
Inferring the annual, seasonal, and spatial distributions of marine species from complementary research and commercial vessels' catch rates

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Abstract :

The objective of this study is to analyse at fine scale the annual, seasonal and spatial distributions of several species in the Eastern English Channel (EEC). On the one hand, data obtained from scientific surveys are not available all year through, but are considered to provide consistent yearly and spatially resolved abundance indices. On the other hand, on-board commercial data do cover the whole year, but generally provide a biased perception of stock abundance. The combination of scientific and commercial catches per unit of effort (CPUEs), standardized using a delta-generalized linear model, allowed to infer spatial and monthly dynamics of fish distributions in the EEC, which could be compared with previous knowledge on their life cycles. Considering the scientific survey as a repository, the degree of reliability of commercial CPUEs was assessed with survey-based distribution using the Local Index of Collocation. Large scale information was in agreement with literature, especially for cuttlefish. Fine scale consistency between survey and commercial data was significant for half of the 19 tested species (e.g. whiting, cod). For the other species (e.g. plaice, thornback ray), the results were inconclusive, mainly owing to poor commercial data coverage and/or to particular aspects of the species biology.

Keywords : commercial data, Eastern English Channel, seasonality, spatial distribution, survey data.

31 **1. Introduction**

32 Ecosystem-Based Fisheries Management (EBFM) requires enhancing knowledge of
33 ecosystem functioning, therefore allowing forecasting the impact of fisheries on salient
34 ecosystem components (Long *et al.*, 2015) and to design future management plans and tools
35 including Marine Protected Areas (Meyer *et al.*, 2007) or fishing closures (Hunter *et al.*,
36 2006). This necessitates a stepwise approach, the first tier of which, and one of the most
37 important, is to gain fine scale knowledge on the seasonal and geographic distribution of
38 marine organisms, in general, and fish stocks in particular (Booth, 2000).

39 Scientific surveys have been implemented for decades to derive spatially- and yearly-resolved
40 abundance indices of commercial fish and shellfish species (e.g. van Keeken *et al.*, 2007).
41 Surveys provide abundance indices, derived from standardized and controlled protocols,
42 which allow for a wide spatial coverage associated with a weak selectivity (Verdoit *et al.*,
43 2003). Survey data, however, are costly to obtain and therefore rarely provide for adequate
44 seasonal coverage of the resource distribution. In contrast, information derived from
45 commercial fisheries are generally available all year through. Consequently, the catch per unit
46 of effort (CPUE), the most common and easily collected fishery-dependent index of
47 abundance (Maunder and Punt, 2004), has the potential to reflect fish distributions. However,
48 commercial CPUEs can generally not be used directly as abundance indicators. This is
49 because fishers target rather than sample fish densities, and continuously adapt their activities
50 to prevailing conditions, through technological development and tactical adaptations (Marchal
51 *et al.*, 2006), including discarding practices on which information is often limited (Rijnsdorp
52 *et al.*, 2007).

53 A major challenge for fisheries scientists is then to reconcile fisheries-independent and -
54 dependent information into abundance indices that consistently mirror the annual, seasonal
55 and spatial dynamics of commercial marine species. Kristensen *et al.* (2014) have

56 reconstructed spatial and seasonal cohorts of cod (*Gadus morhua*) in Skagerrak by kriging, in
57 both time and space, data provided by survey and also by fisheries subject to a survey-like
58 sampling protocol. To our best knowledge, however, no method has yet been developed to
59 estimate spatio-temporal distributions of fish at high resolution, by combining survey and true
60 commercial fisheries data.

61 The main objective of this paper is to provide detailed annual, seasonal and spatial
62 distributions of major Eastern English Channel (EEC) commercial fisheries resources, using a
63 novel approach combining fisheries-independent and -dependent information. The gain in
64 knowledge on fine scale temporal and spatial fish distribution in the EEC will expand the
65 scope of earlier results (e.g. Vaz *et al.*, 2007), and strengthen the science support to an EBFM
66 in this area. To that purpose, we (i) inferred the seasonal and spatial abundance distribution
67 based on survey and commercial abundance data for several species in the EEC, (ii)
68 investigated the degree of similarity of fine scale spatial distributions derived from these two
69 data sources and (iii) investigated abundance indices derived from these data sources.

70

71 **2. Material and methods**

72 **2.1. Study area**

73 The Eastern English Channel (ICES subdivision VIIId) is delimited by latitudes 49.3°N and
74 51°N and longitudes 2°W and 2°E (Figure 1). This shallow area constitutes a corridor
75 between the northeast Atlantic Ocean and the North Sea, and a strategic region in the
76 northeast Atlantic, as it hosts a very intense maritime traffic and human activities such as
77 mixed fisheries, aggregate extraction and wind farms (Dauvin, 2012). This area is also
78 important for several commercially important migratory species, e.g. red mullet (*Mullus*
79 *surmuletus*) (Mahé *et al.*, 2005), cuttlefish (*Sepia officinalis*) (Royer *et al.*, 2006), mackerel

80 (*Scomber scombrus*) (Eltink *et al.*, 1986), herring (*Clupea harengus*) (ICES, 2015), or
81 European seabass (*Dicentrarchus labrax*) (Pawson *et al.*, 2007).
82 Fishing is a key socio-economic activity in the region (Carpentier *et al.*, 2009), which has also
83 generated a strong pressure on its marine ecosystem (Molfese, 2014).

84 **2.2. Data**

85 This study is supported by two main data sources: a scientific survey (the Channel Ground
86 Fish Survey – CGFS; Coppin and Travers-Trolet, 1989) and observations on-board
87 commercial vessels (hereby referred to as the OBSMER French programme; Cornou *et al.*,
88 2015).

89 The CGFS has sampled the entire EEC demersal community annually since 1988. The survey
90 occurs every year in October, with a systematic fixed sampling design of 88 trawling stations
91 located between 49.3°N and 51.3°N. The sampling gear is a GOV trawl with 3 m vertical
92 opening, 10 m horizontal opening and a 20 mm codend. For each haul, all fish caught are
93 sorted, identified and measured to the nearest inferior centimetre. In case of large catch,
94 random subsampling is performed while ensuring representativeness of species and length
95 distributions. For the current study only survey data from 1998 to 2014 were retained as this
96 period corresponds to a relatively stable state of the community structure with no detected
97 regime shift in species spatial distributions (Auber *et al.*, 2015).

98 The CGFS provides information for a large panel of economically valuable demersal fishes
99 and cephalopods, i.e. European seabass, red mullet, cod, whiting (*Merlangius merlangus*),
100 plaice (*Pleuronectes platessa*), cuttlefish, squids (*Loligo* spp.) and thornback ray (*Raja*
101 *clavata*). Other commercially important species such as common sole (*Solea solea*), herring
102 or sardine (*Sardina pilchardus*), are poorly sampled by the GOV trawl (Carpentier *et al.*,
103 2009), and thus have not been considered in this study.

104 On-board observer programmes allow estimating catch and effort for a sample of fishing
105 operations. Unlike other fisheries data collection programmes, e.g. building on port sampling
106 and/or mandatory logbooks, observer's data are precisely geo-referenced and allow inferring
107 the total catch, including the discarded fraction, and more accurate measurements of effective
108 fishing effort. Although on-board fisheries data can generally not be collected for all the
109 vessels belonging to a given fleet, and although the presence of observers may be perceived as
110 overly intrusive to fishers, they offer an opportunity to derive CPUE-based abundance
111 indicators, at a fine spatial and temporal scale.

112 The OBSMER programme covers the period 2003-2015. It was developed to better estimate
113 the discards' quantity and assess catch composition. Precise information on ship
114 characteristics (e.g. homeport, length, engine power), fishing activity (time, latitude,
115 longitude, gear, fishing effort, targeted species assemblage) and catch composition (landings
116 and discards of fish and commercial invertebrates) are collected for each fishing operation by
117 scientific observers. For each fishing operation, a subsample of the catch (including both the
118 part to be landed and the part to be discarded) is sorted, identified and measured. This data
119 compilation has already been operated to characterize pressures exerted on communities,
120 discarded fractions of catches, or discarding drivers (Fauconnet *et al.*, 2015).

121 Spatio-temporal species distributions estimated using OBSMER data are primarily expected
122 to corroborate previous knowledge on these species' life cycles. In addition, they could reflect
123 species distributions as observed using scientific surveys (considered as a reference) in
124 converging time lapse. However, because species' spatial distributions are dynamic and vary
125 from one time step to another, and because fishers continuously adapt to prevailing conditions
126 (Eigaard *et al.*, 2014), time and spatial variations in CPUE reflect two entangled signals
127 prompted by fisher's plasticity and stock fluctuations. Using CPUEs to reflect time changes in

128 stock abundance therefore requires to preliminarily filter out the skipper effect signal it
129 originally contains (Maunder and Punt, 2004).

130 **2.3. Standardizing survey and commercial catch rates**

131 Surveys and commercial fisheries operate at different temporal and spatial scales, with
132 different gears and strategies, thereby targeting dissimilar species assemblages and/or size
133 ranges. The first step of this study was to identify common temporal and spatial scales, then to
134 select a common pool of representative species and size ranges, and finally to standardize
135 survey and commercial catchabilities using a delta- Generalized Linear Model (GLM)
136 approach.

137 The temporal scale retained is the month, while the spatial scale considered is cells of $0.3^\circ \times$
138 0.3° (~ 700 km²). These seasonal and spatial scales result from a trade-off between having a
139 sufficient amount of data and maintaining a sufficient level of precision, as described further.

140 Based on these small-scale spatio-temporal units, a mean CPUE index in number of
141 individuals caught per hour is calculated separately from OBSMER data for each month and
142 from CGFS data (only for October) for a set of demersal species (Table 1). These species
143 have been selected based on their economic importance, relative abundance and/or
144 catchability by the survey gear being considered. Survey data were only kept from 2005 to
145 2014 for the cephalopods (i.e. *Sepia officinalis* and *Loligo* spp.), as no length information is
146 available for these species before 2005. To harmonize the survey and commercial gears'
147 selectivities of the species being considered, we used a common length threshold (L_s) above
148 which a species is considered to be correctly selected by the different gears (Table 1). L_s was
149 graphically determined from length distribution for each species following the method used
150 by Ravard *et al.* (2014): in commercial data most of the length-frequency were unimodal and
151 L_s was approximately set for each species at the length of the highest mode of the different
152 gears combined. In our study, L_s mainly corresponded to the official minimum landing sizes

153 for the few species concerned. The potential case of a different selectivity of large individuals
154 to particular gears (e.g. Bertignac *et al.*, 2012) is not considered in this study.

155 OBSMER data were filtered to avoid abundance overestimation. Thus, for each species and
156 each size, only hauls with all the subsamples representing at least 5% of the total catch
157 weights each were kept for further calculations. Furthermore, to obtain a clear overview of
158 abundance for each demersal species being studied, only fishing gears sufficiently represented
159 (i.e. > 10 observations for a given species) were kept in the analysis.

160 Finally, we adjusted the remaining catchability differences by standardizing CPUE values
161 derived from both OBSMER and survey data. This was operated by applying a delta-GLM to
162 the CPUEs of each species under consideration. The delta-GLM first fits the probability of
163 observing a zero catch as a function of the explanatory variables, and then fits another GLM
164 to the non-zero catches (Maunder and Punt, 2004; Meissa *et al.*, 2008; among others).

165 The probability of presence is based on the binomial distribution after a binary recoding
166 (0=absence and 1=presence). For hauls with positive CPUE a logarithmic transformation was
167 first applied on data in order to homogenize variances and to transform the multiplicative
168 effects into additive effects (Meissa *et al.*, 2008).

169 The delta-GLM for OBSMER data contains a maximum of six explanatory variables:

$$170 \text{logit}(p_{i,a,m,y}^{>0}) = \beta_a \delta_m + \lambda_y + \rho_g \tau + v_s \quad (1)$$

$$171 \text{log}(IA_{i,a,m,y}) = \beta_a \delta_m + \lambda_y + \rho_g \tau + v_s + \varepsilon_{i,a,m,y} \quad (2)$$

172 where $p_{i,a,m,y}^{>0}$ is the mean presence probability and $IA_{i,a,m,y}$ the CPUE of a species caught by
173 vessel i of length τ rigged with gear g (e.g. bottom otter trawl, trammel net), fishing in (0.3° x
174 0.3°) area a , year y and month m . β_a is the area effect of the fishing operation (treated as
175 factor), δ_m is the month effect of the fishing operation, ρ_g is the gear effect, λ_y is the annual
176 effect, v_s is the sediment effect, which accounts for small scale habitat variability and is

177 decomposed into five categories s : mud, fine sand, coarse sand, gravel and pebble, based on a
178 sediment map of EEC from Larssonneur *et al.* (1982), and $\varepsilon_{i,a,m,y}$ a term of residual error.

179 Sediments are kept because they proved to have the strongest influence on the distribution of
180 species in the shallow Eastern English Channel, compared with, e.g. depth, temperature and
181 salinity (see Carpentier *et al.*, 2009). Engine power information was also available but only
182 vessel length was kept as these two variables are usually highly correlated for bottom otter
183 trawlers ($r = 0.94$ using OBSMER data), the main size-varied vessels of the available
184 commercial data.

185 CGFS survey data are always collected in October (i.e. no month effect) with the same
186 research vessel (i.e. no vessel or gear effects), hence the previous formula was reduced to the
187 following, with a maximum of three explanatory variables:

$$188 \text{logit}(p_{a,y}^{>0}) = \beta_a + \lambda_y + \nu_s \quad (3)$$

$$189 \text{log}(\text{IA}_{i,a,m,y}) = \beta_a + \lambda_y + \nu_s + \varepsilon_{a,y} \quad (4)$$

190 Models' retained explanatory variables were selected for each species based on Akaike
191 information criterion (AIC). Model selection was largely influenced by the previous choice of
192 the spatial resolution for *area* variable.

193 In none of the models (1-4) an interaction term between area (or area-by-month) and year
194 effects was considered. This requires some clarifications, given such an interaction term could
195 potentially reveal spatial shifts in fish distribution over time.

196 In the analysis of commercial CPUE indices, spatio-temporal interactions were partly covered
197 by introducing an area-by-month term. It was, however, not possible to explore the effect of
198 introducing the higher-ranked interaction area-by-month-by-year, partly owing to the limited
199 amount of observations available but also to opportunistic fisher's behaviour, which in
200 combination resulted in a variable inter-annual coverage of the OBSMER dataset. In the
201 analysis of survey abundance indices, only area-by-year effects could potentially be

202 considered, since the CGFS is operated in October only. Auber *et al.* (2015) concluded that
203 although October EEC fish communities were subject to a substantial spatial shift in 1997, no
204 significant change was observed during 1998-2014, i.e. the period being considered in this
205 analysis. Still, we did investigate a model including a spatio-annual effect. According to the
206 AIC none of the presence/absence models and only 3 out of the 19 abundance models showed
207 improved goodness of fit performances when an area-by-year interaction term was added
208 (poor cod, starry smooth-hound and thornback ray), without statistically significant
209 differences in the distribution outputs (Table S1 and S2). Furthermore, 14 out of the 19
210 presence/absence models did not converge with an area-by-year interaction term.

211 Final predictions are obtained by the product of presence probabilities and CPUE. Knowing
212 the sediment characteristics of each area, the total abundance in each cell is computed by
213 reallocating the environmental effects in proportions to sediment types coverage.

214 Finally a limit of 10 observations per cell in both OBSMER and CGFS was determined as the
215 threshold above which the square was kept in the analysis, resulting from a trade-off between
216 a sufficient coverage of the EEC and a consistent number of observations (Figure 2). By
217 applying this limit and our spatial resolution to survey data, 88% of the EEC is covered (for
218 OBSMER data this percentage is variable among month and species). In comparison, using
219 cells of $0.4^{\circ} \times 0.4^{\circ}$ instead of $0.3^{\circ} \times 0.3^{\circ}$ leads to the representation of 90% of the Eastern
220 English Channel, while using smaller cells of $0.2^{\circ} \times 0.2^{\circ}$ only allows representing 68% of the
221 Eastern English Channel. Thus our choice seems to be the best trade-off between precision
222 and coverage.

223 Importantly, the explained variables presented above are likely to include inherent spatial
224 dependence (spatial autocorrelation SAC; Legendre, 1993), owing to the nature of the data at
225 hand. As a result, the values of the dependent variables are unlikely to be conditionally
226 independent as assumed in these models. The SAC inherent to both CGFS and OBSMER data

227 was here accounted for by applying the Moran's Eigenvectors (MEV) mapping method
228 following the protocol described by Cormon *et al.* (2014) with R packages {spdep} (Bivand
229 *et al.*, 2013), {spacemakeR} (Dray, 2013) and {packfor} (Dray *et al.*, 2013). The concept of
230 this method is to allow the translation of the spatial arrangement of the data into a set of
231 explanatory variables through the eigenvector decomposition of data coordinate connectivity
232 matrix previously built (Dormann *et al.*, 2007). For OBSMER data, MEV are computed and
233 selected for each month separately, and then integrated in the whole model set of parameters.
234 Temporal dependencies were not examined in the study.

235 **2.4. Assessing the similarity between fisheries- and survey-based spatial abundance**

236 The data treatment described above allows to produce monthly maps of species abundance
237 distribution. While the global seasonal patterns obtained can be compared with disparate
238 knowledge available for some species, the degree of reliability of the fine scale spatial
239 distribution derived from commercial data can be addressed through comparison to survey-
240 based maps.

241 To quantitatively determine how similar spatial distribution derived from commercial and
242 survey data are at fine scale, we estimated, for October, the local overlap between
243 distributions, using the geostatistical index Local Index of Collocation (LIC, Woillez *et al.*,
244 2009):

$$245 \text{ LIC} = \frac{\sum z_{obsmer}(i)z_{survey}(i)}{\sqrt{\sum z_{obsmer}^2(i) \times \sum z_{survey}^2(i)}} \quad (5)$$

246 where $z_{obsmer}(i)$ and $z_{survey}(i)$ are the computed abundances in area i , as provided by OBSMER
247 and CGFS data, respectively. LIC was computed using R package {RGeostats} (Renard *et al.*,
248 2014). This spatial indicator is considered appropriate to assess local overlapping between
249 two densities of population, without taking the mean abundance into account (Woillez *et al.*,
250 2009).

251 This index theoretically ranges between 0, showing absolutely no match between the two
252 spatial distributions ($z_{obsmer}(i) = 0$ if $z_{survey}(i) > 0$, $z_{survey}(i) = 0$ if $z_{obsmer}(i) > 0$, $\forall i$), and 1,
253 demonstrating a perfect match between them ($z_{obsmer}(i) = z_{survey}(i)$, $\forall i$).

254 The significance of index values was assessed using random permutations of OBSMER
255 abundance values against constant CGFS ones. This procedure is repeated 5000 times, and the
256 spatial distributions derived from commercial data were considered to overlap spatial
257 distributions derived from the CGFS survey when the actual LIC value was above the 95th
258 percentile of the LIC randomly permuted values.

259 The Horn's index (Horn, 1966) was also tested for the study, but it provides approximately
260 the same results and is less efficient with extreme values of abundance, thus only results
261 based on LIC are presented.

262 Finally, to assess the sensitivity of our results to the set of areas being considered, a jackknife
263 resampling was operated for all species, by removing sequentially each area, and by
264 evaluating its impact on LIC significance.

265 **2.5. Comparing yearly abundance indices**

266 Additionally to the spatial abundance, the model provides a year effect that can be used to
267 derive an inter-annual abundance index in both survey and OBSMER data following the
268 method of Lo *et al.* (1992). The time series ranges from 1998 to 2014 for survey data (2005-
269 2014 for cephalopods series) and from 2003 to 2015 for OBSMER data. It is obtained by
270 varying only the year parameter on the computation of CPUEs, and taking the mean of all
271 areas in natural space to avoid variance disparities. Pearson's correlation index was computed
272 to quantify the correlation between abundance indices from the two data sources.

273

274 **3. Results**

275 **3.1. Monthly spatial distribution patterns**

276 In the delta-GLM applied to commercial CPUEs, every parameters were kept, with an
277 exception for the sediment parameter in the presence/absence model of cuttlefish (Table S3).
278 However, area-by-month was replaced *by* month alone in the presence/absence models of
279 starry smooth-hound, flounder and John Dory. In the delta-GLM applied to survey CPUEs,
280 the parameters selection is more variable (Table S4). For example, the year parameter is not
281 kept in both presence/absence and abundance models for tub gurnard, and the sediment one is
282 not kept for three species: cod, pouting and tub gurnard. The area parameter was always
283 significant and kept. The monthly spatial distribution of cuttlefish derived from the delta-
284 GLM models applied to commercial and survey CPUEs is presented in Figure 3. This species
285 has been chosen for illustration because it is one of the main species in terms of yields in the
286 EEC (Royer *et al.*, 2006). These maps are partial and do not cover the same areas over all
287 months, owing to varying fisheries distributions. The map presented for October results from
288 survey-based information, hence explaining its wider spatial coverage. Some informative
289 spatial patterns can be evidenced for cuttlefish: their quasi-absence in the EEC from January
290 to March, a coastal aggregation along the French coast in May-June, and a more offshore
291 distribution in October-November indicate the existence of a seasonal migration pattern for
292 this species.

293 **3.2. Comparison of fine scale spatial distributions from survey data and commercial** 294 **data**

295 The fine scale match between the spatial abundances estimated from fisheries and survey has
296 been quantified for each species by computing the LIC value, and testing its significance with
297 5000 random permutations of CPUE abundances. Of the 19 tested species, 9 had a LIC
298 significance above 95%, 6 between 75% and 95%, and only 4 under 75% (Figure 4).
299 Considering 95% significance threshold, survey- and fisheries-based spatial distributions were
300 therefore found to overlap for half of the species under investigation. Although the

301 distribution of LIC values resulting from the permutation tests is variable among species, the
302 results highlight that almost all species with a LIC above 0.6 showed high significance
303 (except John Dory for which the LIC value of 0.67 falls just below the third quartile of
304 permutations), while species with a LIC value smaller than 0.6 showed no significant overlap
305 (except cod with a LIC of 0.52). It can also be noted that John Dory, the only species showing
306 no significant overlap despite a LIC above 0.6, shows a very low variability of LIC in the
307 permutation test.

308 Thornback ray, poor cod, plaice and pouting had the lowest LIC values, under 0.4.
309 Cephalopods species, cuttlefish and squids, had intermediate LIC values of 0.50 and 0.54,
310 respectively, and both were between the median and the 95th percentile. Finally, of the four
311 flatfish species, i.e. common dab, lemon sole, European flounder and plaice, only common
312 dab and lemon sole had a significant LIC.

313 **3.3. Sensitivity to areas**

314 In order to assess the sensitivity of the results obtained, a jackknife resampling was performed
315 and results were analysed in regard to some characteristics of sensitive areas (Table 2). Of the
316 10 species for which no overlap could be evidenced, red mullet was the only one for which
317 LIC became significant by removing one area. Red mullet original LIC significance value
318 compared with permutations was close to 0.05, and dropped below that threshold with the
319 removal of either the first or second top abundance areas as derived from CGFS information
320 (ranked 8th and 4th building on OBSMER data).

321 Among the nine species for which the LIC was significant for all areas being considered, the
322 LIC of seven species became not significant when removing one area (Table 3). The LIC of
323 tub gurnard, common dab, lemon sole, starry smooth-hound and lesser-spotted dogfish were
324 thus sensitive to the absence of one particular area, ranked first or second in abundance. The
325 LIC of cod and black seabream became not significant with the removal of one area among a

326 list of 6 and 8, respectively. Their original p-values, close to the 0.05 threshold (i.e. 0.046 and
327 0.043), can partially explain the high number of sensitive areas.

328 **3.4. Rebuilding of yearly abundance index**

329 The *year* effect derived from each delta-GLM analysis can be considered as a yearly
330 abundance index for each species. Figure 5 displays two examples of different levels of fit
331 between survey and commercial data, ranging from good visual fit, for cod, to poor fit for
332 black seabream. Cod abundance index shows consistent fluctuations in both survey and
333 commercial data, with higher abundance from 2007 to 2009 followed by 4 years of lower
334 abundance. Black seabream abundance index derived from survey displayed a general
335 decrease from 2004 until 2014. in contrast, the index derived from commercial CPUEs shows
336 an increase over this period. The Pearson's correlation index was computed to quantify the
337 link between the two abundance indices produced for each species (Table 4). The results
338 indicated that spatial overlap represented by LIC's significance is not necessarily related to
339 concordant abundance indices time series, as most of the species with a significant LIC value
340 have an intermediate correlation (Figure S1). Black seabream, with a significant LIC, has
341 even the third lowest value for Pearson's correlation metrics.

342

343 **4. Discussion**

344 **Seasonal distribution patterns of the main fishing resources in the EEC**

345 Our results show the usefulness of fisheries data to infer, in combination with surveys, the
346 spatial and seasonal distributions of several species. The spatial and seasonal distribution of
347 cuttlefish, one of the main commercial species for French fleets (Royer *et al.*, 2006), is in
348 agreement with literature. Indeed, from the examination of landings data, cuttlefish adults are
349 known to start migrating in October to spend winter in the Central and Western English
350 Channel, and to be inshore in the Eastern English Channel during summer for feeding and

351 reproduction (Royer *et al.*, 2006). Other remarkable life distribution can be derived from the
352 maps (see Figures S2-S19), like the high winter abundance of squids in the EEC, confirming
353 previous knowledge (Royer *et al.*, 2002), or the quasi-absence of red mullet in the East of the
354 EEC in the beginning of the year while it concentrates in the East central part of the EEC in
355 the end of the year, which adheres to the conclusions of Mahé *et al.* (2005) based on fishers'
356 interviews. On the contrary the spatial distribution of other species remains more stable
357 through the year, e.g. red gurnard in the centre of the EEC, or European flounder inshore
358 except during the winter period, as described by Skerritt (2010). Finally punctual abundance
359 or absence can be detected, like the high concentration of cod along the English coast in June
360 and in the Dover Strait in November, or the high presence of black seabream in the centre of
361 the EEC in February, contrasting with its absence in the eastern part, consistent with Pawson
362 (1995).

363 **Coherence between fisheries-dependent and -independent abundance indices**

364 In addition to the accordance between the global seasonal pattern produced here and the
365 available literature, our results also show that half of the species' spatial distributions
366 exhibited good coherence at fine scale across the two data sources. This conclusion built on
367 an analysis of the LIC overlap metric, the statistical significance of which was quantified
368 using a permutation test. Prior to this study, LIC values were compared with and have been
369 found very close to Horn index values. The Horn index is another overlap metric that is
370 commonly used in trophic ecology, and for which a value > 0.6 is usually considered
371 significant, without further testing (Scrimgeour and Winterbourn, 1987). Our results cross-
372 checked this approach. Except for John Dory (i.e. LIC = 0.67) and cod (i.e. LIC = 0.52), every
373 species' distribution with a LIC above 0.6 were significant. The unexpected outcome obtained
374 for John Dory reveals a shortcoming of the method we applied to assess overlap significance.
375 Indeed, when abundance is homogeneously spread in the entire study area (here the EEC),

376 LIC can be above 0.6 and still non-significant when compared with values resulting from the
377 permutation test. Actually, the LIC (as well as the Horn index) random permutation test can
378 only be efficient with areas of contrasted abundance, as demonstrated by lemon sole or
379 common dab with one area of high abundance contrasting with relatively low values.
380 Therefore, for the evenly distributed John Dory spatial distributions derived from survey and
381 fisheries data can be considered to be close.

382 Concerning the remaining half of species with lower coherence, a number of reasons can be
383 invoked to explain the discrepancies observed. The results of jackknife analysis demonstrated
384 the impact of some influential areas on the result of the LIC, which cannot be observed
385 depending on the fishers' spatial distribution in October, and highlight the sensitivity of using
386 fine scale comparison when high abundance areas are not available. Another issue is a
387 possible non-proportionality between CPUE and abundance (Hilborn and Walters, 1992).

388 Indeed, commercial fisheries are expected to concentrate their activities into attractive areas (
389 Gillis, 2003). This issue was addressed by standardizing CPUEs using a delta-GLM, and by
390 filtering out spatial auto-correlation. Owing to the limited amount of data, however, SAC
391 correlations could not be computed separately for each year. This could be a concern, as
392 species presence in a precise area/season may vary from one year to another. Thus, a more
393 realistic approach could consist of computing SAC separately for each year, which could not
394 be achieved in this study owing to the low number of observations in the dataset. For similar
395 reasons, the CPUE delta-GLM could not be applied to each gear separately. Instead,
396 observations from the different gears were analysed through the same model, where gear type
397 was treated as an explanatory variable. This approach allowed to estimate the overall impact
398 of gears on CPUE. However, more specific effects of gear types on CPUEs (e.g. selectivity,
399 saturation) could not be fully addressed. In particular, the selectivity of large individuals
400 could be a challenge, as the trawl selectivity ogive is sigmoid-shaped, while that of gillnets

401 could be bell-shaped, or bi-normal, reducing the catch of larger individuals (Dickson *et al.*,
402 1995). Among other potential limits, the soaking time of gillnets is much longer compared
403 with trawls, and it is more subject to saturation effect, which could result in an asymptotic
404 relationship between catches and fishing time (Hickford and Schiel, 1996).

405 Still, the lack of overlap between the spatial distributions derived from fisheries-dependent
406 and -independent abundance indices for some species could also be explained by their actual
407 biological and ecological characteristics. These could have strong impact on abundance
408 estimations, particularly if only few observations are available within an area. Based on a
409 scientific protocol, the CGFS sampling strategy is fixed and the timing of the survey almost
410 does not vary from one year to the other. However, the EEC ecosystem constitutes for several
411 species a migration path between the North Sea and the Atlantic Ocean, and this can lead to
412 biased estimates of abundance based on survey conducted at a fixed period. For example, red
413 mullet migrates during fall from the southern part of the North Sea to the Western English
414 Channel (Mahé *et al.*, 2005), but its migration timing appears variable across years
415 (Carpentier *et al.*, 2009), which could lead to high variance in some areas and thus causes
416 difficulties to obtain a clear static mean distribution.

417 Pouting, poor cod, thornback ray and plaice have the lowest LIC in our results. Various
418 species are known to change their behaviour between day and night (Pitcher, 1992), which
419 may affect our results (Fréon *et al.*, 1993). Indeed, pouting are known to have diel activity
420 patterns, forming shoals near wrecks or rocks during the day and disperse during the night for
421 feeding (Jensen *et al.*, 2000). Thornback rays predate also at night and burry in the sand
422 during the day (Wilding and Snowden, 2008). There is evidence that poor cod is mainly
423 caught at night (Gibson *et al.*, 1996). Concerning plaice, differences in catches between day
424 and night are less clear and vary across studies (De Groot, 1971; Arnold and Metcalfe, 1995).

425 Surveys like CGFS occur only during daylight, while about half of the fishing operations are

426 conducted during the night. Including explicitly the time of the day in our model would be a
427 way forward, which would require a larger set of data (Benoît and Swain, 2003). Finally,
428 variability in species distribution can occur by environmentally-driven spatial and annual
429 shifts (Verdoit *et al.*, 2003). As previously evoked, with sufficient data, dealing with these
430 shifts would require interaction parameters, introduced by fixed effects (with associated
431 restrictions, e.g. Thorson and Ward, 2013) or random effects (with corresponding bias-
432 correction, e.g. Thorson and Kristensen, 2016). The high number of presence/absence models
433 that did not converge with an area-by-year interaction can be explained by the small number
434 of observations for each occurrence (i.e. on average 2 per area-by-year), often 0 or 1 for a
435 substantial part of the new parameters. Increasing the number of iteration failed to improve
436 model convergence.

437 In the coming years, the growing collection of data may allow for accommodating such
438 processes, but also fine-scale targeting (e.g. Thorson *et al.*, in press), and hence lead to more
439 reliable abundance estimates per area for a broader coverage of the EEC. A next step could
440 then be to derive spatially-explicit estimations of fish lengths, building on innovative
441 approaches (e.g. Petitgas *et al.*, 2011; Nielsen *et al.*, 2014). These could help to distinguish
442 between mature and non-mature individuals, which are driving fish movement (Pittman and
443 McAlpine, 2001).

444 **Uses of data collected on-board commercial vessels**

445 Another objective of this study was to provide annual series of abundance indices. The
446 comparison between fisheries-dependent and -independent time series suggested contrasted
447 results across species.

448 For species like cod (Figure 5a) and lemon sole, both the spatial and annual abundance
449 distributions derived from fisheries and survey data were reasonably consistent. However,
450 consistent annual trends across the two data sources were not necessarily linked with spatially

451 overlapping distributions, e.g. cuttlefish or red mullet. Potential reasons for the lack of spatial
452 overlap for such species were discussed above.

453 For other species, a good spatial overlap between fisheries-dependent and -independent
454 abundance distributions was not necessarily associated with synchronous time series (e.g.
455 black seabream, Figure 5b). This could be owing to data limitations, but also to some
456 hyperstable relationship between abundance and CPUE (Hilborn and Walters, 1992), that
457 could not be completely filtered out by our standardization approach. In addition, the species
458 which present a good spatial overlap can be subject to intra-annual fluctuations of abundance
459 owing to high exploitation, migrations and recruitment (Gillis and Peterman, 1998), that could
460 strongly impact the mean annual abundance value.

461 Finally, abundance indices derived from fisheries data could be an appropriate source of
462 information to provide seasonal and spatial distributions, particularly during periods where
463 surveys do not operate. A better overview of species migrations is first a progress in current
464 knowledge on species ecology, which could further be linked with seasonally-explicit abiotic
465 and biotic environmental conditions. Secondly such information could be linked with fishers'
466 movement throughout year, which could enhance our knowledge on fishers-resource
467 interactions. Thirdly, seasonally- and spatially-resolved information such as that output from
468 this study could also serve to calibrate complex end-to-end models such as Atlantis (Fulton *et al.*,
469 2007), OSMOSE (Shin and Cury, 2001), ISIS-Fish (Pelletier *et al.*, 2009) or Ecospace
470 (Walters *et al.*, 1999), and enhance their capacity to evaluate ecosystem-based management
471 strategies (e.g. closed areas and seasons). Finally, further studies could validate the
472 assumptions that on-board commercial data give a better overview of spatial distributions than
473 survey for a small portion of species (e.g. pouting). However, the distributions derived for
474 species presenting strong variability in selectivity or behavioural pattern (e.g. diel variations
475 or migrations) should be interpreted with caution.

476 In addition to spatial distributions, annual abundance indices derived from fisheries data could
477 potentially complement the survey-based series used in stock assessments. This would
478 require, as a follow-up to this study, to structure those fisheries-based annual indices by
479 length and/or age, and perhaps to try to obtain such indices on a shorter duration than year.
480 Previously, fisheries-based abundance indices should be closely examined, on a case-by-case
481 basis, cognisant of the life cycle and exploitation features of the species under investigation.

482

483 **5. Conclusion**

484 This study shows the potential of combining fisheries-dependent and -independent data to
485 increase our knowledge on the seasonal and spatial distribution of several marine species.
486 Even if the comparisons realized during this study showed that fisheries-dependent data did
487 not always mirror the time and spatial survey-based distribution of some species, they still
488 remain a valid source of information. Fisheries-dependent data are relatively abundant,
489 opportunistic and cheaper than survey data, and their use should be encouraged, especially to
490 reflect abundance distributions in areas and seasons that are not covered by surveys.
491 Moreover, some species are poorly sampled by surveys owing to their diel behaviour, and the
492 use of at-night observations on-board commercial vessels could help better inferring their
493 spatial distributions. The method we used here is relatively simple compared with, e.g. log-
494 Gaussian Cox model method developed by Kristensen *et al.* (2014). Still, the quality of the
495 resulting outputs we presented was assessed, and these provide valuable information on
496 spatial and temporal species distributions, which concur with existing ecological knowledge.
497 This approach would benefit from a better spatial representation along the English coastline,
498 and further cooperation, data sharing and on-board observation program strengthening could
499 substantially enhance our understanding of the spatio-temporal distribution of marine species
500 in the Eastern English Channel.

501 **Supplementary material**

502 The following supplementary material is available at ICESJMS online: one table for
503 parameters of survey data models incorporating spatio-temporal interactions, one table for
504 comparison between models with and without spatio-temporal interactions and two tables of
505 parameters chosen for each species in the commercial data and survey data Delta-GLM. It
506 also contains additional abundance index from the two sources of data. Finally it contains
507 additional maps of the 18 species not presented in the study.

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518

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697

698 **Table 1.** List of species considered in this study, with their minimum total length L_s (cm),
 699 above which individuals are considered to be equally selected by survey and commercial
 700 gears, and Minimum Landing Size (MLS) during the 2003-2014 period in Eastern English
 701 Channel when relevant.

species	L_s (cm)	MLS (cm)	Common name
<i>Chelidonichthys cuculus</i>	22	-	Red gurnard
<i>Chelidonichthys lucerna</i>	26	-	Tub gurnard
<i>Dicentrarchus labrax</i>	36	36	European seabass
<i>Gadus morhua</i>	35	35	Atlantic cod
<i>Limanda limanda</i>	21	-	Common dab
<i>Loligo</i> spp.	14 ^a	-	Squids
<i>Merlangius merlangus</i>	24	27	Whiting
<i>Microstomus kitt</i>	25	-	Lemon sole
<i>Mullus surmuletus</i>	20	-	Red mullet
<i>Mustelus asterias</i>	60	-	Starry smooth-hound
<i>Platichthys flesus</i>	29	-	European flounder
<i>Pleuronectes platessa</i>	25	27	European plaice
<i>Raja clavata</i>	49	-	Thornback ray
<i>Scyliorhinus canicula</i>	54	-	Lesser-spotted dogfish
<i>Sepia officinalis</i>	13 ^a	-	Common cuttlefish
<i>Spondylisoma cantharus</i>	17	-	Black seabream
<i>Trisopterus luscus</i>	25	-	Pouting
<i>Trisopterus minutus</i>	13	-	Poor cod
<i>Zeus faber</i>	21	-	John Dory

^a mantle length

702

703

704

705 **Table 2.** Jackknife results and main data attributes for species that did not initially
706 demonstrate significant overlap between OBSMER and Channel Ground Fish Survey (CGFS)
707 distributions. LIC: original value of Local Index of Collocation. p-value: situation of the LIC
708 value related to the distribution of permutation tests (values below 0.05 indicate significant
709 overlap). JK: number of areas which prevented from having significant overlap (with total
710 number of areas). % abundance OBSMER & CGFS: percentage of abundance represented by
711 these sensitive areas among all OBSMER and CGFS areas respectively (with ranking among
712 all areas).

	LIC	p-value	JK	% abundance OBSM	% abundance CGFS
Seabass	0.49	0.156	0 (24)	/	/
Squids	0.54	0.440	0 (20)	/	/
Red mullet	0.58	0.063	2 (23)	5.8 (4/23) 3.7 (8/23)	12.4 (2/23) 19.2 (1/23)
Flounder	0.47	0.118	0 (21)	/	/
Plaice	0.32	0.194	0 (24)	/	/
Thornback ray	0.22	0.703	0 (22)	/	/
Cuttlefish	0.50	0.248	0 (21)	/	/
Pouting	0.39	0.108	0 (23)	/	/
Poor cod	0.10	0.768	0 (21)	/	/
John Dory	0.67	0.259	0 (24)	/	/

713

714

715 **Table 3.** Jackknife results and main data attributes for species that did initially demonstrate
716 significant overlap between OBSMER and Channel Ground Fish Survey (CGFS)
717 distributions. LIC: original value of Local Index of Collocation. p-value: situation of the LIC
718 value related to the distribution of permutation tests (values below 0.05 indicate significant
719 overlap). JK: number of areas which allowed having significant overlap (with total number of
720 areas). % abundance OBSMER & CGFS: percentage of abundance represented by these
721 sensitive areas among all OBSMER and CGFS areas respectively (with rank among all areas).

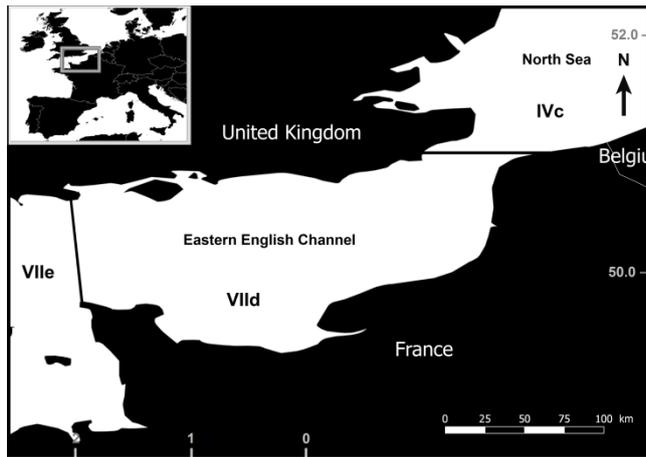
	LIC	p-value	JK	% abundance OBSM	% abundance CGFS
Red gurnard	0.83	6e-04	0 (24)	/	/
Tub gurnard	0.79	0.016	1 (24)	11.1 (2/24)	11.3 (1/24)
				1.9 (2/24)	0.7 (19/24)
				0.0 (23/24)	1.2 (14/24)
Cod	0.52	0.046	6 (24)	45.3 (1/24)	10.6 (2/24)
				0.2 (20/24)	0.5 (20/24)
				3.8 (7/24)	2.3 (12/24)
				0.0 (24/24)	3.4 (10/24)
Common dab	0.66	0.019	1 (23)	22.2 (1/23)	43.1 (1/23)
Whiting	0.71	0.030	0 (23)	/	/
Lemon sole	0.65	0.021	1 (22)	25.5 (1/22)	27.1 (1/22)
Starry smooth-hound	0.62	0.046	1 (22)	14.9 (3/22)	25.9 (1/22)
Lesser-spotted dogfish	0.63	0.020	1 (24)	27.9 (1/24)	12.2 (2/24)
				0.2 (18/23)	1.0 (17/23)
				0.0 (20/23)	0.1 (22/23)
				0.0 (21/23)	0.1 (21/23)
Black seabream	0.67	0.043	8 (23)	0.2 (17/23)	0.3 (20/23)
				0.0 (22/23)	0.0 (23/23)
				7.8 (5/23)	12.6 (3/23)
				0.0 (23/23)	1.6 (13/23)
				14.8 (2/23)	12.7 (2/23)

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724 **Table 4.** Correlation between Channel Ground Fish Survey (CGFS) and OBSMER annual
725 abundance indices assessed by Pearson's correlation index (Pearson). LIC values are also
726 reported for 18 species Eastern English Channel species. Tub gurnard is not represented
727 because the year effect was not significant ($p > 0.05$) in the survey model. * emphasizes
728 species for which spatial overlap was significant ($p < 0.05$).

Common name	Pearson	LIC
Poor cod	0.81	0.10
Cod	0.72	0.52*
John Dory	0.71	0.67
Red mullet	0.66	0.58
Plaice	0.65	0.32
Lemon sole	0.63	0.65*
Cuttlefish	0.51	0.50
Common dab	0.24	0.66*
Red gurnard	0.20	0.83*
Whiting	-0.01	0.71*
Starry smooth-hound	-0.05	0.62*
Thornback ray	-0.08	0.22
Squids	-0.12	0.54
Pouting	-0.13	0.39
Lesser-spotted dogfish	-0.22	0.63*
Black seabream	-0.23	0.67*
Flounder	-0.27	0.47
Seabass	-0.50	0.49

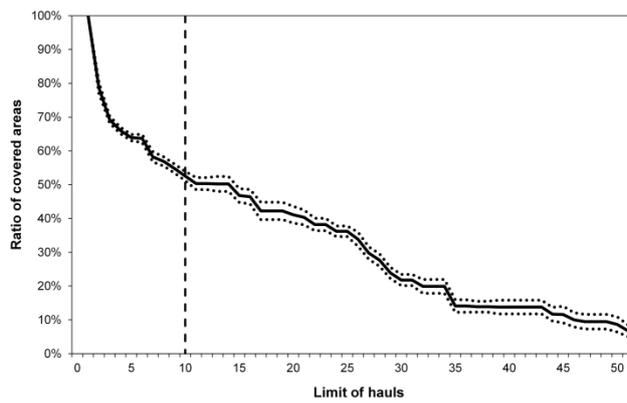


730

731 **Figure 1.** Study area of the Eastern English Channel, corresponding to the ICES division

732 VIIId.

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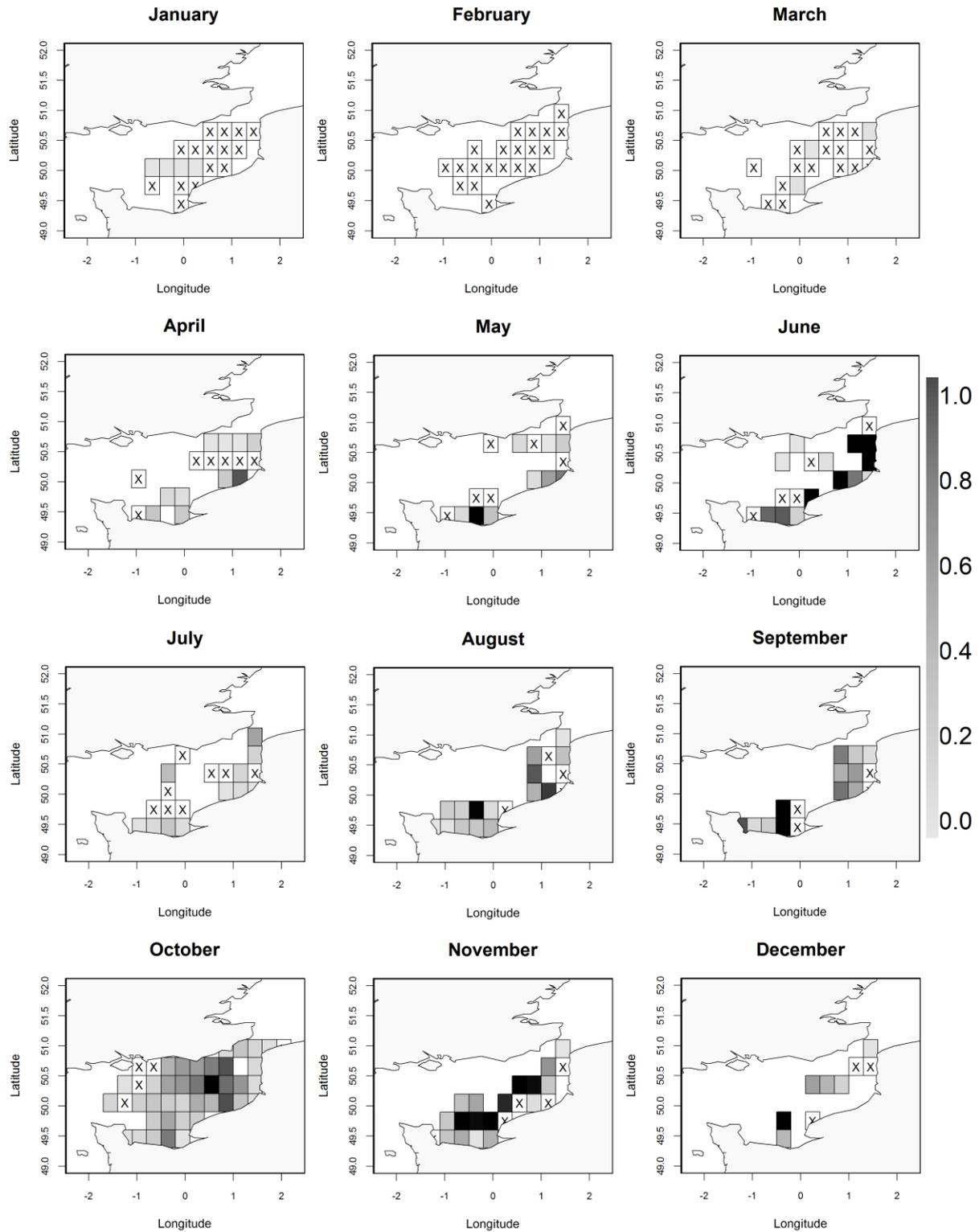
734

735 **Figure 2.** Mean percentage of cells kept in the analysis according to the minimal threshold of

736 hauls set per cell. Dotted lines represent the standard deviation along the 19 species. Dashed

737 vertical line represents the chosen limit of 10 observations.

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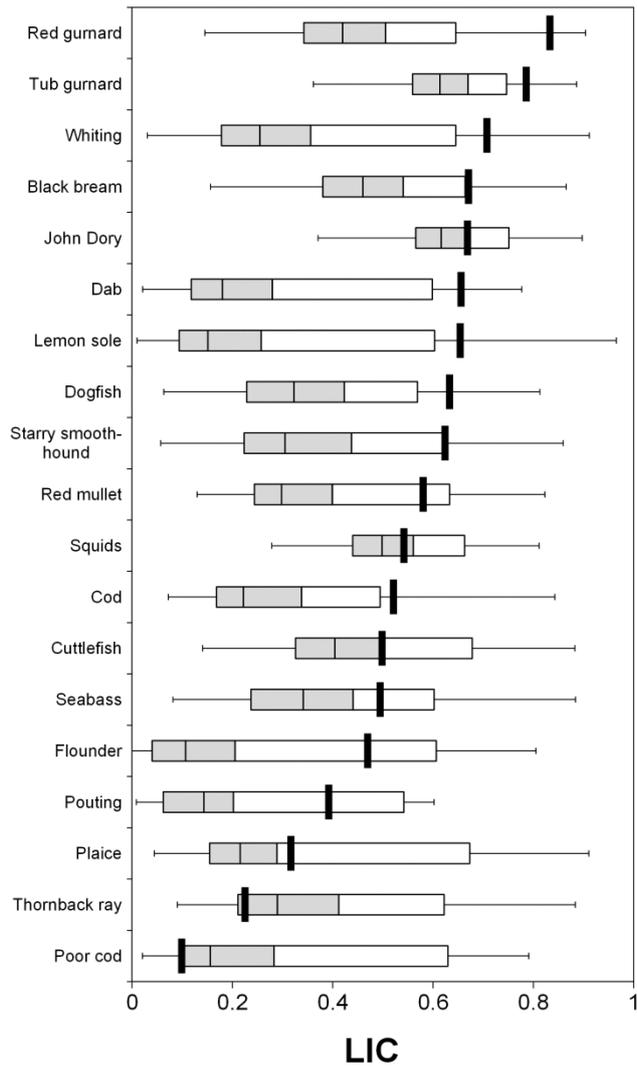
Figure 3. Monthly spatial abundance distribution estimated from OBSMER and CGFS for

741

cuttlefish. 'X' represents areas where no cuttlefish was ever fished during a month in the

742

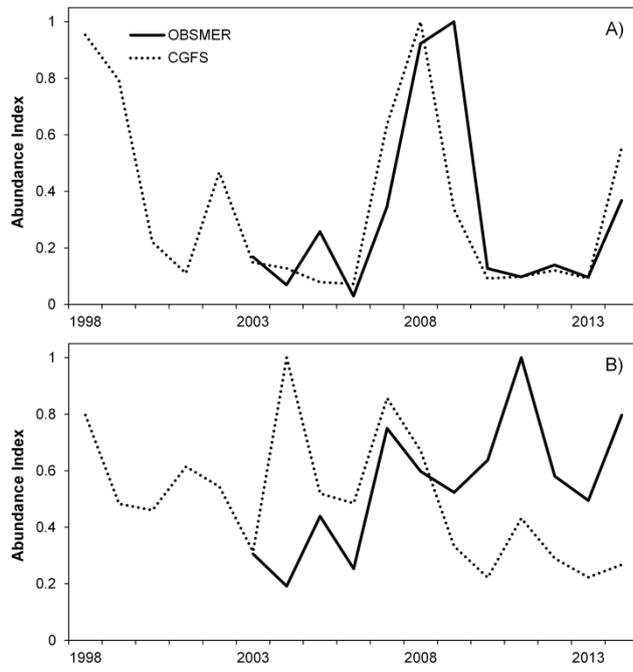
database.



743

744 **Figure 4.** Actual Local Index of Collocation of the 19 species investigated in the Eastern
 745 English Channel (bold black line), compared to the distribution of 5000 randomly simulated
 746 LICs (permutation test). Minimum and maximum simulated LIC are represented by the short
 747 segments. Grey boxes represent Q1, median and Q3 ranges of simulated LICs. The white box
 748 represents the range of values between Q3 and the 95th percentile of simulated LICs.

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750

751 **Figure 5.** Annual abundance index estimated from Channel Ground Fish Survey (CGFS;
 752 dotted line) and OBSMER (solid line) for A) cod and B) black seabream.

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