates since there is no biological sampling programme that would enable conversion of weights into
344 numbers and, indeed, the high variability in growth rate means that length-weight relationships are also
345 variable, thus requiring more frequent and intense sampling than would otherwise be the case.

346 **(a) LPUE standardization**

347 Standardized LPUE indices (computed per month and rectangle) were compared to the only (survey-
348 based) series of observations available: biomass indices derived from the CGFS surveys carried out in
349 October. Results of correlation analyses suggested that LPUE standardized by the vector autoregressive
350 spatio-temporal method (VAST, Thorson 2019) shows the best match with squid biomass estimated
351 from survey data, in comparison with non-standardized LPUE or LPUE that was standardized based on
352 engine power. The value of this delta-glm model is that it takes into account both the probability of
353 encounter and the positive catch rate and allows the integration of co-variables that influence biomass
354 or catches (such as vessel power). Data from trawl surveys have also drawbacks (Knijn et al., 1993;
355 Baudrier et al., 2018), mainly related to selectivity issues and to the fact that fishing operations were not

356 designed specifically for catching squid. The VAST standardization method has been compared to other
357 standardization procedures like GLMs or GAMs and, although this was not the objective of our study,
358 it is worth mentioning that in these other comparisons VAST provided the best fits (Grüss et al., 2019).
359 This procedure has enabled us to obtain for the first time in the analysis of these resources, biomass
360 indices per month (from 2000 to 2021) and per statistical rectangle in the English Channel which is the
361 first step in studying spatio-temporal variations in squid stocks. It is applicable in other short-lived
362 species provided that the stock's range is regularly explored by a commercial fleet.

363 Variations in the timing of the appearance of *L. forbesii* in the local area off Plymouth had already been
364 studied (Sims et al., 2001). However, this study is the first decomposition of temporal trends in 30 ICES
365 rectangles of the English Channel.

366 **(b) General interannual trend**

367 Temporal analyses of biomass indices suggest a relatively stable trend during the first decade, with ups
368 and downs. In the last decade, there was an increasing trend from 2014 and 2018 followed by a
369 decreasing trend in 2019 and 2020. This decline in the 2019-2020 observations coincided with a drop in
370 total landings from the same area, and suggests that the status of loliginid populations in the English
371 Channel may be of concern (Figure 1, ICES, 2023). Environmental drivers of this variability may be
372 sought as relationship with temperature have already been established (e.g. Waluda and Pierce, 1998;
373 Robin and Denis, 1999; Challier et al., 2005). However, observations in the period 2000-2021 do not
374 suggest that English Channel squid undergo long-term cycles of abundance. The hypothesis of the
375 influence of the 10-12 years solar cycle on English Channel communities (Southward et al., 1975) do
376 not seem to apply to squid populations. The hypothesis that its effect would be masked by other factors,
377 e.g. the global warming context (Southward et al., 1995) is not supported by time series decomposition.

378 **(c) Seasonality**

379 The present findings also indicated the existence of a seasonal fluctuations. Seasonal peaks and trough
380 are consistent with the annual life-cycle of Loliginid squids (Holme, 1974; Guerra and Rocha, 1994;
381 Moreno et al., 2007). The slight shift in the timing of seasonal cycles in the Western and Eastern parts

382 of the Channel seems likely related to the presence of the two species *Loligo forbesii* and *Loligo vulgaris*
383 in the resource with different timings of their life-cycles (Holme, 1974; Robin and Boucaud-Camou,
384 1995; Royer, 2002, Laptikhovsky et al., 2022) and with differing importance in the Western and Eastern
385 parts of the Channel. Within each year, the beginning of an increase in abundance in June is likely to
386 correspond to the recruitment to the fishery of *L. forbesii* and a second increase in October then
387 corresponds to *L. vulgaris* recruitment. Again, time series decomposition of VAST standardized indices
388 provides for the first-time evidence that the seasonal pattern is consistently repeated. A similar
389 seasonality over more than 20 fishing seasons illustrates that the life-cycle of both species is repeating
390 in a regular way and that sub-cohorts or variable timing of recruitment peaks as observed in *L. forbesii*
391 in Scottish waters (Pierce et al., 1994) are of minor importance in Channel stocks.

392 (d) Spatial patterns

393 Cluster analysis identify two distinct geographical patterns (West/East) among ICES rectangle time
394 series. Low and stable biomass indices were found in the Western English Channel and most of the
395 fluctuations and seasonal variations were found in Eastern English Channel. This result is different from
396 the clustering with spatial contiguity constraint applied by Royer (2002). This is likely a difference
397 related to the temporal window analysed since *L. forbesii* was more abundant in 1992-1999 (Chen et al.,
398 2006).

399 Analysis of monthly centres of gravity provide a quantitative view of squid distribution shifts. From
400 June to September squid biomass is centred in the West, the deepest part of the English Channel (Dauvin,
401 2012), and the area where the recruitment of *L. forbesii* begins in June (Holme, 1974). From October,
402 squid concentrations move eastwards, probably corresponding to the appearance of *L. vulgaris* in fishery
403 catches (Robin and Boucaud-Camou, 1995). These observations are consistent with the fact that *L.*
404 *forbesii* has a deeper, more offshore, distribution than its congener *L. vulgaris* (Lordan and Casey, 1999;
405 Hastie et al., 2009). The Eastward shift in the location of centre of gravity and the increase of inertia (a
406 measure of dispersion) in October is likely the result of a combination of two phenomena: the autumn
407 recruitment of *L. vulgaris* and the eastward migration of immature *L. forbesii* (Holme, 1974; Royer,
408 2002; Vaz et al., 2008). *L. forbesii* gradually migrate eastward, while foraging, into the Eastern Channel

409 and then return to the Western approaches in autumn. Females *L. forbesii* reach maturity in November,
410 spawn in December - January, and the juveniles are seen in the catches around May after hatching from
411 the eggs. Royer (2002) made the first trial to quantify migratory fluxes of the two squid species within
412 the English Channel using spatialized cohort analysis. This preliminary trial was done using strong
413 assumptions (equal catchability and the proportions of both species in catches being the same in all
414 locations, varying according to results of monthly sampling in a single fish market). In comparison,
415 changes in the location of the centre of gravity offer a rather direct quantification of spatial patterns that
416 can be used to better understand interannual variation. The advantage of quantitative parameters like
417 centres of gravity can be seen by comparing the difficulties of analyzing 264 maps like those in Figure
418 4 with the trends clearly visible in Figure 8.

419 Such a quantitative approach to the distribution of cephalopod resources could be used in other migrating
420 species like *Sepia officinalis* whose wintering grounds vary according to minimal temperatures (Wang
421 et al., 2003).

422 **(e) Shift in squid biomass distribution from 2014**

423 Analysis of yearly centres of gravity suggested an eastward shift in squid concentration since 2014.
424 These observations coincided with an increase of seasonal variations in biomass indices trends since
425 2014, with a decrease of the monthly average biomass indices in summer and an increase in autumn-
426 winter.

427 We hypothesize that these observations reflect a decrease in the biomass of *L. forbesii* present from June
428 to September and localized in the west of the English Channel and an increase in the biomass of *L.*
429 *vulgaris* present from October and localized in the east. This squid biomass shift is consistent with
430 observations of fishery landings at the Port-en-Bessin fish market suggesting that the proportion of *L.*
431 *forbesii* is decreasing while *L. vulgaris* is increasing over time in the English Channel (Royer 2002;
432 Marcout et al. in prep). Our findings are also consistent with the findings of Oesterwind et al. (2022)
433 who found that the distribution range of *L. forbesii* has declined in the English Channel, but has
434 increased in the North Sea, suggesting a northward shift in population range.

435 **Conclusion**

436 The present study highlights the advantages of using commercial fishing data to derive abundance
437 indices, particularly due to its extensive spatial coverage and fine temporal resolution. It requires adapted
438 standardization tools but the resulting index provides new insights on squid distribution and stock
439 structure suggesting an East/West division of the resource with a decrease in *L. forbesii* population. Our
440 results highlight the importance of taking into account spatio-temporal changes in stock structure,
441 knowledge of which could be helpful for fishery managers to give adaptative responses in local and
442 regional fisheries.

443 Climate change may be contributing to the recent eastward shift in squid distribution in the English
444 Channel, as is the case for distribution shifts in other cephalopod populations (Oesterwind et al., 2022)
445 and indeed in the distributions of various fish species in this region (Auber et al., 2017; McLean et al.,
446 2018; Lima et al., 2022). Continued monitoring will be needed to confirm this hypothesis.

447

448 **Acknowledgements**

449 This work was supported by France Filière Pêche (FFP) and by the Conseil Régional de Basse
450 Normandie. We would like to thank the Système d'Information Halieutique (SIH) of the Ifremer for
451 providing us with French commercial landings and the French Direction des Pêches Maritimes et de
452 l'Aquaculture (DPMA) for granting permission for using commercial data.

453 **References**

- 454 Aghabozorgi, S., Shirkhorshidi, A. S., & Wah, T. Y. (2015). Time-series clustering—a decade review.
455 Information systems, 53, 16-38.
- 456 Albouy, C., Velez, L., Coll, M., Colloca, F., Le Loc'h, F., Mouillot, D., & Gravel, D. (2014). From
457 projected species distribution to food-web structure under climate change. Global change biology,
458 20(3), 730-741.
- 459 Arkhipkin, A. I., Rodhouse, P. G., Pierce, G. J., Sauer, W., Sakai, M., Allcock, L., . . . Zeidberg, L. D.
460 (2015). World squid fisheries. Reviews in Fisheries Science & Aquaculture, 23(2), 92-252.
- 461 Arkhipkin, A. I., Hendrickson, L. C., Payá, I., Pierce, G. J., Roa-Ureta, R. H., Robin, J. P., & Winter,
462 A. (2021). Stock assessment and management of cephalopods: advances and challenges for short-
463 lived fishery resources. *ICES Journal of Marine Science*, 78(2), 714-730.
- 464 Auber, A., Gohin, F., Goascoz, N., & Schlaich, I. (2017). Decline of cold-water fish species in the
465 Bay of Somme (English Channel, France) in response to ocean warming. *Estuarine, Coastal and*
466 *Shelf Science*, 189, 189-202.
- 467 Baudrier, J., Lefebvre, A., Galgani, F., Sarau, C., & Doray, M. (2018). Optimising French fisheries
468 surveys for marine strategy framework directive integrated ecosystem monitoring. Marine Policy,
469 94, 10-
- 470 Berkeley, S. A., Hixon, M. A., Larson, R. J., & Love, M. S. (2004). Fisheries sustainability via
471 protection of age structure and spatial distribution of fish populations. *Fisheries*, 29(8), 23-32.19.
- 472 Berndt DJ, Clifford J (1994). Using dynamic time warping to find patterns in time series. In: KDD
473 workshop, vol 10, pp 359–370
- 474 Boyle, P., Rodhouse, P. (2005). Cephalopods: ecology and fisheries. Oxford: Blackwell Science.
- 475 Cadrin, S. X. (2020). Defining spatial structure for fishery stock assessment. *Fisheries Research*,
476 221, 105397.

477 Cao, J., Thorson, J. T., Punt, A. E., & Szuwalski, C. (2020). A novel spatiotemporal stock assessment
478 framework to better address fine-scale species distributions: development and simulation testing.
479 *Fish and Fisheries*, 21(2), 350-367.

480 Carpentier, A., Coppin, F., Curet, L., Dauvin, J.-C., Delavenne, J., Dewarumez, J.-M., Dupuis, L.,
481 Foveau, A., Garcia, C., Gardel, L., Harrop, S., Just, R., Koubbi, P., Lauria, V., Martin, C., Meaden,
482 G., Morin, J., Ota, Y., Rostiaux, E., Smith, B., Spilmont, N., Vaz, S., Villanueva, C.-M., Verin, Y.,
483 Walton, J., Warembourg, C., (2009). Channel Habitat Atlas for Marine Resource Management—
484 CHARM II, URL <http://archimer.ifremer.fr/doc/00000/7377/>.

485 Challier, L., Royer, J., Pierce, G. J., Bailey, N., Roel, B., Robin, J. P. (2005). Environmental and
486 stock effects on recruitment variability in the English Channel squid *Loligo forbesi*. *Aquatic Living*
487 *Resources*, 18(4), 353-360.

488 Chen, C. S., Pierce, G. J., Wang, J., Robin, J. P., Poulard, J. C., Pereira, J., ... & Orsi-Relini, L. (2006).
489 The apparent disappearance of *Loligo forbesi* from the south of its range in the 1990s: trends in *Loligo*
490 spp. abundance in the northeast Atlantic and possible environmental influences. *Fisheries Research*,
491 78(1), 44-54.

492 Cheng, M. L. H., Rodgveller, C. J., Langan, J. A., & Cunningham, C. J. (2023). Standardizing fishery-
493 dependent catch-rate information across gears and data collection programs for Alaska sablefish
494 (*Anoplopoma fimbria*). *ICES Journal of Marine Science*, 80(4), 1028-1042.

495 Chu, S., Keogh, E., Hart, D., & Pazzani, M. (2002). Iterative deepening dynamic time warping for
496 time series. In *Proceedings of the 2002 SIAM International Conference on Data Mining* (pp. 195-
497 212). Society for Industrial and Applied Mathematics.

498 Cleveland, R. B., Cleveland, W. S., McRae, J. E., & Terpenning, I. J. (1990). STL: A seasonal-trend
499 decomposition procedure based on loess. *Journal of Official Statistics*, 6(1), 3-
500 33. <http://bit.ly/stl1990>

501 Coppin, F., Carpentier, A., Delpech, J.-P., Schlaich, I., (2002). Manuel des protocoles de campagne
502 halieutique. Campagnes CGFS. V3, URL <http://archimer.ifremer.fr/doc/00036/14705/12011.pdf>

503 Cotter, J., Petitgas, P., Abella, A., Apostolaki, P., Mesnil, B., Politou, C. Y., ... Woillez, M. (2009).
504 Towards an ecosystem approach to fisheries management (EAFM) when trawl surveys provide the
505 main source of information. *Aquatic Living Resources*, 22(2), 243-254.

506 Dauvin, J. C. (2012). Are the eastern and western basins of the English Channel two separate
507 ecosystems?. *Marine Pollution Bulletin*, 64(3), 463-471

508 Denis, V., Lejeune, J., & Robin, J. P. (2002). Spatio-temporal analysis of commercial trawler data using
509 General Additive models: patterns of Loliginid squid abundance in the north-east Atlantic. *ICES Journal*
510 *of Marine Science*, 59(3), 633-648.

511 Fletcher, R. J., T. J. Hefley, E. P. Robertson, B. Zuckerberg, R. A. McCleery, and R. M. Dorazio. (2019).
512 A practical guide for combining data to model species distributions. *Ecology* 100: e02710.

513 Giorgino, T. (2009). Computing and visualizing dynamic time warping alignments in R: the dtw
514 package.

515 Grosselin, M. D., & Laurec, A. (1982). Bottom trawl surveys design, operation and analysis. FAO,
516 CECAF/ECAF Series, 1014-9228

517 Grüss, A., Walter III, J. F., Babcock, E. A., Forrestal, F. C., Thorson, J. T., Lauretta, M. V., & Schirripa,
518 M. J. (2019). Evaluation of the impacts of different treatments of spatio-temporal variation in catch-per-
519 unit-effort standardization models. *Fisheries Research*, 213, 75-93

520 Guerra, A., Rocha, F. (1994). The life history of *Loligo vulgaris* and *Loligo forbesi* (Cephalopoda:
521 Loliginidae) in Galician waters (NW Spain). *Fisheries Research*, 21, 43-69.

522 Hastie, L. C., Pierce, G. J., Wang, J., Bruno, I., Moreno, A., Piatkowski, U., & Robin, J. P. (2009).
523 Cephalopods in the north-eastern Atlantic: species, biogeography, ecology, exploitation and
524 conservation. *Oceanography and marine biology*, 123-202

525 Holme, N. A. (1974). The biology of *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda) in the
526 Plymouth area. *Journal of the Marine Biological Association of the United Kingdom*, 54(2), 481-503.

527 ICES. (2011). Report of the Working Group on Cephalopod Fisheries and Life History (WGCEPH).
528 ICES CM 2011/SSCEF:03, 122 pp.

529 ICES. (2017). Interim Report of the Working Group on Cephalopod Fisheries and Life History
530 (WGCEPH). In : . 2017. p. 135.

531 ICES. (2020). Working Group on Cephalopod Fisheries and Life History (WGCEPH; outputs from 2019
532 meeting). ICES Scientific Reports. 2:46. 121 pp. <http://doi.org/10.17895/ices.pub.6032>

533 ICES. (2023). Working Group on Cephalopod Fisheries and Life History (WGCEPH; Outputs from
534 2022 meeting). ICES Scientific Reports. 5:01. 163 pp. <https://doi.org/10.17895/ices.pub.2197671>

535 Kerr, L. A., Cadrin, S. X., & Secor, D. H. (2010). The role of spatial dynamics in the stability, resilience,
536 and productivity of an estuarine fish population. *Ecological Applications*, 20(2), 497-507.

537 Knijn, R. J., Boon, T. W., Heessen, H. J., & Hislop, J. R. (1993). Atlas of North Sea fishes-Based on
538 bottom-trawl survey data for the years 1985-1987. ICES Cooperative Research Reports (CRR).

539 Laptikhovsky, V., Allcock, A. L., Barnwall, L., Barrett, C., Cooke, G., Drerup, C., .Firmin, C., Lozach,
540 S., MacLeod, E., .Oesterwind, D., Petroni, M., Robin, J.P., Sheerin, E., Power, A.M., Pierce, G. J.
541 (2022). Spatial and temporal variability of spawning and nursery grounds of *Loligo forbesii* and *Loligo*
542 *vulgaris* squids in ecoregions of Celtic Seas and Greater North Sea. *ICES Journal of Marine Science*,
543 79(6), 1918-1930.

544 Lima, A. R., Baltazar-Soares, M., Garrido, S., Riveiro, I., Carrera, P., Piecho-Santos, A. M., ... & Silva,
545 G. (2022). Forecasting shifts in habitat suitability across the distribution range of a temperate small
546 pelagic fish under different scenarios of climate change. *Science of the Total Environment*, 804, 150167.

547 Lordan, C., & Casey, J. (1999). The first evidence of offshore spawning in the squid species *Loligo*
548 *forbesi*. *Journal of the Marine Biological Association of the United Kingdom*, 79(2), 379-381

549 Mahevas, S., Trenkel, V.M., Doray, M. and Peyronnet, A. (2011) Hake catchability by the French
550 trawler fleet in the Bay of Biscay: estimating technical and biological components. *ICES Journal of*
551 *Marine Science*. 1 janvier 2011. Vol. 68, n° 1, p. 107-118. (doi 10.1093/icesjms/fsq140).

552 McLean, M., Mouillot, D., Lindegren, M., Engelhard, G., Villéger, S., Marchal, P., ... & Auber, A.
553 (2018). A climate-driven functional inversion of connected marine ecosystems. *Current Biology*, 28(22),
554 3654-3660.

555 Moreno A., Pereira J., Arvanitidis C., Robin J.P., Koutsoubas D., Perales-Raya C., Cunha M.M.,
556 Balguerias E., Denis V., (2002). Biological variation of *Loligo vulgaris* (Cephalopoda Loliginidae) in
557 the Eastern Atlantic and Mediterranean. *Bulletin of Marine Science* 71 (1):3-7, 515-534.

558 Moreno, A., Azevedo, M., Pereira, J. M. F., Pierce G. J., (2007). Growth strategies in the European
559 squid *Loligo vulgaris* from Portuguese waters. *Marine Biology Research*, 3: 49–59.

560 Morrison, W.E., and V. Termini. (2016) A Review of Potential Approaches for Managing Marine
561 Fisheries in a Changing Climate. U.S. Dept. of Commer., NOAA. NOAA Technical Memorandum
562 NMFS-OSF-6, 35 p.

563 Moullec, F., Asselot, R., Auch, D. et al. Identifying and addressing the anthropogenic drivers of global
564 change in the North Sea: a systematic map protocol. *Environ Evid* 10, 19 (2021).
565 <https://doi.org/10.1186/s13750-021-00234-y>

566 National Research Council. (2000.) Improving the collection, management and use of marine fisheries
567 data. National Academy Press, Washington, D.C. <https://doi.org/10.17226/9969>

568 Oesterwind, D., Barrett, C. J., Sell, A. F., Núñez-Riboni, I., Kloppmann, M., Piatkowski, U., ... &
569 Laptikhovsky, V. (2022). Climate change-related changes in cephalopod biodiversity on the North East
570 Atlantic Shelf. *Biodiversity and Conservation*, 31(5-6), 1491-1518.

571 Pierce, G. J., Boyle, P. R., Hastie, L. C., & Key, L. (1994). The life history of *Loligo forbesi*
572 (Cephalopoda: Loliginidae) in Scottish waters. *Fisheries Research*, 21(1-2), 17-41.

573 R Development Core Team. (2023). R: A language and environment for statistical computing. R
574 Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>

575 Rijnsdorp, A. D., W. Dekker, and N. Daan. (2006). Partial fishing mortality per fishing trip: a useful
576 indicator for effective fishing effort in management of mixed demersal fisheries. *ICES Journal of Marine*
577 *Science* 63:556-566.

578 Roa-Ureta, R. H. (2012). Modeling in-season pulses of recruitment and hyperstability-hyperdepletion
579 in the *Loligo gahi* fishery of the Falkland Islands with generalized depletion models. *ICES Journal of*
580 *Marine Science*, 69: 1403–1415.

581 Robin, J. P., & Boucaud-Camou, E. (1995). Squid catch composition in the English Channel bottom
582 trawl fishery: proportion of *Loligo forbesi* and *Loligo vulgaris* in the landings and length-frequencies of
583 both species during the 1993–1994 period. ICES CM 1995/K: 36, 12pp.r

584 Robin, J. P., & Denis, V. (1999). Squid stock fluctuations and water temperature: temporal analysis of
585 English Channel Loliginidae. *Journal of Applied Ecology*, 36(1), 101-110.

586 Rodhouse, P. G., Pierce, G. J., Nichols, O. C., Sauer, W. H., Arkhipkin, A. I., Laptikhovskiy, V. V., ...
587 & Downey, N. (2014). Environmental effects on cephalopod population dynamics: implications for
588 management of fisheries. *Advances in marine biology*, 67, 99-233.

589 Rosenberg, A.A., Kirkwood, G.P., Crombie, J.A. and Beddington, J.R., 1990. The assessment of stocks
590 of annual squid species. *Fisheries Research.*, 8: 335-350.

591 Royer, J. (2002) Modélisation des stocks de céphalopodes de Manche. PhD thesis, University of Caen,
592 243pp.

593 Royer, J., Périès, P., & Robin, J. P. (2002). Stock assessments of English Channel loliginid squids:
594 updated depletion methods and new analytical methods. *ICES Journal of Marine Science*, 59(3), 445-
595 457.

596 Sims, D. W., Genner, M. J., Southward, A. J., & Hawkins, S. J. (2001). Timing of squid migration
597 reflects North Atlantic climate variability. *Proceedings of the Royal Society of London. Series B:*
598 *Biological Sciences*, 268(1485), 2607-2611.

599 Southward, A. J., Butler, E. I., & Pennycuik, L. (1975). Recent cyclic changes in climate and in
600 abundance of marine life. *Nature*, 253(5494), 714-717.

601 Southward, A. J., Hawkins, S. J., & Burrows, M. T. (1995). Seventy years' observations of changes in
602 distribution and abundance of zooplankton and intertidal organisms in the western English Channel in
603 relation to rising sea temperature. *Journal of thermal Biology*, 20(1-2), 127-155.

604 Thorson JT, Cunningham CJ, Jorgensen E, Havron A., Hulson PJF, Monnahan CC., von Szalay P.
605 (2021). The surprising sensitivity of index scale to delta-model assumptions: Recommendations for
606 model-based index standardization. *Fisheries Research*, 233, 105745.
607 <https://doi.org/10.1016/J.FISHRES.2020.105745>

608 Thorson, JT. (2019). Guidance for decisions using the Vector Autoregressive Spatio-Temporal (VAST)
609 package in stock, ecosystem, habitat and climate assessments. *Fish. Res.* 210: 143-161.

610 Tinbergen, L., & Verwey, J. (1945). Zur Biologie von *Loligo vulgaris* Lamarck. *Archives Néerlandaises*
611 *Zoologie*, 7, 186-213.

612 van der Hammen, T.; Poos, J.J.; Quirijns, F.J. (2011). Data availability for the evaluation of stock status
613 of species without catch advice: Case study: turbot (*Psetta maxima*) and Brill (*Scophthalmus rhombus*).
614 IJmuiden: IMARES, (Report C109/11) - p. 35.

615 Vaz, S., Martin, C. S., Eastwood, P. D., Ernande, B., Carpentier, A., Meaden, G. J., & Coppin, F. (2008).
616 Modelling species distributions using regression quantiles. *Journal of Applied Ecology*, 204-217.

617 Waluda, C. M., & Pierce, G. J. (1998). Temporal and spatial patterns in the distribution of squid *Loligo*
618 *spp.* in United Kingdom waters. *African Journal of Marine Science*, 20.

619 Wang, J., Pierce, G. J., Boyle, P. R., Denis, V., Robin, J. P., & Bellido, J. M. (2003). Spatial and temporal
620 patterns of cuttlefish (*Sepia officinalis*) abundance and environmental influences—a case study using

621 trawl fishery data in French Atlantic coastal, English Channel, and adjacent waters. ICES Journal of
622 Marine Science, 60(5), 1149-1158.

623 **Figure captions**

624 Figure 1. Loliginid landings in the English Channel from 2000 to 2021 by national fleet (Data from
625 ICES, 2023)

626 Figure 2. The 33 ICES rectangles of the English Channel (division 7E and 7D). Four rectangles (30E6,
627 30E7, 30E8 in the English coast and 27F0) were excluded from the analysis because very few data were
628 available. Rectangle 27E8 overlaps into ICES division (27E8.E and 27E8.D) and because of this, is split
629 into two distinct rectangles. In total, 30 rectangles were considered in the analysis. Red crosses represent
630 the barycentres associated with each rectangle.

631 Figure 3. CGFS indices (kg/km²; in red), LPUE_{basic} (kg/h; in green), LPUE_{vessel} (kg/h; in blue) and
632 LPUE_{VAST} (kg/h; in purple) in October from 2000 to 2021. LPUE indices are plotted against the left
633 vertical axis and CGFS indices against the right axis.

634 Figure 4. Squid biomass indices in the English Channel for two years: 2012 (a and b) and 2017 (c and
635 d) in two seasons: summer (a and c) and in winter (b and d).

636 Figure 5. Seasonal and global trends in the squid biomass index in the English Channel between 2000
637 and 2021 with (a) the original time series decomposed in three components: (b) the global trend, (c) the
638 seasonal component and (d) the remainder component.

639 Figure 6. The monthly average biomass squid index in the English Channel over all years (a) and
640 between 2000 and 2021 (b).

641 Figure 7. Time series clustering of the biomass index using time series of the biomass index for each
642 ICES rectangle. The dendrogram (a) reveals two main clusters of rectangles and the map (b) shows the
643 location of each group of rectangles within the English Channel. For each cluster seasonal time series
644 decompositions are shown in c and d and are as described in fig. 5.

645 Figure 8. Centre of gravity for squid biomass indices: (a) for each month for all years (2000-2021) and
646 (b) the average location of gravity centre for each month using symbol size scaled according to the
647 monthly biomass indices averaged over the 22 years.

648 Figure 9. Location of the average centre of gravity by year for squid biomass indices in the English
649 Channel

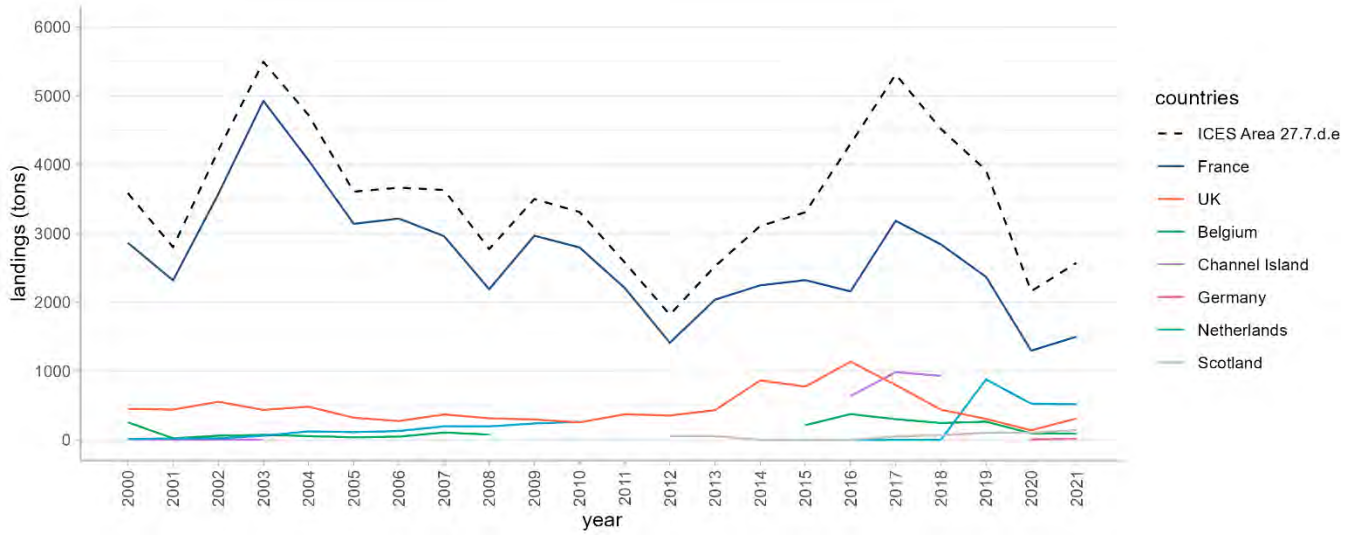


Figure 1

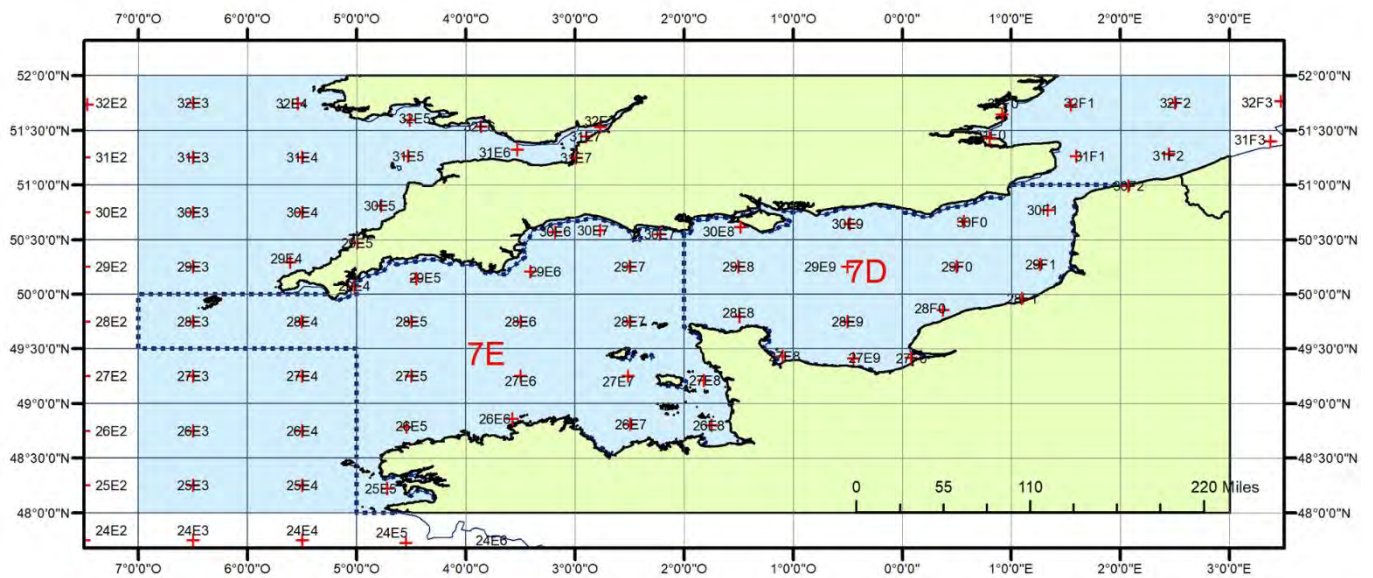


Figure 2

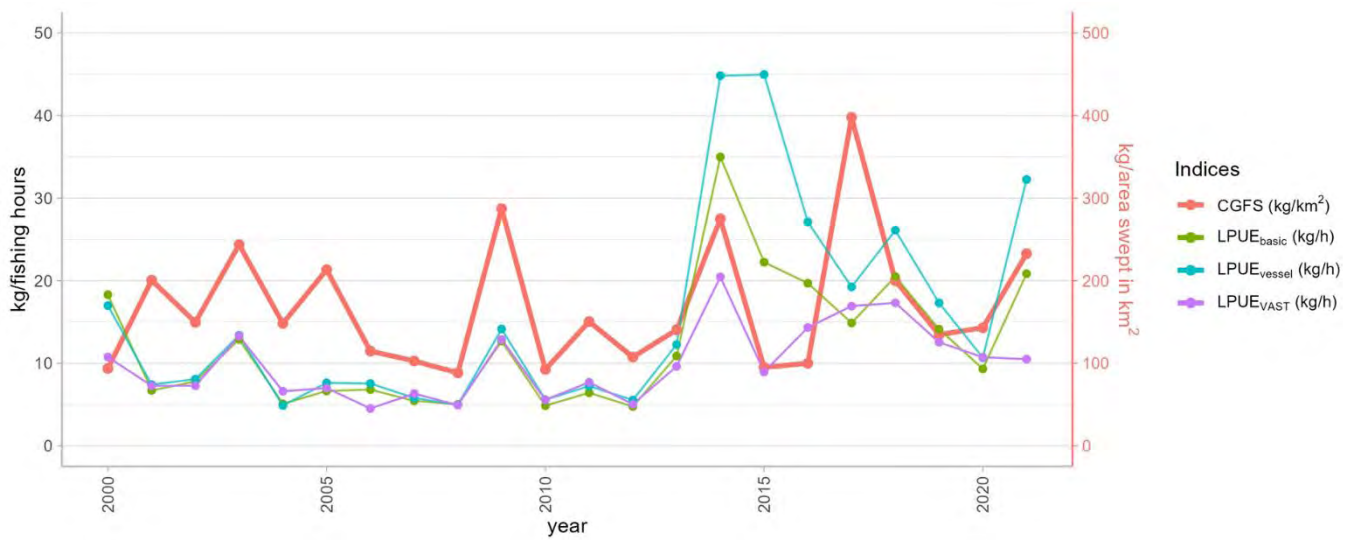
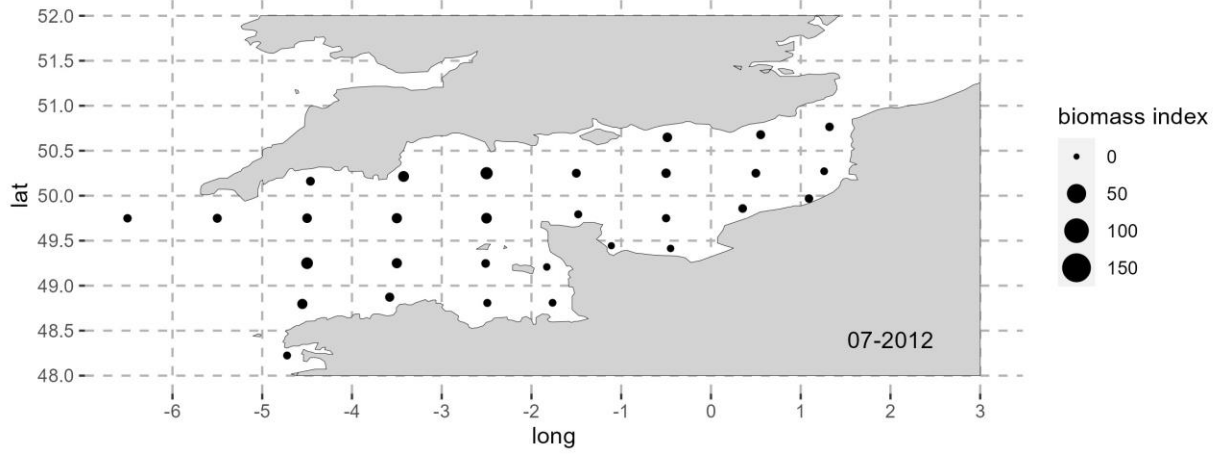


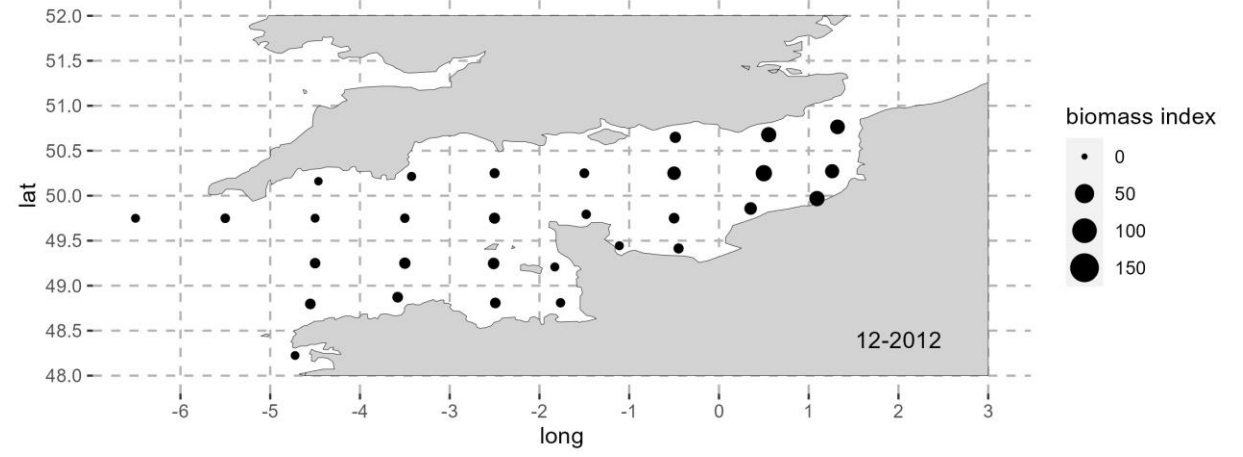
Figure 3

FIGURE 4

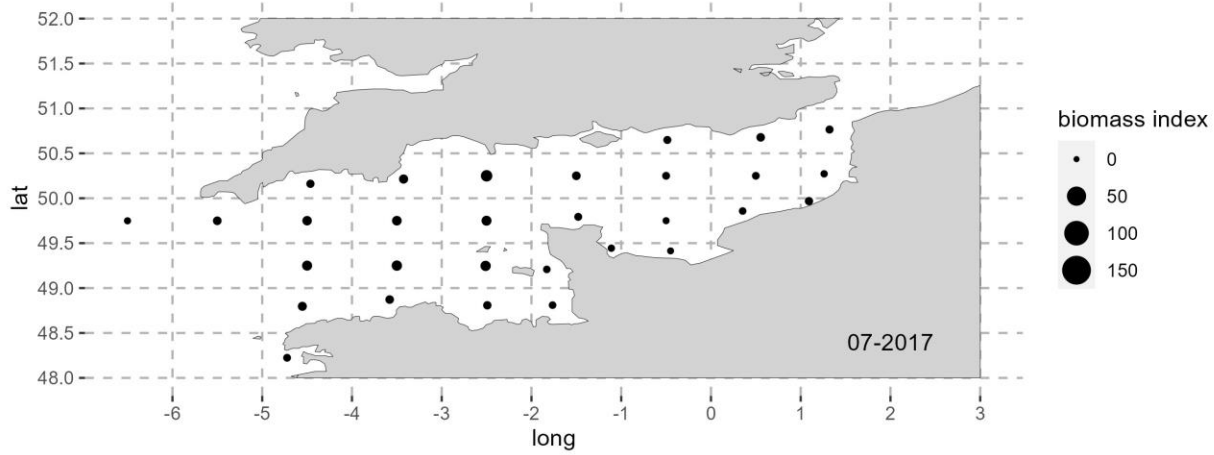
(a)



(b)



(c)



(d)

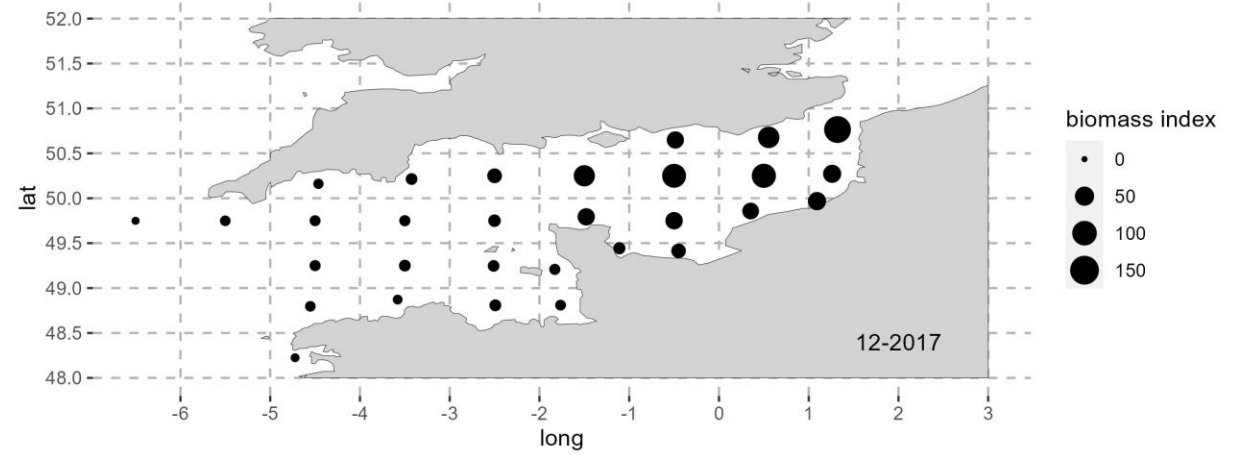


FIGURE 5

STL decomposition

biomass index = trend + seasonal + remainder

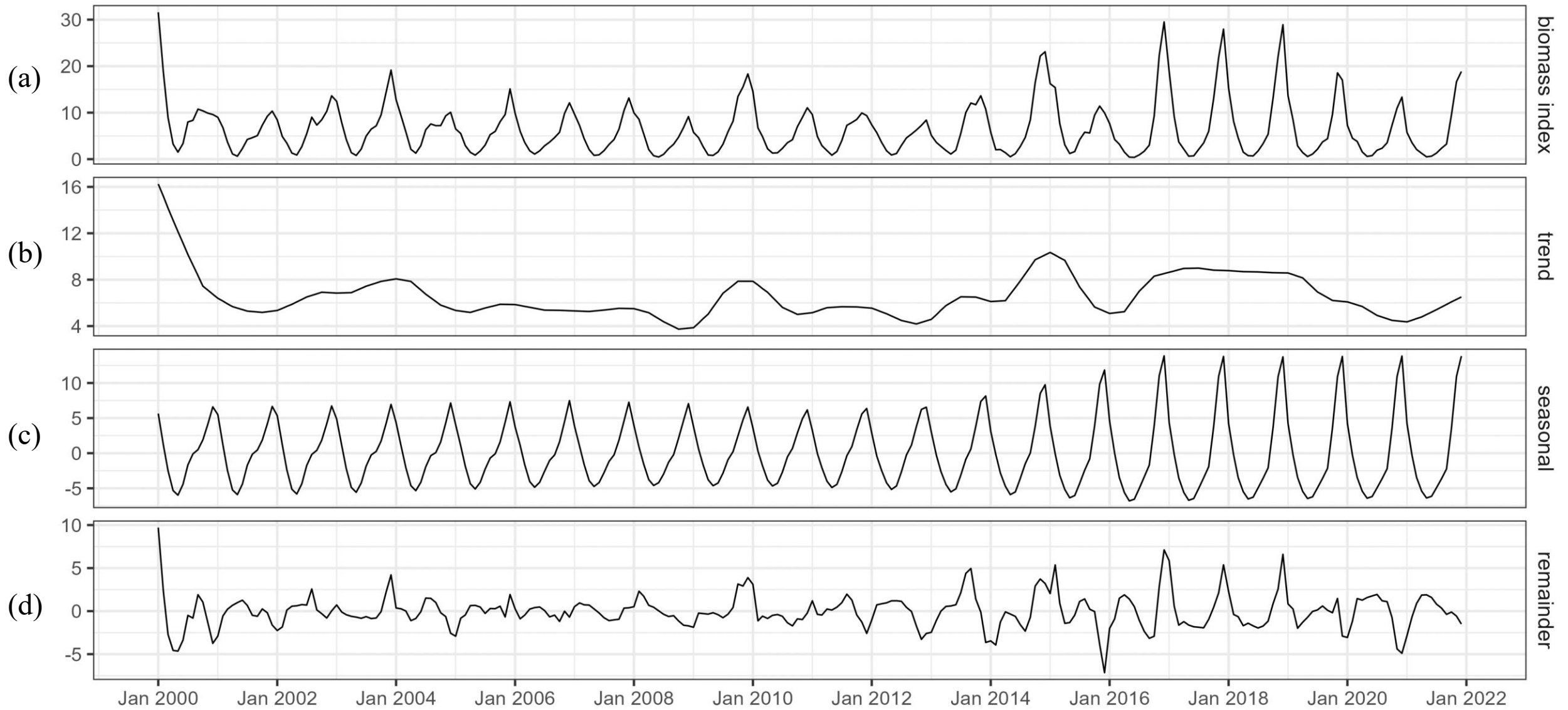
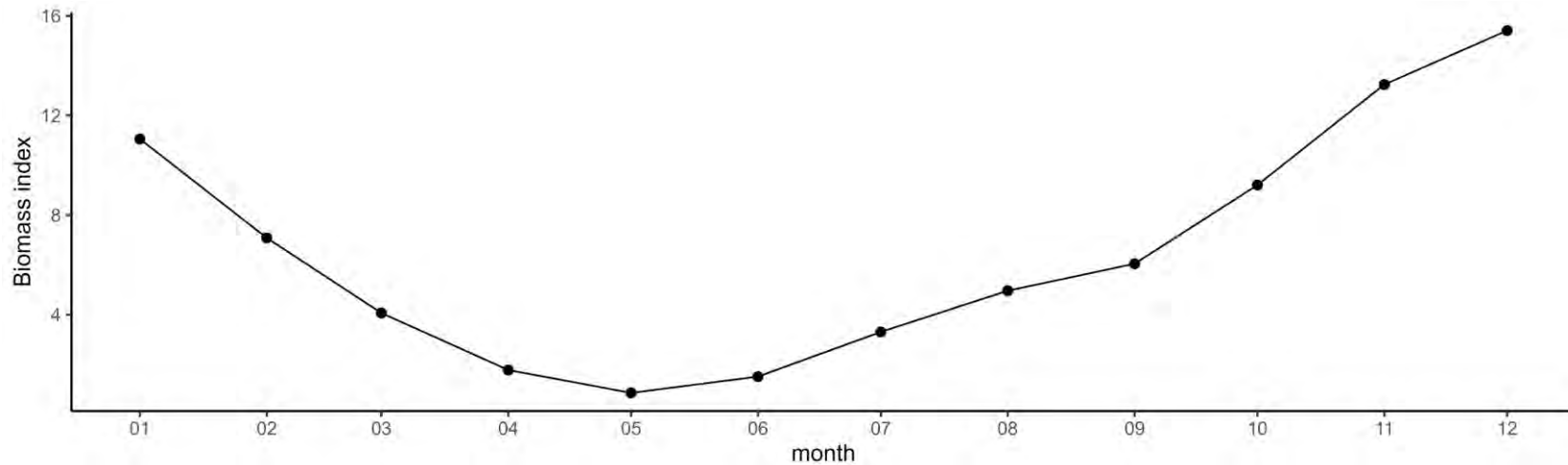


FIGURE 6

(a)



(b)

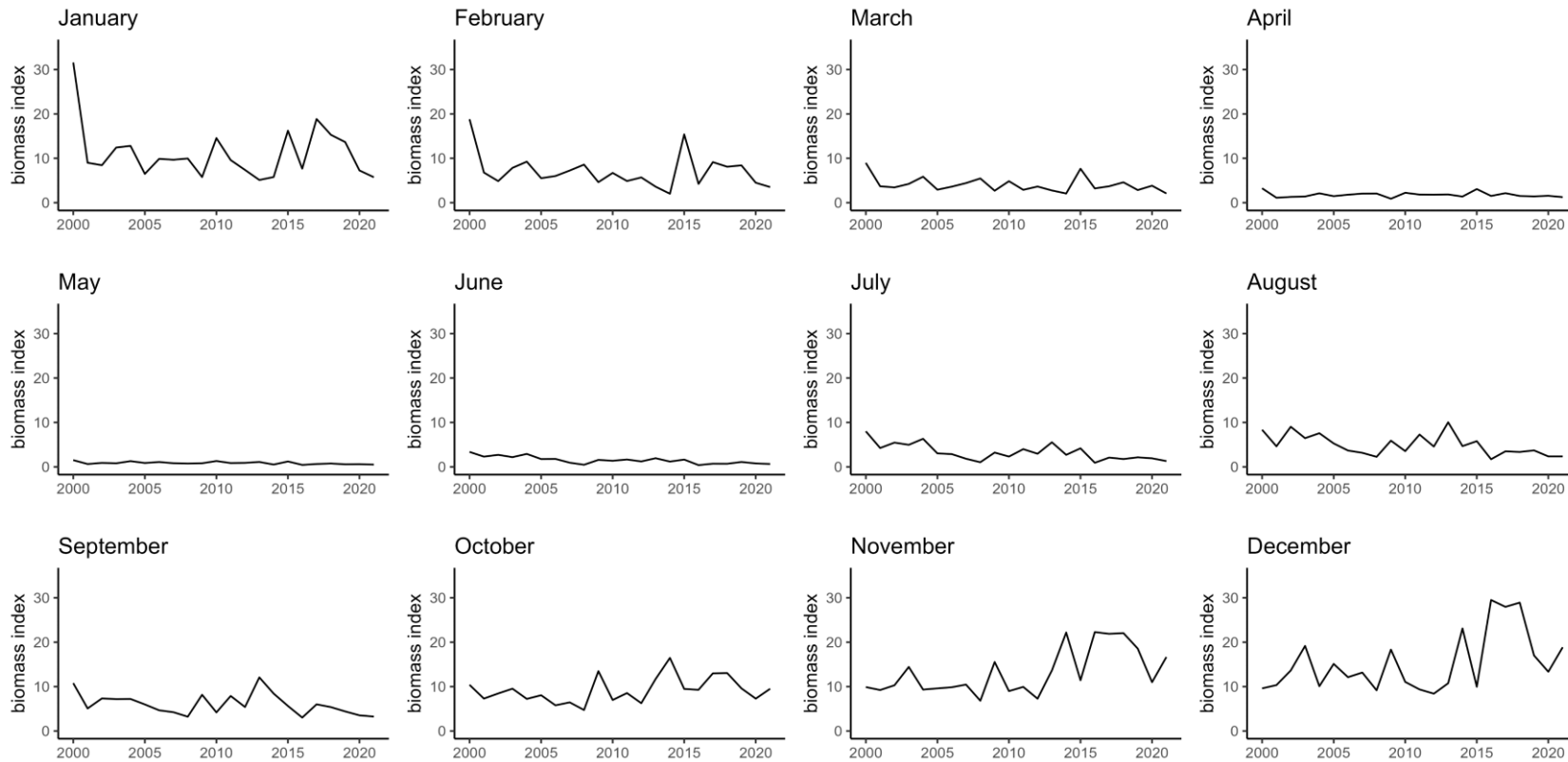
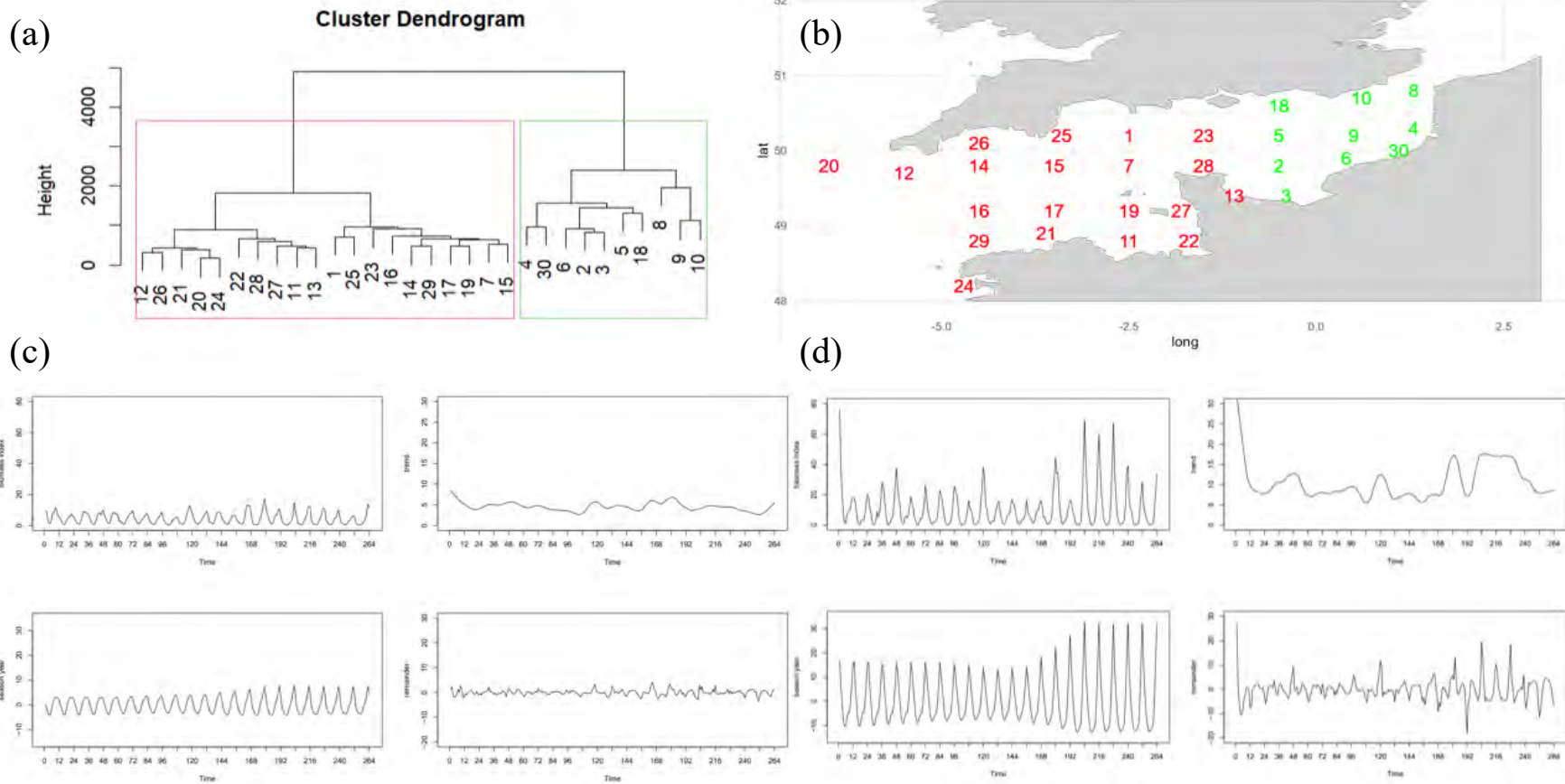


FIGURE 7



(a)

FIGURE 8

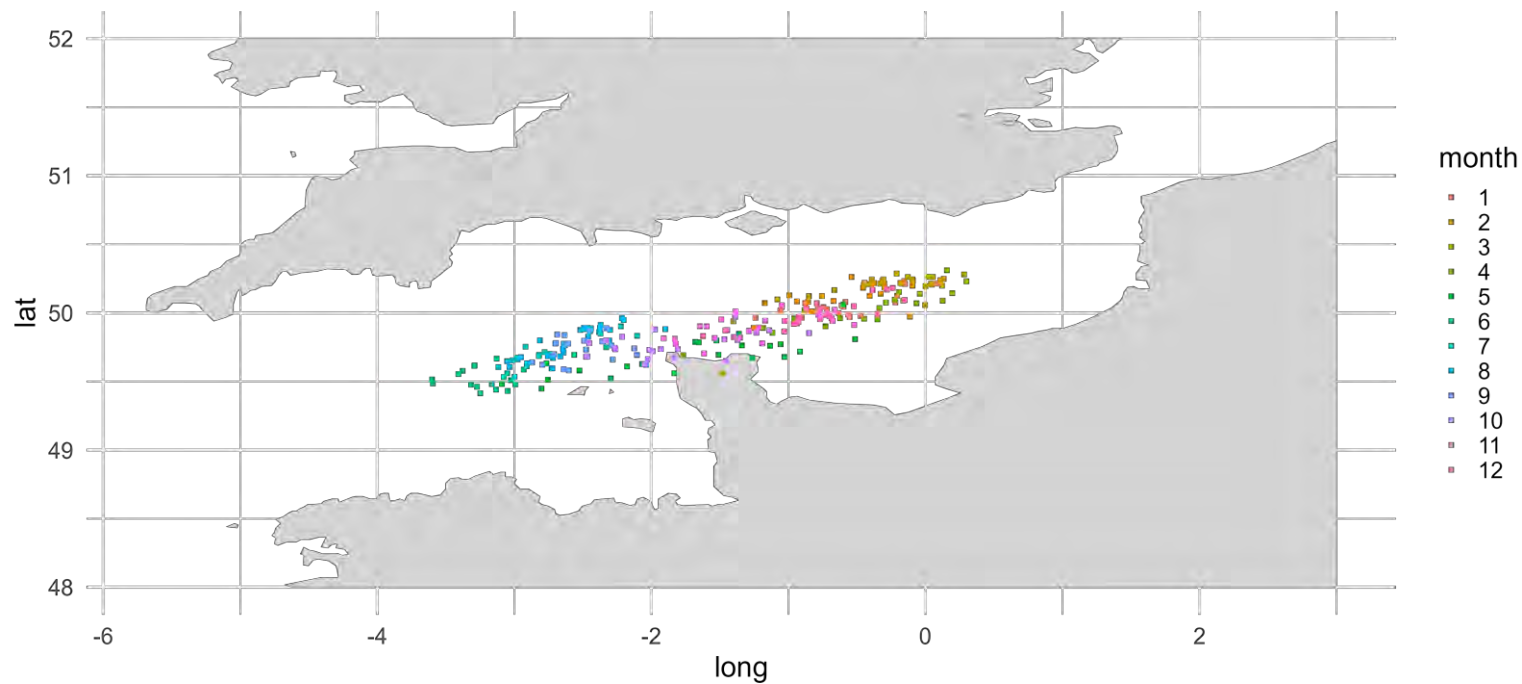
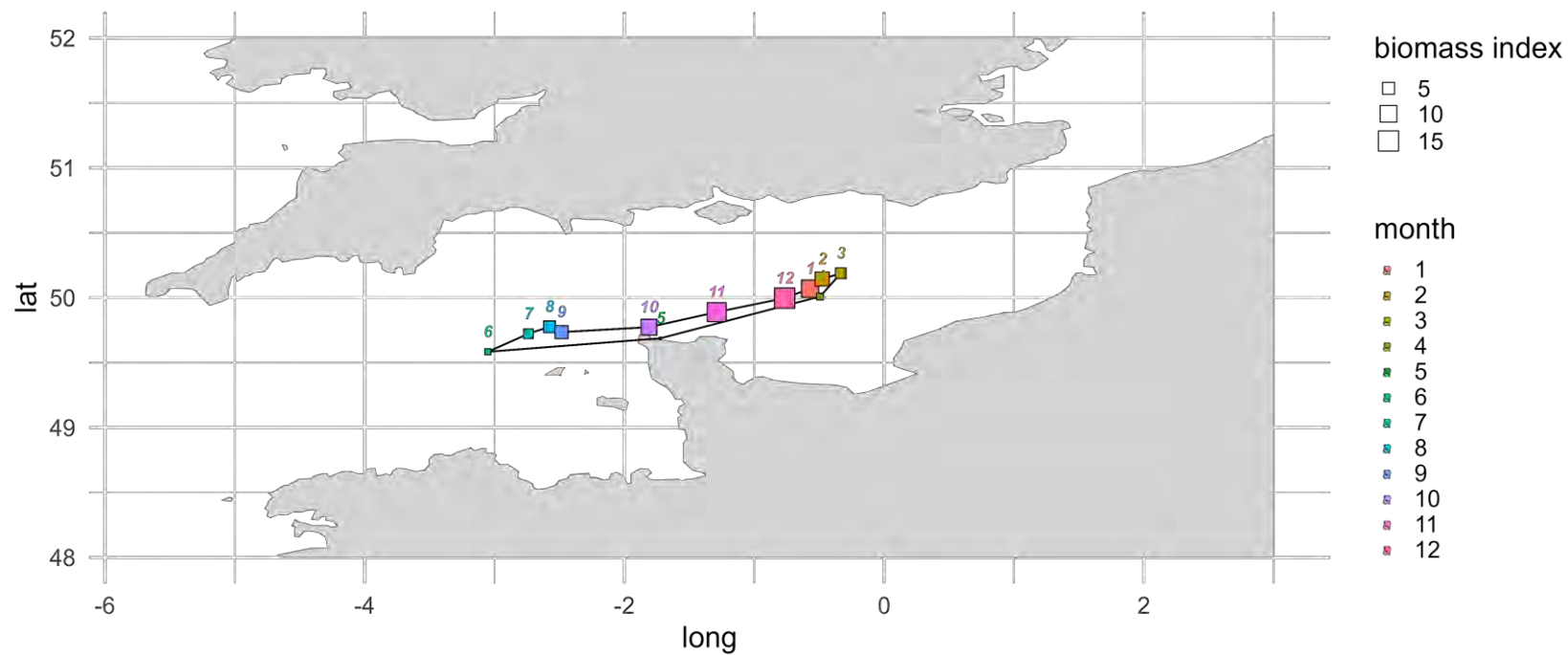
**(b)**

FIGURE 9

