

Modelled distributions of ten demersal elasmobranchs of the eastern English Channel in relation to the environment

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Abstract:

Generalised Linear Models, combined with a Geographic Information System, were used to map the habitats of ten demersal elasmobranch taxa (five skates, four sharks and a stingray) in the eastern English Channel, based on an annual fishery-independent bottom trawl survey conducted each October, and covering 21 years. Habitat models showing mean density levels were developed for the most frequently occurring species, whilst binomial occurrence habitat models were built for less frequent species. The main predictors of elasmobranch habitats in the eastern English Channel were depth, bed shear stress and salinity, followed by seabed sediment type and temperature. Habitat maps highlighted contrasting habitat utilisation across species. *Raja clavata*, and to a lesser extent *Scyliorhinus canicula*, showed ontogenetic differences in habitat utilisation, with early life history stages found in shallow coastal waters, sheltered from strong tidal currents and typically with softer sediments. Spatial segregation by sex was also evident for *S. canicula*, with females found at higher densities on some harder grounds in the study area. An improved knowledge of habitat utilisation by elasmobranchs (particularly for important life history stages and all seasons) is required if spatial management is to be considered for these species.

Highlights

► GLMs and GIS were used to map the habitats of five skates, four sharks and a stingray. ► Predictors used included depth, sediment type, bed stress, temperature and salinity. ► Habitat maps highlighted contrasting habitat utilisation across elasmobranch species. ► Two species showed ontogenetic differences in habitat utilisation. ► Spatial segregation by sex was found for one species.

Keywords: Channel Ground Fish Survey ; Chondrichthyes ; Elasmobranchii ; GLM ; Grande Overture Verticale ; Trawl survey

1. Introduction

Species distribution modelling is widely used in terrestrial and aquatic systems to predict species occurrence and to better understand the processes influencing their geographical distributions. It can also be used to assist in conservation planning and population management, and to study the effects

49 of changing environmental conditions on biogeographical patterns (Guisan and Zimmermann, 2000;
50 Thuiller et al., 2005; Guisan and Thuiller, 2005; Ramirez-Bastida et al., 2008; Vaz et al., 2008; Seo
51 et al., 2009). Species distribution models have also been called habitat models (Elith and Leathwick,
52 2009) and, in the present study, habitat is seen as species-centred and environment-based, i.e. how
53 the environment controls the spatial distribution of a species (Planque et al., 2011). This description
54 of habitat is derived from the theoretical niche concept, in which the niche is defined as a property
55 of the species in relation to its environment (Hutchinson, 1957).

56

57 Habitat models are commonly developed from numerical estimates of species' responses (e.g.
58 occurrence, density) to changes in one or more environmental variables. A number of approaches
59 have been developed to model the habitat of terrestrial and aquatic species, such as Generalized
60 Additive Models (GAMs), neural networks, environmental envelopes and boosted decision trees
61 (Guisan and Zimmermann, 2000; Elith et al., 2006). Generalized Linear Models (GLMs,
62 McCullagh and Nelder, 1989), in particular, have been used successfully to predict the mean
63 response of various species to environmental predictors. When different processes are thought to
64 govern occurrence and density levels, a two-step approach can be followed (Stefánsson, 1996;
65 Lauria et al., 2011) whereby a *binomial* occurrence model (obtained through logistic regression) is
66 used to balance a non-null density (or *positive*) model. The binomial model predicts the probability
67 of presence of the species from input data either coded as presence (1)/absence (0), or from
68 proportions, while the positive model predicts densities from the presence subset of the input data,
69 i.e. sampling points with non-null density. The resulting combined, or *delta*, model predicts mean
70 density levels for that species.

71

72 GLMs are flexible in that they can be applied to data that are not necessarily normally distributed,
73 such as those collected during fishery-independent trawl surveys. This is achieved through a link
74 function that ensures data transformation towards linearity and maintains model predictions within a

75 range of values coherent with the original data (Guisan and Zimmermann, 2000). Furthermore,
76 GLMs are suited to cases where there are a large number of zero occurrences in the modelled
77 dataset (Welsh et al., 1996), which is often the case of species sampled during fishery-independent
78 trawl surveys. These surveys, which were designed to optimise the sampling of commercial teleosts,
79 provide some of the only detailed, species-specific information on demersal elasmobranchs (e.g.
80 dogfish, skates and rays) in European waters (Daan et al., 2005; Ellis et al., 2005a,b; Maxwell and
81 Jennings, 2005; Martin et al., 2010), and are also used to evaluate stock status (ICES, 2010b).

82

83 The eastern English Channel (Figure 1A) is a shallow sea area, characterised by a heterogeneous
84 environment (Figure 2) that supports feeding, spawning and nursery areas for a number of marine
85 species, including fish (Pawson, 1995; Vaz et al., 2007; Carpentier et al., 2009). The bathymetry
86 slopes down gradually from the coast, and the depths in mid-channel are 60–80 m. The local
87 hypertidal regime (i.e. the tidal range is > 6 m), and to a lesser extent winds, result in strong
88 hydrodynamics and alternating currents. The French and UK coastlines contribute to forming steep
89 gradients of tidal amplitude, and current speeds (and associated seabed stress) are greatest where the
90 two coastlines are closest (i.e. the Dover Strait and the "narrows", Figure 1A). These tidal gradients
91 also influence the seabed sediments, with harder substrata (gravel and pebbles) where currents are
92 strong, and softer ones (sand and muddy-sand) in areas more sheltered from strong tidal currents
93 (e.g. some bays). The tidal regime, winds and relatively shallow depths result in a well mixed water
94 column throughout the year, meaning that there is neither a thermocline nor major differences
95 between near bottom and surface temperatures and salinities (Pingree, 1980). Offshore waters in
96 October are slightly warmer than the shallow, coastal areas, and there is an arm of less saline water
97 along the French coast due to freshwater inflow from French rivers (Brunet et al. 1992). The eastern
98 English Channel, and its local biodiversity, are also subject to numerous anthropogenic impacts,
99 including shipping, aggregate extraction, aquaculture and fisheries, and eutrophication (Dauvin,

100 2008; Martin et al., 2009). In this context, it is essential to conserve the habitats of sensitive species
101 such as elasmobranchs.

102

103 Elasmobranchs are known to be more vulnerable to over-exploitation than many teleost fish, due to
104 the slow population growth resulting from a late age at maturity, longevity, low fecundity and long
105 gestation period (Stevens et al., 2000; Compagno et al., 2005; Ellis et al., 2008). In the English
106 Channel, a number of elasmobranchs are commercially exploited, including thornback ray *Raja*
107 *clavata*, blonde ray *R. brachyura*, spotted ray *R. montagui* and starry smooth-hound *Mustelus*
108 *asterias* (Pawson, 1995; Carpentier et al., 2009). Although mainly a by-catch in mixed demersal
109 fisheries, some of the larger skates (e.g. *R. clavata*) are targeted in some areas (Carpentier et al.,
110 2009). Other species are of conservation interest, for example undulate ray *Raja undulata* is classed
111 as *Endangered* by the International Union for the Conservation of Nature (IUCN, 2010). Many
112 elasmobranchs segregate by size and/or sex (e.g. Springer, 1967; Pawson, 1995; Wearmouth and
113 Sims, 2008; Bansemer and Bennett, 2011) or aggregate at ecologically-important habitats (e.g. areas
114 of high prey abundance; Jacoby et al., 2011), meaning that important components of the population
115 (e.g. reproductively active females or juveniles) can be distributed more discretely and so
116 potentially subject to localised over-exploitation (Wearmouth and Sims, 2008). However, little is
117 known about habitat utilization of elasmobranchs in this regional sea.

118

119 The present study quantitatively investigated the distribution of ten small demersal elasmobranch
120 taxa (Table 1) in the eastern English Channel in relation to five environmental variables. Data from
121 a fishery-independent bottom trawl survey (collected each October for 21 years) were analysed
122 using a standardized GLM approach coupled with a Geographic Information System (GIS), and
123 environment-based habitat models developed, evaluated and mapped. Model performances were
124 examined in relation to catch frequency, as elasmobranch catches are known to occur at contrasting

125 levels in the study area (Ellis et al., 2005a; Martin et al., 2010). For the three most abundant species,
126 sexual and ontogenetic differences in habitat utilization were also investigated.

127

128

129 MATERIAL AND METHODS

130 **Survey data.** Between 1988 and 2008 and under the auspices of the ICES (International Council for
131 the Exploration of the Sea) International Bottom Trawl Survey Working Group (IBTSWG),
132 IFREMER have carried out the fishery-independent Channel Groundfish Survey (CGFS). This
133 trawl survey (described in ICES, 2010a) takes place in the eastern English Channel (ICES Division
134 VIIId) and provides data to support the assessment of the main commercial fish stocks in the area.

135

136 A total of 60–110 stations (haul duration = 30 min hauls; trawl speed = 3.5 knots) were sampled
137 each October (Figure 1B) on board the *RV Gwen-Drez*. The gear was a small GOV (*Grande*
138 *Ouverture Verticale*) bottom trawl with a high (ca. 3 m) headline height and a cod-end liner of 20
139 mm (stretched mesh) to catch juveniles. Trawling depth (m) was recorded by sensors on-board the
140 research vessel. Since 1997, SCANMAR sensors (Scanmar AS, Norway) have been used to record
141 and maintain net geometry, and a Micrel (San Jose, CA, USA) hydrological probe (attached to the
142 headline of the trawl) used to measure temperature (°C) and salinity (Practical Salinity Units, PSU)
143 every 15 seconds.

144

145 At each trawl station, fish species were sorted, weighed, counted and measured (total length, to the
146 whole cm below for elasmobranchs). Since 1991, elasmobranchs were sexed; sex ratio at individual
147 stations was calculated as the proportion of females (%F). Although nominal data for both common
148 smooth-hound *Mustelus mustelus* and *M. asterias* were available, it is now accepted that the
149 identification based on presence/absence of spots on the body is unreliable for identification (Farrell
150 et al., 2009). Data on these morphologically similar congeners were combined and analysed as

151 *Mustelus* spp., of which *M. asterias* is the more abundant. Elasmobranch densities, or relative
152 abundance, from a total of 1,828 trawl hauls covering the period 1988 to 2008, were expressed as
153 numbers of individuals per km² (ind.km⁻²). For this, swept area was based on a theoretical wing
154 spread of 10 m, which was checked to be close to the average effective wing spread. Survey density
155 data were log-transformed (Log₁₀[x+1], x = density) to reduce the skewed distribution (Legendre
156 and Legendre, 1998).

157

158 **Length at age calculation.** Size (total length) was used as a proxy for age. Lengths at age were
159 calculated using the von Bertalanffy (1938) equation:

$$160 \quad L_t = L_\infty - (L_\infty - L_b) e^{-kt}$$

161 where L_t (cm) is length as a function of time t (year), L_∞ (cm) is the theoretical asymptotic length,
162 L_b (cm) is the length at birth, and k (year⁻¹) is the growth rate constant (Cailliet et al., 2006). Based
163 on the estimated lengths at age and length frequency histograms obtained from survey data,
164 densities for the three most abundant species were recalculated for two age groups (neonate and
165 young; sub-adult and adult) and modelled separately.

166

167 **Other datasets used.** The 1988–2008 density dataset was partitioned into two subsets (1988–1996
168 and 1997–2008) due to the absence of *in situ* temperature and salinity data for the first time period.
169 The recent time period was used for model development and internal evaluation, whilst the earlier
170 time period was only used for external model evaluation. Table 2 lists the various datasets used for
171 the main modelling steps: (i) development (and internal evaluation), (ii) mapping of the predictions,
172 and (iii) external evaluation. The depth map (step ii, Figure 2A) merged bathymetry and mean sea
173 level (corresponding to a mid-tide coefficient) derived from a 3D hydrodynamic model (Le Roy and
174 Simon, 2003; Carpentier et al., 2009). Seabed sediment types (steps i to iii, Figure 2B) came from a
175 digital map of the surface sediments in the English Channel, originally developed by Larsonneur et
176 al. (1979), and in which the original 29 sediment classes were aggregated into five broader classes:

177 mud (M), fine sand (FS), coarse sand (CS), gravels (G) and pebbles (P). Bed shear stress (steps i to
178 iii, Figure 2C) came from an 8-km resolution hydrodynamic model developed originally for the
179 Irish Sea (Aldridge and Davies, 1993), but later extended to cover the north-west European shelf.
180 Bed shear stress (Newton.m^{-2}) is an estimate of the pressure exerted across the seabed by tidal
181 forcing (M2 constituent) and often influences the distributions of marine species (Freeman and
182 Rogers, 2003). A mean sea surface temperature map was produced for the month of October for the
183 period 1997–2008 (step ii, Figure 2D) using satellite-derived (AVHRR sensor) temperature data
184 (Casey et al., 2010). The same source was used to produce annual maps for each October between
185 1988 and 1996 (nine maps in total, step iii). A mean sea surface salinity map for the month of
186 October (steps ii and iii, Figure 2E) was produced by averaging annually interpolated survey maps
187 for the period 1997–2006 (Carpentier et al., 2009).

188

189 **Model development.** The five environmental variables were not collinear (Variance Inflation
190 Factor < 5 ; Zuur et al., 2007), and were tested for significant contribution to the models. Depth and
191 sea surface temperature and salinity were those measured *in situ* during the survey, and seabed
192 sediment type and bed shear stress were derived from Figures 2B and C. Seabed sediment types
193 (categorical variable) were introduced to the models as factors (Legendre and Legendre, 1998). The
194 four continuous predictors were tested as first and second order polynomial terms, based on data
195 exploration plots which suggested that the shape of species-environment relationships would often
196 be better described as curvilinear (Austin, 2002). Interactions between first order continuous
197 predictors were also tested.

198

199 Histograms of relative densities indicated that there was recurring discontinuity between the zero
200 values and positive density data, suggesting a two-step modelling approach. Binomial occurrence
201 models were developed using presence-absence data (or proportions for sex ratio models) as the
202 response variable and a logit link function, to predict the mean presence probability of each of the

203 species considered. Positive models were developed using a subset containing only non-null
204 densities and an identity (Gaussian) link function, to predict the mean density on a log scale. The
205 MASS package (version 7.3-5; Venables and Ripley, 2002) in R (R Development Core Team,
206 2009) was used to select the significant variables and to estimate the parameters of the models.
207 Starting from an initial full model, predictors were removed by backward elimination based on
208 Akaike's Information Criterion reduction (AIC; Akaike, 1974).

209
210 A delta model (combining binomial and positive models) was attempted for each species, as this
211 would reveal which variables influenced its occurrence and density. When the delta model was
212 unsatisfactory (see below for evaluation criteria), only the results of the binomial occurrence model
213 were presented (if satisfactory).

214
215 **Model mapping.** Maps of the five environmental variables (Figure 2) were combined with model
216 parameters within a GIS to predict each species' habitat. To illustrate the species response along
217 any given environmental gradient, presence probabilities, or densities, were predicted by each
218 model, whilst keeping all other continuous variables at their mean value. These 'evaluation strips'
219 (Elith et al., 2005; Vaz et al., 2008) were used to examine model behaviour and to help interpret
220 model results, taking into account different seabed sediment types. Model prediction error (or
221 model uncertainty) was computed as the absolute difference between survey and predicted values,
222 relative to the maximum survey value (i.e. a value of 1 corresponded to the maximum possible error
223 in prediction). These errors were spatially auto-correlated and it was possible to estimate them at
224 non-sampled locations using a variogram describing their spatial structure and variation, and to
225 interpolate them by ordinary kriging (Petigas, 2001). In the case of sex ratio models, the binomial
226 occurrence model was used to balance, within a GIS, the corresponding delta model showing both
227 sexes together, to visualize potential spatial segregations by sex, in density levels.

228

229 **Model evaluation.** Though a key step in the development of habitat models, model evaluation and
230 validation are not always undertaken (see Manel et al., 2001). Additionally, some studies that have
231 tested models have often used the same data for both model development and evaluation (Olden et
232 al. 2002). Here, models were evaluated internally by directly comparing predictions with survey
233 values for the same time period (1997–2008). To evaluate models externally, predictions were
234 compared with survey values for an earlier time period (1988–1996), the data for which had not
235 been used for model development. For the latter, sea surface temperature data were extracted from
236 the satellite-derived annual maps produced for October between 1988 and 1996. Salinity data were
237 extracted from Figure 2E and corresponded to the second time period (1997–2008), and it was
238 assumed that salinity patterns were not significantly different over the two decade timescale
239 considered.

240

241 The predictive power of each model was assessed *qualitatively* using a range of diagnostic plots
242 (Zuur et al., 2007), and also *quantitatively*. Firstly, a Spearman’s rank correlation test investigated
243 whether there was a positive and significant correlation between survey data and predicted values:
244 considered passed if $r_s \geq 0.1$ and $p < 0.05$ (Carpentier et al., 2009; Lauria et al., 2011). Secondly, the
245 proportion of deviance explained by the models, adjusted for the number of variables in the model,
246 was considered sufficient if $\text{adj-R}^2 \geq 0.1$ (Carpentier et al., 2009; Lauria et al., 2011), a value
247 deemed suitable for infrequent to moderately abundant species such as elasmobranchs. Finally and
248 for binomial models, the Receiver Operating Characteristic (ROC) curve (Guisan and
249 Zimmermann, 2000) showed the trade off between prediction sensitivity and specificity, and was
250 considered passed if the Area Under the Curve (AUC) ≥ 0.80 and $p < 0.01$. For delta models, a
251 Wilcoxon signed-rank test assessed whether there was a significant difference between survey and
252 predicted values: considered passed if $p \geq 0.05$ (Lauria et al., 2011). Hence, there were three
253 quantitative criteria for each evaluation dataset (internal and external): (i) adj-R^2 , (ii) Spearman's
254 correlation test, and (iii) Wilcoxon signed-rank test or ROC curve. A model was deemed

255 *satisfactory* if, in addition to suitable diagnostic plots (*qualitative* evaluation), it passed at least three
256 of the six *quantitative* evaluations (three internal and three external).

257

258

259 RESULTS

260 **Input datasets**

261 Of the 1,179 trawl stations sampled from 1997 to 2008 that were available for model development
262 and internal evaluation, *in situ* temperature and salinity data were missing at 33 stations (2.8%), due
263 to equipment failure. The remaining 1,146 stations (Table 3) were associated with all five
264 environmental variables (depth, seabed sediment type, bed shear stress, and *in situ* temperature and
265 salinity).

266

267 Similarly, of the 649 stations available for external evaluation of the model (time period 1988–
268 1996), 94 stations (16.7%) had missing temperature data as a result of cloud cover or proximity to
269 land in the satellite images. Hence, a total of 555 trawl hauls from this time period were used for
270 external model evaluation.

271

272 In the case of the sex ratio model for lesser-spotted dogfish *Scyliorhinus canicula*, model
273 development and internal evaluation were carried out on data from 672 stations, and model external
274 evaluation on data from 258 stations. These subsets represented stations where *S. canicula* occurred.

275

276 Habitat modelling by age group (based on the conversion of length data) was undertaken for three
277 species (*R. clavata*, *S. canicula*, and *Mustelus* spp.) for which it was possible to (i) estimate the
278 length at age from published studies (Table 4), and (ii) form two age groups of sufficiently large
279 sample size (based on the length frequency distributions; Figure 3). Where published biological
280 parameters indicated sexual differences (e.g. *S. canicula* and *Mustelus* spp., references in Table 4),

281 an average length at age was used to identify an appropriate length split between 'neonate and
282 young' and 'sub-adult and adult'. The swimming capabilities and behaviours of smaller and/or
283 younger fish are often markedly different to that of larger, mature individuals, and so the
284 distributions of different cohorts may relate differently to the various physical and biological
285 aspects of their environment, and ontogenetic habitat utilisation can be pronounced. Analyses for *R.*
286 *clavata*, *S. canicula* and *Mustelus* spp. used a length split (L_2) that equated with two year old fish.

287

288 **Modelled habitats for all individuals (lengths and sexes combined)**

289 Six binomial occurrence and four delta habitat models were developed (Tables 5 and 6). Delta
290 habitat models were satisfactorily evaluated for the most frequently occurring species: *R. clavata*
291 (present at 33.5% of hauls), *S. canicula* (58.7% of hauls), greater-spotted dogfish *Scyliorhinus*
292 *stellaris* (15.4% of hauls) and *Mustelus* spp. (30.5% of hauls) (Table 3). For the remaining six
293 species, input data for positive models were limited, ranging from 11 positive occurrences (1.0% of
294 hauls) for small-eyed ray *R. microocellata* to 54 (4.7% of hauls) in the case of tope *Galeorhinus*
295 *galeus*. Despite these low occurrence levels, six binomial occurrence models were developed and
296 evaluated satisfactorily.

297

298 Depth, bed shear stress and salinity were significant predictors of all ten habitat models, whilst
299 seabed sediment type and temperature were important in nine models. Furthermore, the four
300 continuous predictors were often present in the models as second order polynomials, thereby
301 indicating curvilinear relationships. The number of first order interactions retained in the models
302 ranged from one to four. The most frequently selected interaction was that of depth with salinity
303 (selected 13 times), followed by bed shear stress with sea surface temperature, and depth with bed
304 shear stress (both selected 8 times).

305

306 The habitat maps (Figures 4 and 5) and model behaviour (Figure 6 shows the example of *S.*
307 *canicula*) derived from the model equations help inform on the relationship between each species
308 and the environment of the eastern English Channel (Figure 2). The modelled habitat maps of
309 stingray *Dasyatis pastinaca*, *G. galeus*, *R. clavata*, *S. canicula*, *S. stellaris*, and *Mustelus* spp.
310 (Figures 4A, 4F and 5A-D) revealed that these species preferred the hard sediments (gravel and
311 pebbles) that occurred in the central parts of the survey area and in the Dover Strait (Figure 2B).
312 These coarse grounds coincided with zones of intermediate to strong tidal currents (Figure 2C), and
313 deeper waters (Figure 2A). *R. clavata* (mostly juveniles) and *S. canicula* (mostly juveniles and
314 females) also occurred, at lower density levels, on some inshore grounds where seabed sediments
315 were comprised of mud, sand and gravel (Figures 5A and B). In contrast, species such as *R.*
316 *brachyura* and *R. microocellata* preferred more coastal habitats with soft sediments (muddy sand,
317 fine and coarse sands), located in shallower areas that were sheltered from strong tidal currents
318 (Figures 4B and C). Although the habitats of *R. montagui* and *R. undulata* were similar (Figures 4D
319 and E), in that suitable grounds were located both inshore and offshore, *R. undulata* tended to prefer
320 slightly harder sediment types (gravel, pebbles) associated with stronger bed shear stress than *R.*
321 *montagui*, and also occurred mainly in the western parts of the study area.

322

323 All ten models presented in Tables 5 and 6 passed at least three of the six evaluation criteria, with
324 *R. montagui* passing only three and *G. galeus* passing all six. Potential relationships between each
325 species' occurrence levels (estimated as the number of positive occurrences relative to the number
326 of trawl stations) and aspects of the performance of the corresponding habitat model were
327 investigated. The proportion of deviance explained by the model and the number of evaluation
328 criteria passed did not correlate significantly with species' occurrence levels (Spearman's
329 correlation, $p > 0.05$, $N = 10$ models), suggesting that it was not influenced by how frequently a
330 species had been caught. In contrast, the correlations between survey and predicted values were
331 positive and significantly stronger (i.e. higher r_s values) as species increased in occurrence

332 (Spearman's correlation, $N = 10$ models, $df = 8$), for both internal ($r_s = 0.88$, $p < 0.001$) and external
333 ($r_s = 0.82$, $p < 0.01$) evaluations. Finally, the internal evaluation (time period 1997–2008) passed an
334 average of 2.7 tests (range 2-3), compared to 1.5 (range 0-3) for the external evaluation (time period
335 1988–1996).

336

337 Prediction errors associated with each habitat map (Figures 4 and 5) tended to be higher in areas
338 where individuals were caught more frequently, suggesting that density variability in these areas
339 was higher. Conversely, errors were lower in areas where individuals were caught less frequently.
340 This indicated that there was little model uncertainty concerning the extent of the areas where the
341 modelled species was absent.

342

343 **Modelled habitats by age group**

344 To enable direct comparison across age groups (neonate and young; sub-adult and adult) of *R.*
345 *clavata*, *S. canicula* and *Mustelus* spp., models were presented as binomial occurrence models
346 (Table 7), although some age groups had satisfactory delta models.

347

348 The habitat model for sub-adult and adult *R. clavata* (Figure 7B) only passed two evaluation
349 criteria, but was retained for comparison with the model for neonates and young (Figure 7A). The
350 mapped models were almost mirror images of each other, i.e. there was very little overlap between
351 them. The younger age groups occurred primarily in shallow waters along the French and UK
352 coasts, especially in bays (and including areas of slightly lower salinity) where bed shear stress was
353 weak. These areas also coincided with muddy and sandy substrates. In contrast, the habitats of the
354 older age groups were more broadly distributed, including those grounds consisting of harder
355 sediments (gravel, pebbles). These ontogenetic differences in habitat utilization were coherent with
356 the habitat map developed for all individuals (Figure 5A), in which there appeared to be little
357 unsuitable habitat evident across the study area.

358

359 Ontogenetic differences in habitat utilization between neonate and young (Figure 7C) and sub-adult
360 and adult (Figure 7D) *S. canicula* were less conspicuous. The habitat of the older age group was
361 more broadly distributed than that of the younger age group. Younger fish were usually located on
362 softer sediment types (mud, fine sand), closer to the UK and French coasts, whilst the main habitats
363 of the older age group were located further offshore, on harder bottoms (gravel, pebbles), including
364 the Dover Strait. Both age groups of *Mustelus* spp. (Figures 7E and F) had suitable habitats located
365 in deep waters with hard bottoms, although the habitat of neonate and young was more broadly
366 distributed, and included the less saline coastal waters where bottom types were softer (muddy-
367 sand).

368

369 **Modelled habitats of male and female *S. canicula***

370 The binomial model predicting the proportion of female *S. canicula* comprised all five tested
371 predictors (Table 7), and passed all six evaluation criteria. The proportion of females was clearly
372 higher in shallow coastal areas, especially along the English coast (Figure 8A). As a result, derived
373 habitat maps showing the density levels of females and males contrasted significantly. Male habitat
374 (Figure 8C) was very similar to the overall habitat (sexes combined, Figure 5B), with the exception
375 of two areas where densities were lower: one south of the Isle of Wight and the other along the
376 coasts of the Dover Strait. It was in these two areas, with coarser substrata, that female densities
377 were at their greatest (Figure 8B). Female were also found at comparatively moderate density levels
378 in the central waters of the eastern English Channel.

379

380

381 DISCUSSION

382 Groundfish survey data were used to improve our understanding of habitat utilization by ten
383 demersal elasmobranchs in the eastern English Channel, based on a standardized GLM approach

384 using data covering broad temporal and spatial (regional sea) scales. Model parameters helped
385 quantify habitat utilization and reveal important combinations of environmental variables for each
386 species' habitat. The associated habitat maps highlighted contrasting habitat utilization between
387 species. For the first time, a combination of habitat modelling and GIS calculation was used to gain
388 new insights into the spatial ecology of these species in this area, and also in terms of segregation
389 by size (three species) and sex (one species). Despite the zero-inflated nature of some species'
390 datasets, the GLM approach was found to be suitable and relatively straightforward to implement
391 (from model development and evaluation, to mapping), hence providing a practical solution to
392 fisheries managers and conservationists. Modelled habitat maps can be used as inputs in systematic
393 conservation planning (Margules and Pressey, 2000), an approach that is widely used in marine
394 spatial planning, including the design of marine protected area networks in multiple-use areas.
395 Decision-support tools (e.g. Delavenne et al., 2011) often require knowledge of the spatial
396 distribution of the features that are to be conserved, e.g. species and/or habitats. In terms of fisheries
397 management, habitat maps by age could be used to select areas for improved regional management
398 or technical measures (Wiegand et al., 2011).

399
400 **Modelled habitats for all individuals (lengths and sexes combined)**

401 The main predictors of elasmobranch habitats in the eastern English Channel in October were
402 depth, bed shear stress and salinity, followed by seabed sediment type and temperature. Spatial
403 habitat models (based on data from 1997 to 2008) were found to be coherent with spatial patterns
404 mapped by geostatistical interpolation based on data from the same survey (period 1988–2008;
405 Martin et al., 2010). Patterns were also consistent with those from other studies reporting on habitat
406 utilization by the various species (e.g. *R. brachyura*, *R. montagui* and *S. stellaris* in Ellis et al.,
407 2005a; *R. clavata* in Rousset, 1990a, and Hunter et al., 2005; *R. undulata* in Coelho et al. 2003; *S.*
408 *canicula* in Vaz et al., 2008). Earlier studies have observed that *Mustelus* spp. were abundant in
409 coastal areas with fine sediment types (Ellis et al., 2005a), although this was based primarily on

410 observations of juvenile fish, and the trawl survey used in the present study (which also samples
411 larger fish) confirm that coarser grounds are important habitats.

412

413 The frequency of occurrence of a species was a factor in model performance. Indeed, based on the
414 strength of correlation between predicted and survey values, models performed better for the
415 species that were captured more frequently. Indeed, satisfactory delta models were presented for the
416 four most frequent species, whilst the less frequent species were only shown as binomial occurrence
417 models. This was because positive models were based on significantly smaller input datasets,
418 making it difficult to obtain a satisfactory combined model, whilst in a binomial occurrence model,
419 even zeros provide information (i.e. the species was not captured at these locations).

420

421 Internal evaluation passed more evaluation tests than external evaluation. It is likely that several
422 factors contributed to this difference in performance. Firstly, external evaluation was based on an
423 input dataset (555 trawl stations) that was smaller than that used for internal evaluation (1,146 trawl
424 stations). Secondly, as *in situ* salinity data were not available in the external evaluation dataset,
425 salinities from the time period 1997 to 2008 (the period for model development and internal
426 evaluation) were used, and it was not possible to assess how much uncertainty was introduced as a
427 result. Finally, some species showed changes in occurrence and/or density level over time (Martin
428 et al., 2010), with possible effects on associated internal and external model evaluations.

429

430 **Modelled habitats by age group**

431 Of the three species for which possible ontogenetic differences in habitat utilization were
432 investigated, such shifts were clearer for *R. clavata* compared to *S. canicula* and *Mustelus* spp.

433 Given the published lengths at 50% maturity (Table 4) and length frequency histograms (Figure 3),
434 each of the two groups contained multiple age classes. The younger one contained neonates and
435 young juveniles, whilst the older group contained older juveniles, sub-adult and adult fish.

436 Consequently, these ontogenetic differences in habitat utilization were related to size (total length)
437 and not maturity status. Modelling results suggested that the younger age groups of *R. clavata* and
438 *S. canicula* were found in shallow coastal waters, sheltered from strong tidal currents and where
439 seabed sediment types were soft (mud and sand). This was consistent with previous studies in this
440 area and elsewhere (Rousset, 1990b, and Ellis et al., 2005a, for *R. clavata*; Compagno, 1984, and
441 Carpentier et al., 2009 for *S. canicula*). Young fish are likely to be limited in their swimming and
442 competitive abilities, and vulnerable to predators in unsuitable habitats (Jacoby et al., 2011). This is
443 consistent with the results presented here, whereby shallow, coastal waters may offer protection
444 against predation, ample food resources (including smaller prey items) and typically with warmer
445 water to encourage growth (Springer, 1967; Speed et al., 2010). Data presented here are insufficient
446 to conclude that these locations were "nursery" areas for these two species, given that not all areas
447 where juveniles occur can be considered nursery areas (Heupel et al., 2007). It should be noted that
448 egg-cases of *S. canicula* and recently-hatched fish are caught on the hard ground south of the Isle of
449 Wight (Ellis et al., 2005a), as the egg cases are often laid on sessile, filter-feeding invertebrates
450 (Ellis and Shackley, 1997). Hence, there may also be different patterns in the habitat utilization of
451 recently-hatched fish and larger juveniles. Results for *Mustelus* spp. did not show any major
452 ontogenetic difference in habitat utilization, although juveniles were more abundant in shallow,
453 coastal environments. *S. stellaris* was the fourth most abundant species during the period of survey.
454 The egg-cases are known to occur in some inshore areas elsewhere around the British Isles, and the
455 youngest fish are only caught occasionally in groundfish surveys (Ellis et al., 2005a). The lack of
456 length at age data for this species prevented further analysis.

457

458 **Modelled habitats of male and female *S. canicula***

459 *S. canicula* showed clear spatial segregation by sex with higher proportions of females in shallow
460 coastal waters, and on some of the harder grounds (e.g. south of the Isle of Wight). Segregation of
461 *S. canicula* by sex has been reported to operate over both small (Sims et al., 2001; Sims, 2003) and

462 larger scales (Rodriguez-Cabello et al., 2007; Martin et al., 2010). When proportions were brought
463 back to density levels, results presented here suggested that segregation could be at least partly
464 habitat-based (Wearmouth and Sims, 2008), i.e. that there were sexual differences in this species'
465 response to variability in environmental conditions, and possibly resource availability, although the
466 latter could not be tested directly in the modelling procedure. Female *S. canicula* have a protracted
467 egg-laying season (Ellis and Shackley, 1997), and egg-cases are often laid on macroalgae (in coastal
468 waters) and on sessile invertebrates (offshore). Although the present study found that female *S.*
469 *canicula* were often in inshore areas, the main sites of high female abundance were near areas of
470 hard (mainly gravel) grounds (e.g. south of the Isle of Wight, along the coasts of the Dover Strait),
471 and so the distribution of females could be related to proximity to potential oviposition areas and
472 also as a refuge from male harassment (Sims et al., 2001).

473

474

475 **Conclusion**

476 One of the necessary elements for the development of coherent marine strategies is the assessment
477 of species distributions and habitats, and such information is an important element of the European
478 Marine Strategy Framework Directive (European Commission, 2010). There is a specific need to
479 make sure that important habitats are of sufficient extent and quality to maintain viable stock, taking
480 into consideration any threats of habitat degradation (e.g. through dredging, aggregate extraction,
481 pollution), from human exploitation (fisheries) and from environmental change. An improved
482 knowledge of the habitat utilization of elasmobranchs (and by their life history stages) is required
483 for the improved management of both commercial stocks and species of conservation interest (Ellis
484 et al., 2008; Speed et al., 2010), and the present study highlighted some of the key areas for the
485 main species during October in the eastern English Channel. Data on seasonal differences in the
486 distributions of elasmobranchs are limited, both for the study area and elsewhere. An earlier study
487 examined the spatial distributions of a variety of fish species in the eastern English Channel,

488 including *R. clavata*, *R. montagui*, *S. canicula* and *S. stellaris*, from surveys undertaken in July and
489 October (Carpentier et al., 2009), which suggested fairly stable distribution patterns at these times
490 of year. Although the present study was limited to October, and *R. clavata* in the southern North
491 Sea have been shown to display seasonal migrations (Hunter et al., 2005), it is considered that the
492 present study should highlight the broad habitat utilization of the demersal species studied, although
493 further studies for the more mobile and migratory species, such as the triakids, are certainly
494 warranted.

495

496

497 *Acknowledgments*: Part of the work was co-financed by the European Union through its European
498 Regional Development Fund (INTERREG 3a CHARM II project 162/039/365). The authors would
499 like to thank the GENAVIR crew and scientific staff of the research vessel Gwen-Drez. The authors
500 are grateful to F. Gohin (IFREMER Brest) and B. Saulquin (Telecom Bretagne) for the sea surface
501 temperature satellite data, to K. Urbantat for English language editing, and to two reviewers for
502 their comments and suggestions. CSM carried out some of the work with funding from the
503 European Union (MC FP7-PEOPLE-IEF-2008, grant 235791).

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- 689

690 Table 1. Elasmobranch species captured during the Channel Groundfish Survey (CGFS, 1988–
 691 2008) and for which habitat models are presented.

692

693	Family	Scientific name	Species authority	Common name
694	Dasyatidae	<i>Dasyatis pastinaca</i>	(Linnaeus, 1758)	Common stingray
695	Rajidae	<i>Raja brachyura</i>	Lafont, 1873	Blonde ray
696		<i>Raja clavata</i>	Linnaeus, 1758	Thornback ray, roker
697		<i>Raja microocellata</i>	(Montagu, 1818)	Small-eyed ray
698		<i>Raja montagui</i>	Fowler, 1910	Spotted ray
699		<i>Raja undulata</i>	Lacepède, 1802	Undulate ray
700	Scyliorhinidae	<i>Scyliorhinus canicula</i>	(Linnaeus, 1758)	Lesser-spotted dogfish
701		<i>Scyliorhinus stellaris</i>	(Linnaeus, 1758)	Greater-spotted dogfish
702	Triakidae	<i>Galeorhinus galeus</i>	(Linnaeus, 1758)	Tope
703		<i>Mustelus</i> spp.		Smooth-hound

704

705 Table 2. Datasets used during modelling, and their sources. CGFS: Channel Groundfish Survey.

706

707	Dataset	Model development (& internal evaluation)	Model mapping	External model evaluation
709	Density	CGFS 1997–2008	Prediction by habitat model	CGFS 1988–1996
710	Depth	CGFS 1997–2008	Hydrodynamic model ^a	CGFS 1988–1996
711	Seabed sediment type	Digital map ^b	Digital map ^b	Digital map ^b
712	Bed shear stress	Hydrodynamic model ^c	Hydrodynamic model ^c	Hydrodynamic model ^c
713	Sea surface temperature	CGFS 1997–2008	Satellite data 1997–2008 ^d	Satellite data 1988–1996 ^d
714	Sea surface salinity	CGFS 1997–2008	CGFS 1997–2008 ^c	CGFS 1997–2008 ^c

715

716 ^a. Le Roy and Simon, 2003; Carpentier et al., 2009 (Figure 2A); ^b. Larssonneur et al., 1979 (Figure 2B); ^c. Aldridge and Davies, 1993 (Figure 2C); ^d.

717 Casey et al., 2010 (Figure 2D shows time period 1997–2008); ^e. Carpentier et al., 2009 (Figure 2E).

718

719

720 Table 3. Details of the analyses undertaken for the ten elasmobranch taxa, giving the number of
 721 trawl hauls that could be associated with a full set of environmental variables for model
 722 development and internal evaluation, and for external evaluation of the model. Hauls: total number
 723 of trawl hauls; Present: number of hauls in which the species occurred (and percentage of total hauls
 724 in parentheses). Analyses were undertaken for all individuals, with additional analyses undertaken
 725 by age group for *Raja clavata*, *Scyliorhinus canicula* and *Mustelus* spp. (0-1 group: neonate and
 726 young; 2+ group: sub-adult and adult). For *S. canicula*, the number of trawl hauls where sex
 727 information was available is also given.

728 Scientific name	729 Dataset type	730 Model development & internal evaluation (1997–2008)			731 Model external evaluation (1988–1996)		
		732 Hauls	733 Present (%)		734 Hauls	735 Present (%)	
736 <i>D. pastinaca</i>	All	1,146	28	(2.4%)	555	18	(3.2%)
737 <i>R. brachyura</i>	All	1, 146	31	(2.7%)	555	8	(1.4%)
738 <i>R. clavata</i>	All	1, 146	384	(33.5%)	555	182	(32.8%)
739	0-1 group	1, 146	124	(10.8%)	555	42	(7.6%)
740	2+ group	1, 146	309	(26.9%)	555	153	(27.6%)
741 <i>R. microocellata</i>	All	1, 146	11	(1.0%)	555	2	(0.4%)
742 <i>R. montagui</i>	All	1, 146	33	(2.9%)	555	45	(8.1%)
743 <i>R. undulata</i>	All	1, 146	43	(3.8%)	555	21	(3.8%)
744 <i>S. canicula</i>	All	1, 146	673	(58.7%)	555	329	(59.3%)
745	0-1 group	1, 146	22	(1.9%)	555	6	(1.1%)
746	2+ group	1, 146	670	(58.5 %)	555	328	(59.1%)
747	Sex (%Females)	672	542	(80.7%)	258	183	(70.9%)
748 <i>S. stellaris</i>	All	1, 146	176	(15.4%)	555	72	(13.0%)
<i>G. galeus</i>	All	1, 146	54	(4.7%)	555	53	(9.5%)
<i>Mustelus</i> spp.	All	1, 146	350	(30.5%)	555	87	(15.7%)
	0-1 group	1, 146	193	(16.8%)	555	38	(6.8%)
	2+ group	1, 146	253	(22.1%)	555	63	(11.4%)

749 Table 4. Parameters used to calculate length at age using the von Bertalanffy equation: length at
750 birth (L_b , cm), growth rate constant (k , year⁻¹) and theoretical asymptotic length (L_∞ , cm). See text
751 for details of the calculations. [F]: female, [M]: male, [F&M]: female and male; L_2 : estimated
752 length at two years old; bold font: length split value used to investigate age group differences in
753 habitat utilization; *: mean of female and male values; †: the parameters of *Mustelus mustelus* were
754 used for *Mustelus* spp.; L_m , the length at 50% maturity, is given for information.

755

756	Scientific name	Sex	L_b	k	L_∞	L_2	L_m
757	<i>R. clavata</i>	[F&M]	12 ^a	0.14 ^b	118 ^b	37.9	[F] 68, [M] 77 ^c
758	<i>S. canicula</i>	[F]	10 ^d	0.15 ^e	75.1 ^e	26.9	
759		[M]	10 ^a	0.12 ^e	87.4 ^e	26.3	
760		[F&M]				26.6*	58 ^f
761	<i>Mustelus</i> spp.†	[F]	22 ^a	0.06 ^g	205 ^g	57.8	
762		[M]	22 ^a	0.12 ^g	145 ^g	61.6	
763		[F&M]				59.7*	80 ^h

764

765 ^a Ellis et al. 2005b (northeast Atlantic); ^b ICES 1997 (northeast Atlantic); ^c Walker 1999 (northeast
766 Atlantic); ^d Whitehead et al. 1986 (northeast Atlantic and Mediterranean); ^e Ivory et al. 2005
767 (northeast Atlantic); ^f Jennings et al. 1999 (northeast Atlantic); ^g Goosen et al. 1997 (southeast
768 Atlantic); ^h Fischer et al. 1987 (Mediterranean).

769 Table 5. Selected models for six demersal elasmobranchs (lengths and sexes combined; maps in Figures 4) using binomial occurrence models.
 770 Predictors include depth (DEP); mud (M), fine sand (FS), gravel (G) and pebbles (P) seabed sediment types (listed from the highest to lowest
 771 coefficients); bed shear stress (STR); sea surface temperature (SST) and salinity (SAL). Predictors suffixed '2' indicate significant second order
 772 polynomials, and 'inter.' indicates interactions between model predictors. Models evaluated by the adjusted proportion of deviance explained (Adj-R²),
 773 Spearman's rank correlation test (coefficient r_s), and Receiver Operating Characteristic (ROC) and Area Under the Curve (AUC). Significance value of
 774 statistical tests (p) given as ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$. Scores of internal (int.) and external (ext.) model evaluations (out of three) also
 775 given (see main text for details). A model was deemed *satisfactory* if, in addition to suitable diagnostic plots, it passed at least three of the six
 776 evaluations (three internal and three external).

777

778

		Model selection		Model evaluation					
Scientific name	Dataset type	Significant predictors	Adj-R ²	Spearman's r_s	p	ROC AUC	p	Evaluation	
								Type	Score
779 <i>D. pastinaca</i>	All	DEP, M-G-FS-P, STR, SST2, SAL, 2 inter.	0.20	0.19	***	0.86	***	int.	3/3
780			0.07	0.15	***	0.74	***	ext.	1/3
781 <i>R. brachyura</i>	All	DEP2, G-FS-M-P, STR2, SST, SAL, 3 inter.	0.12	0.17	***	0.81	***	int.	3/3
782			0.07	0.11	**	0.77	**	ext.	1/3
783 <i>R. microocellata</i>	All	DEP2, STR2, SST2, SAL, 4 inter.	0.47	0.16	***	0.97	***	int.	3/3
784			0.22	0.06	0.10	0.76	0.09	ext.	1/3
785 <i>R. montagui</i>	All	DEP2, FS-G-P-M, STR, SST2, SAL, 4 inter.	0.15	0.18	***	0.81	***	int.	3/3
786			0.07	0.09	0.02	0.59	*	ext.	0/3
787 <i>R. undulata</i>	All	DEP2, P-G-FS-M, STR2, SAL, 1 inter.	0.14	0.20	***	0.81	***	int.	3/3
788			0.02	0.19	***	0.78	***	ext.	1/3
789 <i>G. galeus</i>	All	DEP2, FS-P-G-M, STR, SST, SAL2, 2 inter.	0.26	0.27	***	0.87	***	int.	3/3
790			0.10	0.37	***	0.86	***	ext.	3/3

791

792

793

794 Table 6. Selected models for four demersal elasmobranchs (lengths and sexes combined; maps in Figure 5) using delta models. Predictors, listed in
 795 Table 5, are given for the binomial (top line) and positive (second line) components. Models evaluated by the adjusted proportion of deviance
 796 explained (Adj-R²), Spearman's rank correlation test (coefficient r_s) and Wilcoxon signed-rank test. Significance value of statistical tests (*p*) given as
 797 ***: *p* < 0.001, **: *p* < 0.01, *: *p* < 0.05. Scores of internal (int.) and external (ext.) model evaluations (out of three) also given (see main text for
 798 details). A model was deemed *satisfactory* if, in addition to suitable diagnostic plots, it passed at least three of the six evaluations (three internal and
 799 three external).

800

801			Model selection	Model evaluation					
	802 Scientific name	803 Dataset type	804 Significant predictors	Adj-R ²	Spearman's r _s	p	Wilcoxon p	805 Evaluation Type	806 Score
807	<i>R. clavata</i>	All	DEP2, G-P-M-FS, STR, SAL2, 1 inter.	0.05	0.25	***	0.36	int.	2/3
808			/ DEP, STR2, SST, SAL2, 1 inter.	0.04	0.24	***	0.21	ext.	2/3
809	<i>S. canicula</i>	All	DEP, P-G-M-FS, STR2, SST, SAL2, 2 inter.	0.32	0.59	***	0.98	int.	3/3
810			/ DEP, G-FS-P-M, STR, SST, SAL2, 4 inter.	0.34	0.52	***	***	ext.	2/3
811	<i>S. stellaris</i>	All	DEP2, G-P-M-FS, STR2, SST2, SAL2, 1 inter.	0.32	0.50	***	***	int.	2/3
812			/ DEP2, G-P-FS-M, STR2, SAL2	0.67	0.42	***	***	ext.	2/3
813	<i>Mustelus spp.</i>	All	DEP, P-G-M-FS, STR2, SST2, SAL2, 2 inter.	0.18	0.42	***	**	int.	2/3
			/ DEP, M-P-FS-G, STR2, SAL, 1 inter.	0.72	0.28	***	***	ext.	2/3

814 Table 7. Selected models for three demersal elasmobranchs, by age group (0-1 group: neonates and young; 2+ group: sub-adult and adult; maps in
 815 Figure 7) and by sex (*S. canicula*; maps in Figure 8), using binomial occurrence models. See Table 5 for further information.

816

817

818 Scientific name	819 Dataset type	820 Model selection Significant predictors	817 Model evaluation					818 Evaluation	
			821 Adj-R ²	822 Spearman's r _s	823 p	824 ROC AUC	825 p	826 Type	827 Score
828 <i>R. clavata</i>	829 0-1 group	830 DEP2, STR2, SAL, 1 inter.	831 0.18	832 0.34	833 ***	834 0.81	835 ***	836 int.	837 3/3
			838 0.13	839 0.23	840 ***	841 0.76	842 ***	843 ext.	844 2/3
	845 2+ group	846 DEP2, G-P-FS-M, STR, SAL2, 1 inter.	847 0.08	848 0.30	849 ***	850 0.70	851 ***	852 int.	853 1/3
			854 0.07	855 0.29	856 ***	857 0.69	858 ***	859 ext.	860 1/3
861 <i>S. canicula</i>	862 0-1 group	863 DEP, M-FS-G- P, STR, SST2, SAL, 2 inter.	864 0.20	865 0.17	866 ***	867 0.85	868 ***	869 int.	870 3/3
			871 0.04	872 0.10	873 *	874 0.76	875 *	876 ext.	877 1/3
	878 2+ group	879 DEP, P-M-G-FS, STR2, SST, SAL2, 2 inter.	880 0.24	881 0.54	882 ***	883 0.82	884 ***	885 int.	886 3/3
			887 0.22	888 0.47	889 ***	890 0.78	891 ***	892 ext.	893 2/3
			894 0.24	895 0.56	896 ***	897 0.93	898 ***	899 int.	900 3/3
901 Sex (%Females)	902 DEP2, FS-M-G-P, STR2, SST, SAL2, 2 inter.	903 0.23	904 0.50	905 ***	906 0.87	907 ***	908 ext.	909 3/3	
910 <i>Mustelus</i> spp.	911 0-1 group	912 DEP, G-M-P-FS, STR2, SST, SAL2, 3 inter.	913 0.07	914 0.26	915 ***	916 0.70	917 ***	918 int.	919 1/3
			920 0.44	921 0.16	922 ***	923 0.68	924 ***	925 ext.	926 2/3
	927 2+ group	928 DEP, M-P-G-FS, STR, SST, SAL2, 2 inter.	929 0.17	930 0.41	931 ***	932 0.79	933 ***	934 int.	935 2/3
936			937 0.53	938 0.31	939 ***	940 0.78	941 ***	942 ext.	943 2/3

834

835 Figure 1. The eastern English Channel showing (A) geographical locations mentioned in the text,
836 and (B) trawl stations sampled during the Channel Groundfish Survey (CGFS, 1988–2008).

837

838 Figure 2. The spatial patterns of the environmental variables used to map the habitat models,
839 including (A) depth (m; Le Roy and Simon, 2003; Carpentier et al., 2009); (B) seabed sediment
840 type (M: mud, FS: fine sand, CS: coarse sand, G: gravel and P: pebble; Larssonneur et al., 1979); (C)
841 bed shear stress (N.m^{-2} , Aldridge and Davies, 1993); (D) satellite-derived sea surface temperature
842 for October 1997–2008 ($^{\circ}\text{C}$; Casey et al., 2010); (E) *in situ* sea surface salinity (PSU; Carpentier et
843 al., 2009) for October 1997–2008.

844

845 Figure 3. Length (cm) frequency distributions of (A) *Raja clavata*, (B) *Scyliorhinus canicula* and
846 (C) *Mustelus* spp., illustrating the density ($\text{Log}_{10}[x+1]$, where $x = \text{ind.km}^{-2}$) of fish at length caught
847 in the Channel Groundfish Survey. The vertical arrows indicate the estimated lengths at two years
848 old (L_2), that were used to separate individuals into two age groups (0-1 group: neonate and young;
849 2+ group: sub-adult and adult). Length at 50% maturity (L_m) is shown for information ([F]: female,
850 [M]: male). The abscises for all species start at the approximate length at birth (L_b). Exact values for
851 L_b , L_2 and L_m are listed in Table 4.

852

853 Figure 4. Mapped binomial occurrence models (main figure) and associated prediction error
854 (below) for (A) *Dasyatis pastinaca*, (B) *Raja brachyura*, (C) *R. microocellata*, (D) *R. montagui*, (E)
855 *R. undulata* and (F) *Galeorhinus galeus* in the eastern English Channel during October (lengths and
856 sexes combined). Prediction error: 0 and 1 correspond to the minimum and maximum possible
857 errors, respectively.

858

859 Figure 5. Mapped delta models (main figure) and associated prediction error (below) for (A) *Raja*
860 *clavata*, (B) *Scyliorhinus canicula*, (C) *S. stellaris* and (D) *Mustelus* spp. in the eastern English

861 Channel during October (lengths and sexes combined). Delta model: showing density in
862 $\text{Log}_{10}[x+1]$, $x = \text{ind.km}^{-2}$; prediction error: 0 and 1 correspond to the minimum and maximum
863 possible errors, respectively.

864

865 Figure 6. Model behaviour for each environmental variable tested, taking into account the effect of
866 each of the five seabed sediment types (see Figure 2B). Each plot illustrates the species response
867 (here density x) along one given environmental gradient, all other variables remaining constant at
868 their mean value. This figure corresponds to the delta model of *Scyliorhinus canicula* (see map in
869 Figure 5B). Units: density ($\text{Log}_{10}[x+1]$, $x = \text{ind.km}^{-2}$), depth (m), bed shear stress (N.m^{-2}), surface
870 temperature ($^{\circ}\text{C}$) and surface salinity (PSU).

871

872 Figure 7. Mapped binomial occurrence models (main figure) for (A-B) *Raja clavata*, (C-D)
873 *Scyliorhinus canicula* and (E-F) *Mustelus* spp. by age group, and associated prediction error
874 (below). Prediction error: 0 and 1 correspond to the minimum and maximum possible errors,
875 respectively. The habitat model corresponding to Figure 7B did not pass the evaluation criteria.

876

877 Figure 8. Habitats of female and male *Scyliorhinus canicula*, showing (A) the proportion of females
878 based on a binomial occurrence model (and below: associated prediction error, where 0 and 1
879 correspond to the minimum and maximum possible errors, respectively). This model was used to
880 balance the delta model (see map in Figure 5B) so as to visualise spatial segregations by sex for (B)
881 females and (C) males (density in $\text{Log}_{10}[x+1]$, $x = \text{ind.km}^{-2}$).

Figure 1.

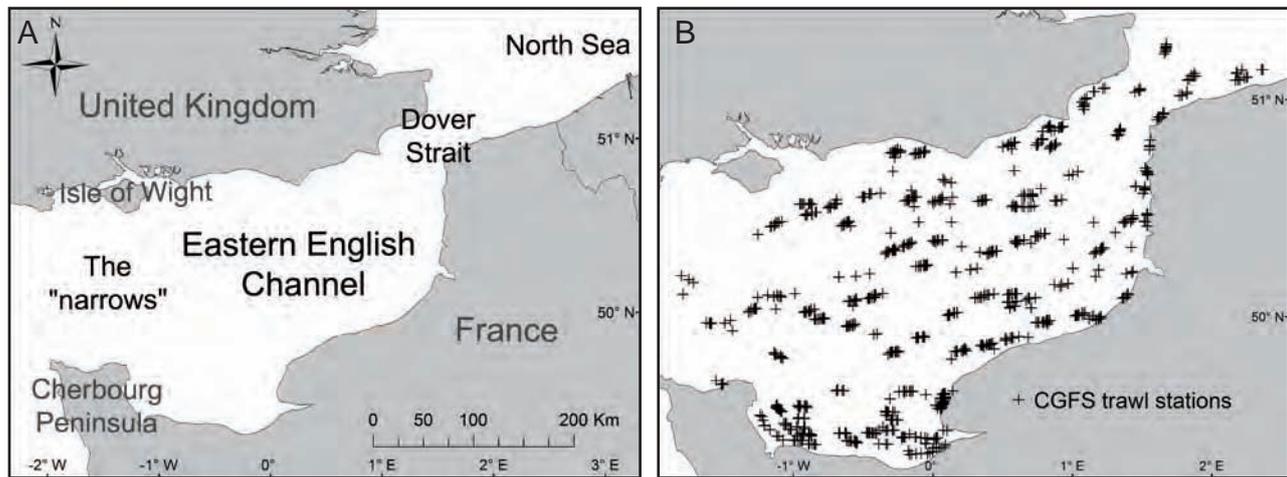


Figure 2.

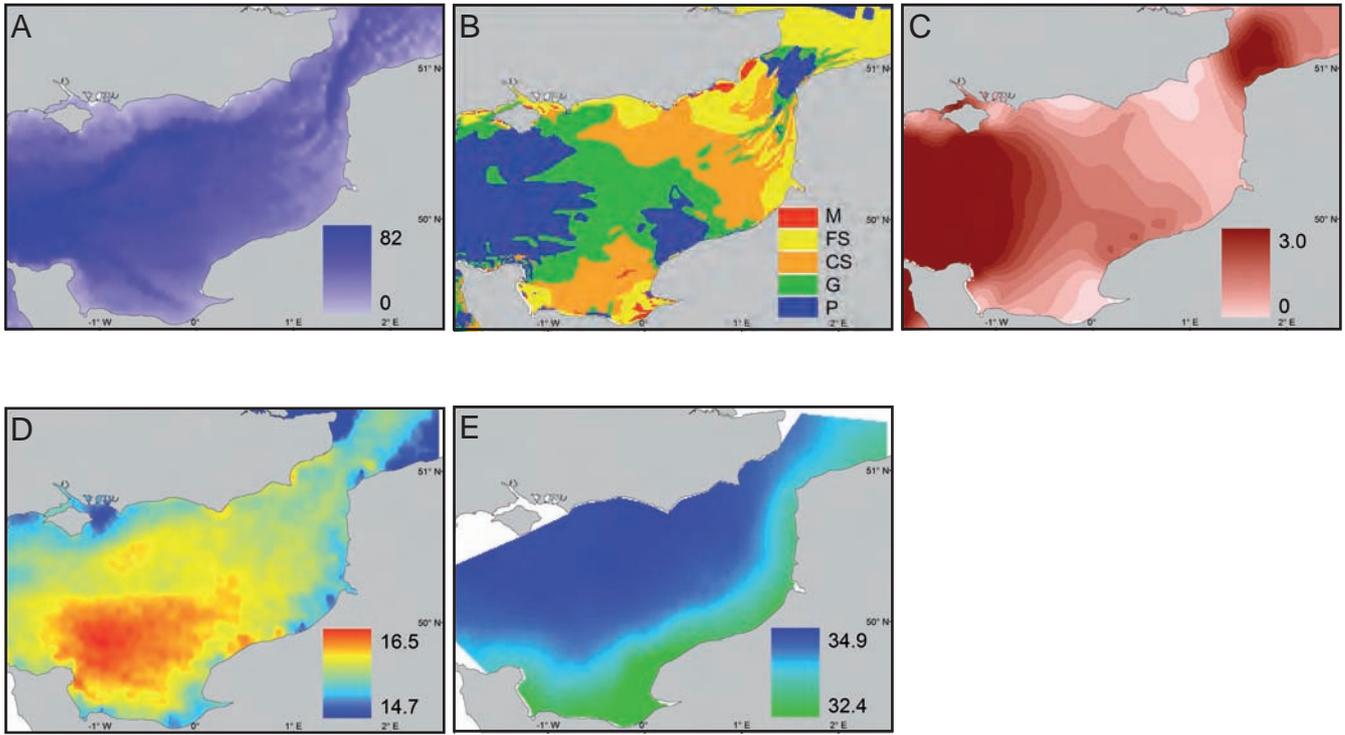


Figure 3.

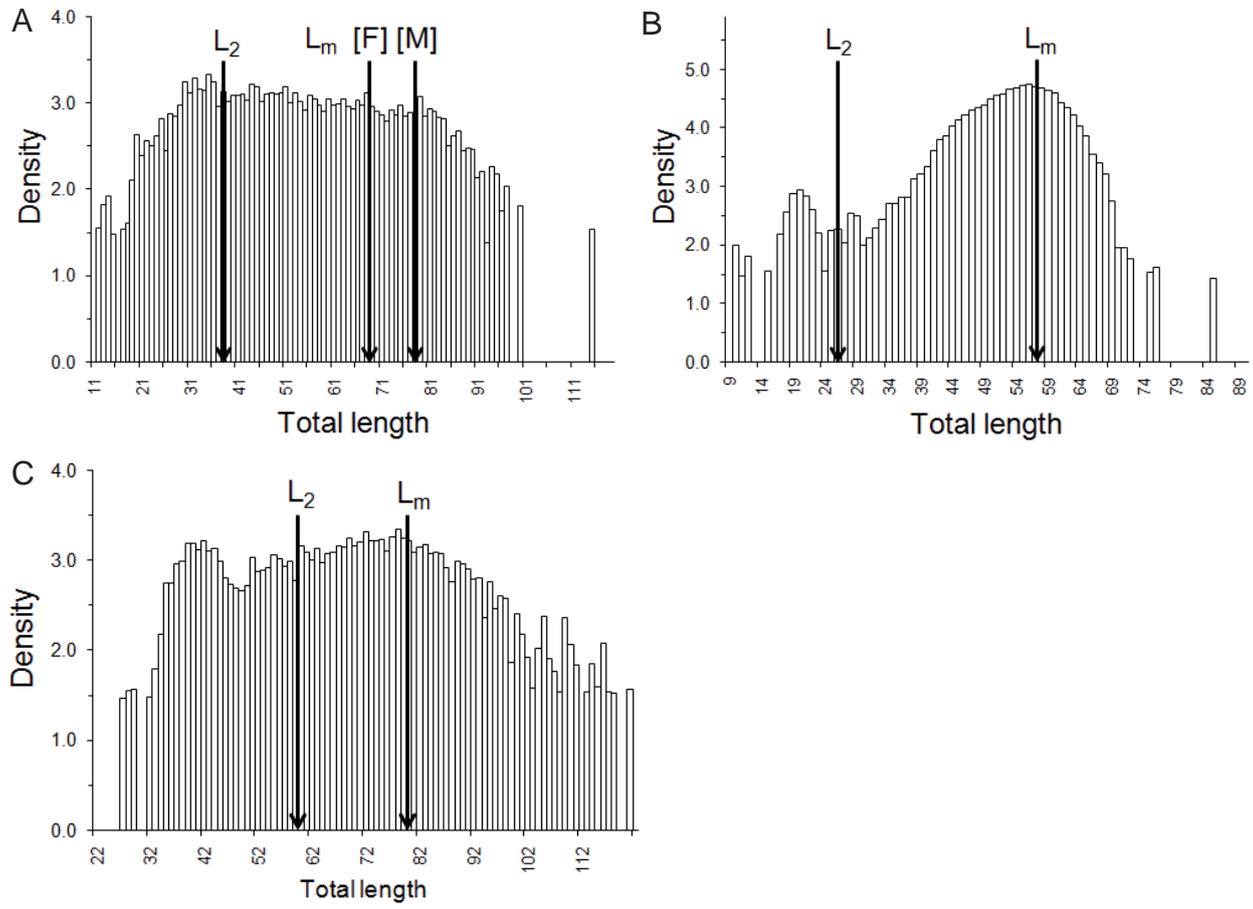


Figure 4.

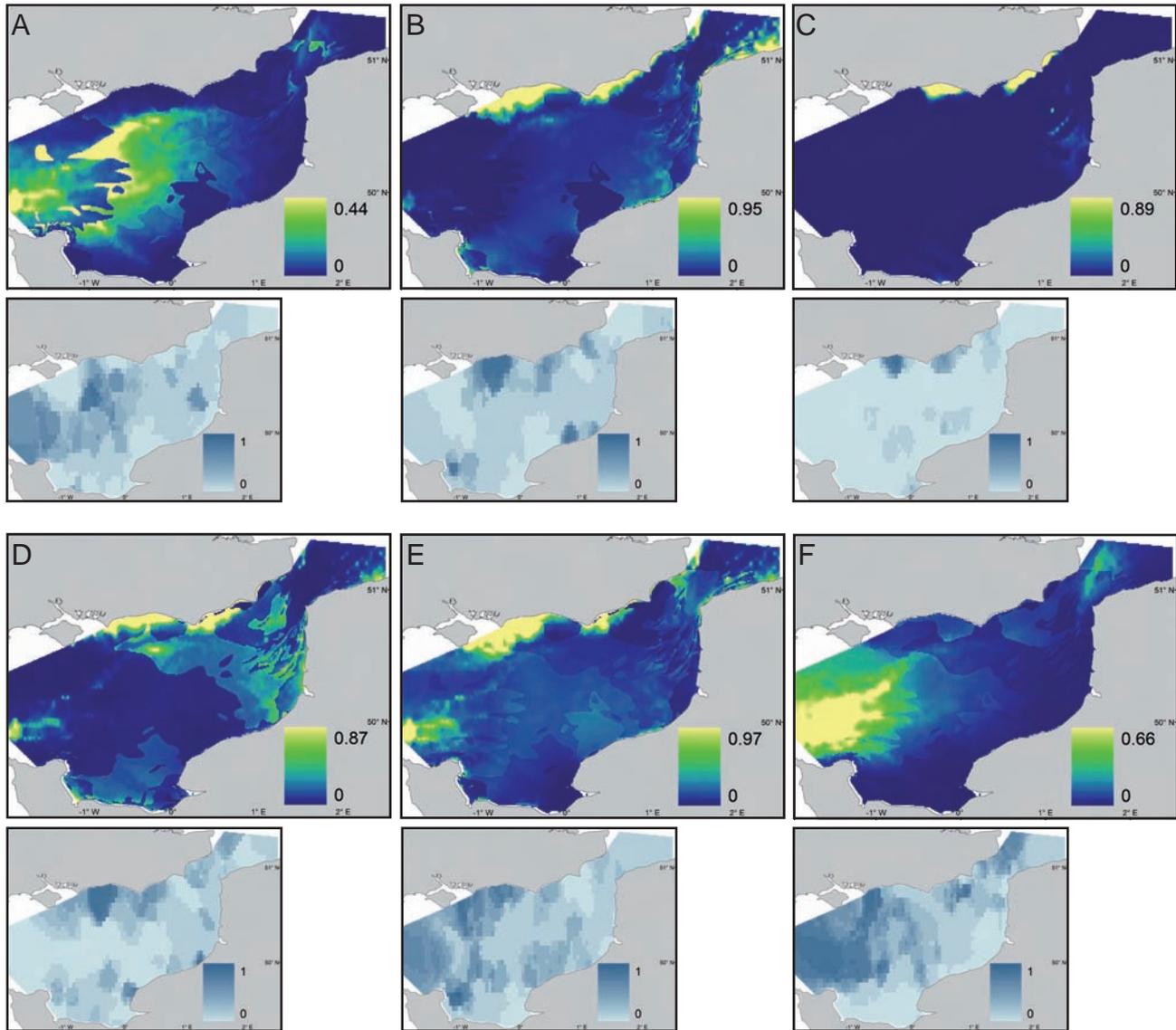


Figure 5.

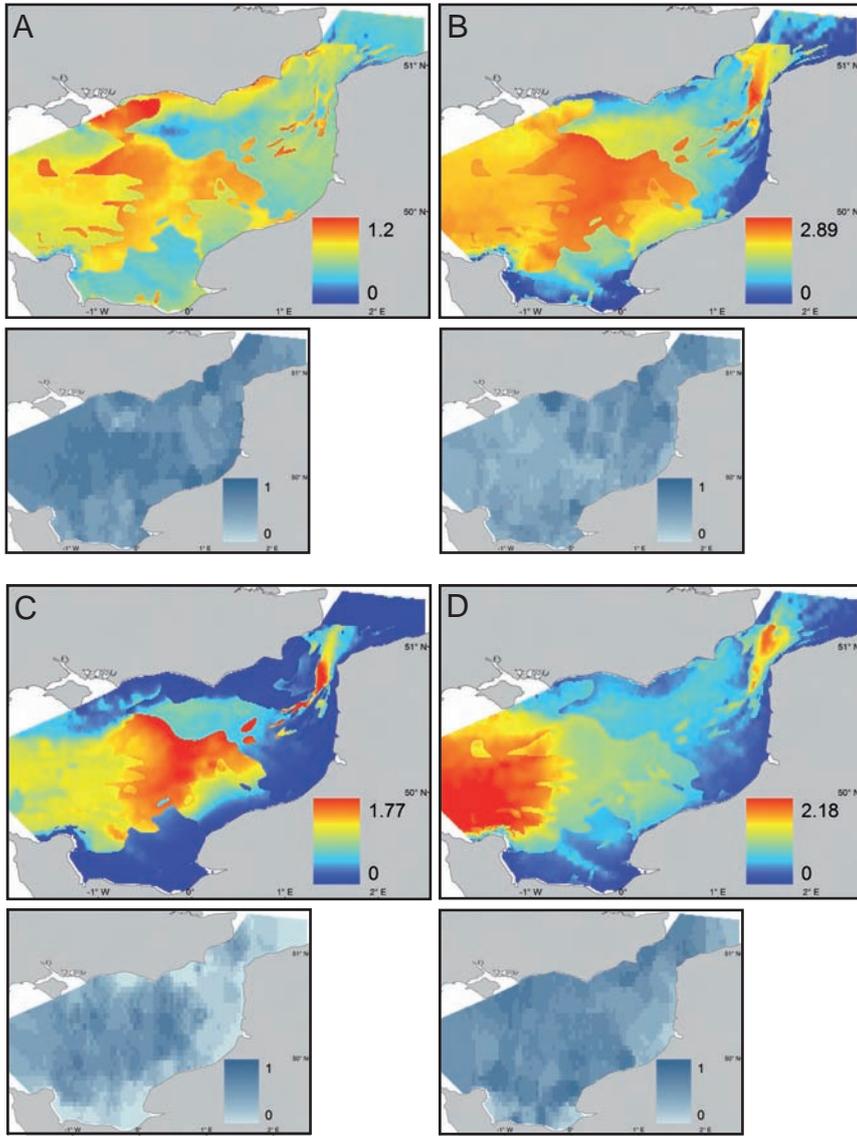


Figure 6.

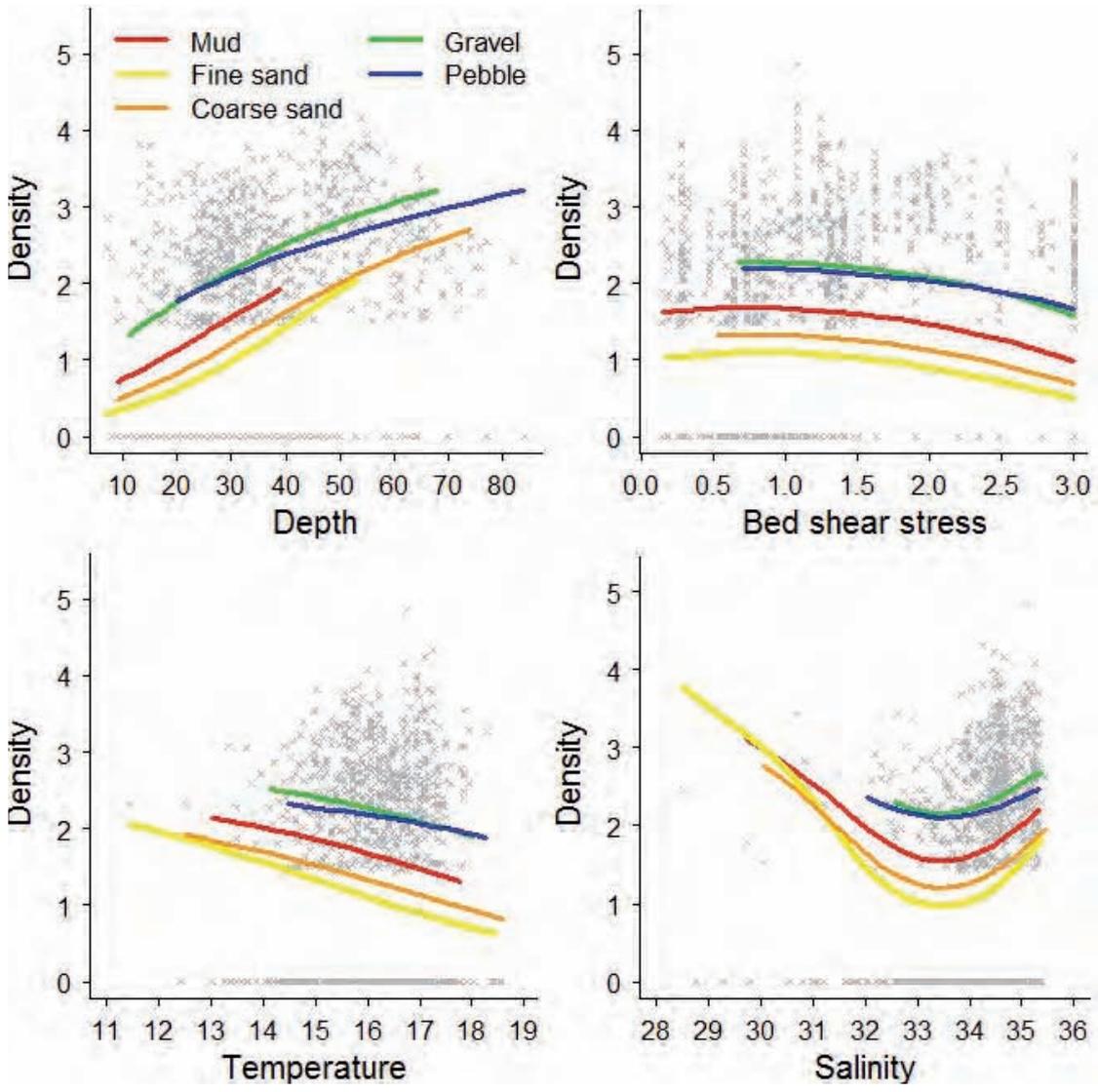


Figure 7.

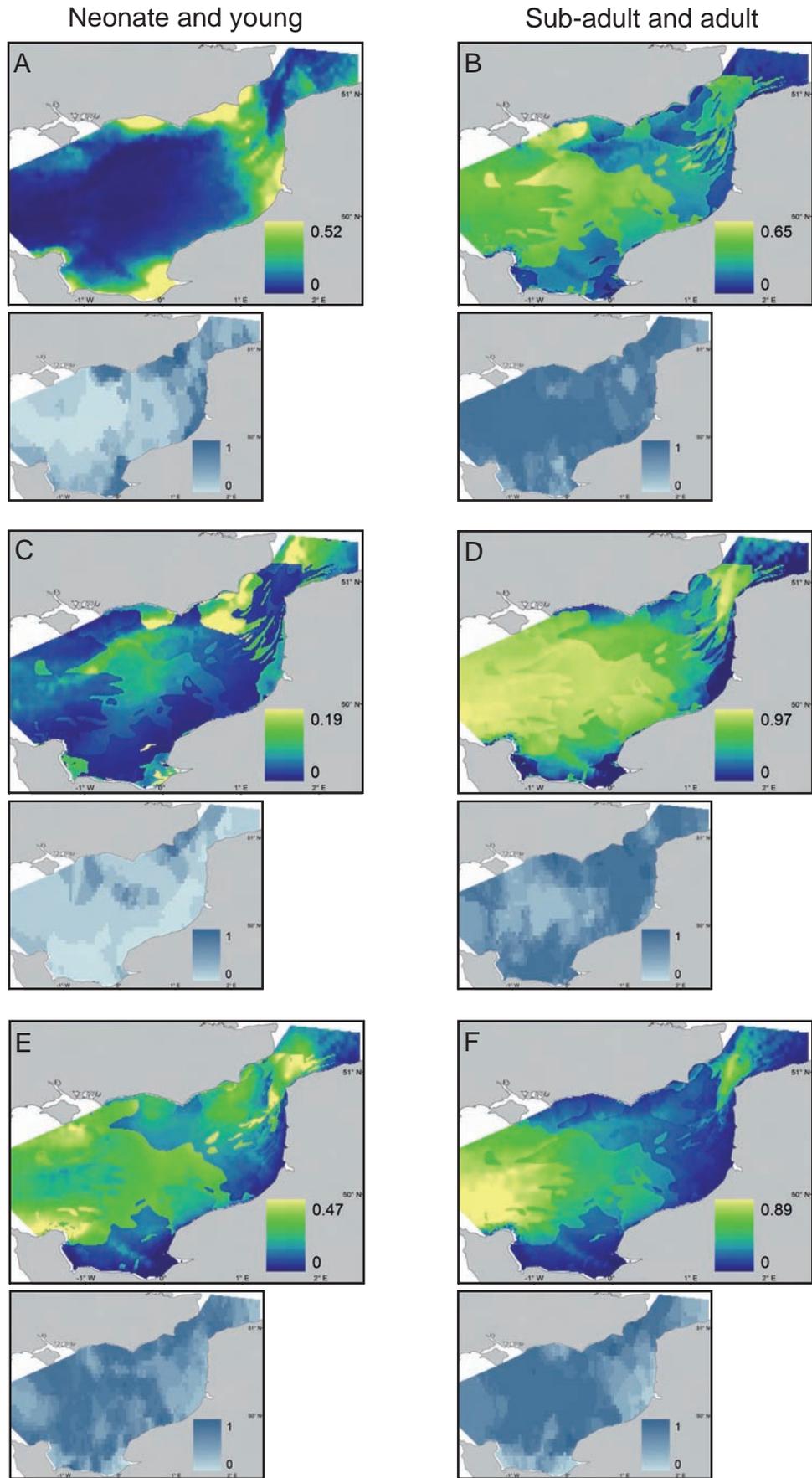


Figure 8.

