

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

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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; Laptikhovskiy 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). Using the
105 European Vessel Registry, vessel engine power (kW) has been associated with each fishing sequence.
106 To characterize squid distribution, we have linked each ICES rectangle to the geographical coordinate
107 of its barycentre using QGIS software and the shapefile: "ICES_Statistical_Rectangles_Eco.shp"
108 downloaded from the ICES website (Figure 2). In total, 927 281 fishing sequences from 1011 different
109 vessels were analyzed.

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

114

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

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

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

124 **2.1 Basic LPUE**

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

$$127 \quad \text{LPUE}_{\text{basic } m,i} = \frac{\sum L_{m,i}}{\sum E_{m,i}}$$

128 Where L is landing in kg, E is effort in hours of fishing.

129 **2.2 LPUE standardization with vessel power**

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

$$135 \quad \text{LPUE}_{\text{vessel } m,i} = \sum \frac{L_{m,i}}{\frac{E_{m,i} * \text{kW}_{m,i}}{400}}$$

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

138 **2.3 LPUE standardization with spatio-temporal model**

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

$$143 \quad (1) \text{ Pr } [c] = \text{ Pr } [C>0] \times \text{ Pr } [C = c | C>0]$$

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

$$148 \quad (2) \Pr [C>0] = p_{m,i}$$

$$149 \quad (3) \Pr [C = c | C>0] = \text{Gamma} (c, \sigma^2, r_{m,i} \sigma^2)$$

150 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
 151 terms of the Gamma distribution.

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

$$156 \quad (4) \text{logit } p_{m,i} = \beta_m^{(p)} + L_\omega^{(p)} \omega_i + L_\varepsilon^{(p)} \varepsilon_{m,i} + L_\eta^{(p)} \eta_{m,i}$$

$$157 \quad (5) \log r_{m,i} = \beta_m^{(r)} + L_\omega^{(r)} \omega_i + L_\varepsilon^{(r)} \varepsilon_{m,i} + L_\eta^{(r)} \eta_{m,i}$$

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

$$163 \quad (6) \text{LPUE}_{\text{VAST } m,i} = \text{logit}^{-1} (\beta_m^{(p)} + L_\omega^{(p)} \omega_i + L_\varepsilon^{(p)} \varepsilon_{m,i} + L_\eta^{(p)} \eta_{m,i}) \times \exp (\beta_m^{(r)} + L_\omega^{(r)} \omega_i + L_\varepsilon^{(r)} \\ 164 \quad \varepsilon_{m,i} + L_\eta^{(r)} \eta_{m,i})$$

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

167 **2.4 CGFS index**

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

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

$$171 \text{CGFS}_{m,i} = \frac{C_{m,i}}{A_{m,i}}$$

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

173

174 **3. Statistical analysis**

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

176 **3.1 Assessing the accuracy of standardization by comparing with indices from scientific surveys**

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

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

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

185 **3.2 Seasonal decomposition of time series**

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

$$193 \quad Y_t = T_t + S_t + R_t \quad 1 \leq t \leq n$$

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

195 **3.3 Time series Clustering**

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

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

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

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

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

212 **3.4 Spatial parameters**

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

- 216 • Centre of gravity of the biomass indices

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

$$219 \quad W_{m,i} = \frac{LPUE_{m,i}}{\sum_{i=1}^n (LPUE_{m,i})} \text{ and } \sum W_{m,i} = 1$$

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

$$222 \quad X_{gm} = \sum_{i=1}^n (X_i * W_{m,i}) \text{ and } Y_{gm} = \sum_{i=1}^n (Y_i * W_{m,i})$$

- 223 • Inertia

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

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

$$226 \quad D_{m,i} = \sqrt{(X_i - X_{gm})^2 + (Y_i - Y_{gm})^2}$$

227

228 and the inertia of all biomass indices in month m is:

$$C_m = \frac{\sum (LPUE_{m,i} * D_{m,i}^2)}{\sum LPUE_{m,i}}$$

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

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

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

234
$$L_m = \Sigma (L_i * W_{m,i})$$

235 **Results**

236 ***1. Comparison of squid biomass indices***

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

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

253 2. Seasonal decomposition of time series

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

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

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

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

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

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

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

288 **4. Analysis of spatial parameters**

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

291 **4.1 Seasonal variations of squid centre of biomass**

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

302 Longitude (X_g) and latitude (Y_g) of the monthly gravity centres are highly correlated ($r = 0.88$, $p <$
303 0.0001) suggesting homogeneous shift north-east and south-west. Squid biomass indices are positively

304 correlated to the gravity centres coordinates (longitude: $r = 0.31$, $p < 0.0001$; latitude: $r = 0.39$, $p <$
305 0.0001) reflecting highest squid concentration in the north-east of the English Channel. Over the course
306 of an average fishing season (between June and March, Figure 8.b) the squid resource moves more than
307 110 nautical miles.

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

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

316

317 ***4.2 Interannual variations of squid concentration***

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

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

328 **Discussion**

329 The starting point for this study was the lack of data to describe changes in the spatial distribution of
330 English Channel squid on an appropriate timescale. In such short-lived migrating populations (Holme,
331 1974, Tinbergen and Verwey, 1945, Sims et al., 2001, Royer, 2002), it is necessary to take into account
332 distribution changes during the course of a fishing season and at all stages of cohort exploitation, as well
333 as between years (i.e. between annual cohorts). In the absence of scientific surveys designed at a relevant
334 temporal scale it is rather common to derive indices from commercial fishery data (Rosenberg et al.,
335 1990; Roa-Ureta, 2012). Indices derived from landings per unit of effort (LPUE) of commercial trawlers
336 are biomass estimates rather than abundance estimates since there is no biological sampling programme
337 that would enable conversion of weights into numbers and, indeed, the high variability in growth rate
338 means that length-weight relationships are also variable, thus requiring more frequent and intense
339 sampling than would otherwise be the case.

340 **(a) LPUE standardization**

341 Standardized LPUE indices (computed per month and rectangle) were compared to the only (survey-
342 based) series of observations available: biomass indices derived from the CGFS surveys carried out in
343 October. Results of correlation analyses suggested that LPUE standardized by the vector autoregressive
344 spatio-temporal method (VAST, Thorson 2019) shows the best match with squid biomass estimated
345 from survey data, in comparison with non-standardized LPUE or LPUE that was standardized based on
346 engine power. The value of this delta-glm model is that it takes into account both the probability of
347 encounter and the positive catch rate and allows the integration of co-variables that influence biomass
348 or catches (such as vessel power). Data from trawl surveys have also drawbacks (Knijn et al., 1993;
349 Baudrier et al., 2018), mainly related to selectivity issues and to the fact that fishing operations were not
350 designed specifically for catching squid. The VAST standardization method has been compared to other
351 standardization procedures like GLMs or GAMs and, although this was not the objective of our study,
352 it is worth mentioning that in these other comparisons VAST provided the best fits (Grüss et al., 2019).
353 This procedure has enabled us to obtain for the first time in the analysis of these resources, biomass

354 indices per month (from 2000 to 2021) and per statistical rectangle in the English Channel which is the
355 first step in studying spatio-temporal variations in squid stocks. It is applicable in other short-lived
356 species provided that the stock's range is regularly explored by a commercial fleet.

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

360 **(b) General interannual trend**

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

372 **(c) Seasonality**

373 The present findings also indicated the existence of a seasonal fluctuations. Seasonal peaks and trough
374 are consistent with the annual life-cycle of Loliginid squids (Holme, 1974; Guerra and Rocha, 1994;
375 Moreno et al., 2007). The slight shift in the timing of seasonal cycles in the Western and Eastern parts
376 of the Channel seems likely related to the presence of the two species *Loligo forbesii* and *Loligo vulgaris*
377 in the resource with different timings of their life-cycles (Holme, 1974; Robin and Boucaud-Camou,
378 1995; Royer, 2002, Laptikhovsky et al., 2022) and with differing importance in the Western and Eastern
379 parts of the Channel. Within each year, the beginning of an increase in abundance in June is likely to

380 correspond to the recruitment to the fishery of *L. forbesii* and a second increase in October then
381 corresponds to *L. vulgaris* recruitment. Again, time series decomposition of VAST standardized indices
382 provides for the first-time evidence that the seasonal pattern is consistently repeated. A similar
383 seasonality over more than 20 fishing seasons illustrates that the life-cycle of both species is repeating
384 in a regular way and that sub-cohorts or variable timing of recruitment peaks as observed in *L. forbesii*
385 in Scottish waters (Pierce et al., 1994) are of minor importance in Channel stocks.

386 (d) Spatial patterns

387 Cluster analysis identify two distinct geographical patterns (West/East) among ICES rectangle time
388 series. Low and stable biomass indices were found in the Western English Channel and most of the
389 fluctuations and seasonal variations were found in Eastern English Channel. This result is different from
390 the clustering with spatial contiguity constraint applied by Royer (2002). This is likely a difference
391 related to the temporal window analysed since *L. forbesii* was more abundant in 1992-1999 (Chen et al.,
392 2006).

393 Analysis of monthly centres of gravity provide a quantitative view of squid distribution shifts. From
394 June to September squid biomass is centred in the West, the deepest part of the English Channel (Dauvin,
395 2012), and the area where the recruitment of *L. forbesii* begins in June (Holme, 1974). From October,
396 squid concentrations move eastwards, probably corresponding to the appearance of *L. vulgaris* in fishery
397 catches (Robin and Boucaud-Camou, 1995). These observations are consistent with the fact that *L.*
398 *forbesii* has a deeper, more offshore, distribution than its congener *L. vulgaris* (Lordan and Casey, 1999;
399 Hastie et al., 2009). The Eastward shift in the location of centre of gravity and the increase of inertia (a
400 measure of dispersion) in October is likely the result of a combination of two phenomena: the autumn
401 recruitment of *L. vulgaris* and the eastward migration of immature *L. forbesii* (Holme, 1974; Royer,
402 2002; Vaz et al., 2008). *L. forbesii* gradually migrate eastward, while foraging, into the Eastern Channel
403 and then return to the Western approaches in autumn. Females *L. forbesii* reach maturity in November,
404 spawn in December - January, and the juveniles are seen in the catches around May after hatching from
405 the eggs. Royer (2002) made the first trial to quantify migratory fluxes of the two squid species within
406 the English Channel using spatialized cohort analysis. This preliminary trial was done using strong

407 assumptions (equal catchability and the proportions of both species in catches being the same in all
408 locations, varying according to results of monthly sampling in a single fish market). In comparison,
409 changes in the location of the centre of gravity offer a rather direct quantification of spatial patterns that
410 can be used to better understand interannual variation. The advantage of quantitative parameters like
411 centres of gravity can be seen by comparing the difficulties of analyzing 264 maps like those in Figure
412 4 with the trends clearly visible in Figure 8.

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

416 (e) Shift in squid biomass distribution from 2014

417 Analysis of yearly centres of gravity suggested an eastward shift in squid concentration since 2014.
418 These observations coincided with an increase of seasonal variations in biomass indices trends since
419 2014, with a decrease of the monthly average biomass indices in summer and an increase in autumn-
420 winter.

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

429 **Conclusion**

430 The present study illustrates the benefits of using commercial fishing data to derive abundance indices,
431 with the advantage of its large spatial coverage and fine temporal resolution. It requires adapted
432 standardization tools but the resulting index provides new insights on squid distribution and stock
433 structure suggesting an East/West division of the resource with a decrease in *L. forbesii* population. Our
434 results highlight the importance of taking into account spatio-temporal changes in stock structure,
435 knowledge of which could be helpful for fishery managers to give adaptative responses in local and
436 regional fisheries.

437 Climate change may be contributing to the recent eastward shift in squid distribution in the English
438 Channel, as is the case for distribution shifts in other cephalopod populations (Oesterwind et al., 2022)
439 and indeed in the distributions of various fish species in this region (Auber et al., 2017; McLean et al.,
440 2018; Lima et al., 2022). Continued monitoring will be needed to confirm this hypothesis.

441

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617 **Figure captions**

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

620 Figure 2. The 33 ICES rectangles of the English Channel (division 7E and 7D). Four rectangles (30E6,
621 30E7, 30E8 in the English coast and 27F0) were excluded from the analysis because very few data were
622 available. Rectangle 27E8 overlaps into ICES division (27E8.E and 27E8.D) and because of this, is split
623 into two distinct rectangles. In total, 30 rectangles were considered in the analysis. Red crosses represent
624 the barycentres associated with each rectangle.

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

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

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

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

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

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

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

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