

1 **Abundance and Spatial Distribution of Brown Crab (*Cancer pagurus*) from Fishery-**  
2 **Independent Dredge and Trawl surveys in the North Sea**

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14 population dynamics of shellfish”), which took place in November 2019 in Tromsø, Norway.

15 **Abstract**

16

17 Spatial information is important to understand the distribution, population structure and dynamics  
18 of commercially important marine species. Brown crab (*Cancer pagurus*) is a crustacean that  
19 supports important commercial fisheries along the British coastline. There have been no specific  
20 studies based on fishery-independent surveys documenting the habitat preferences of brown crab  
21 around Scotland. This paper provides an analysis of dredge and trawl fisheries surveys in the North  
22 Sea (2008-2018) with the aim of describing the spatial distribution of brown crab and developing  
23 abundance and recruitment indices for the species. The distribution of brown crab is investigated  
24 using geostatistical methods, and generalized additive models (GAMs) are used to model crab  
25 catch rates in relation to a number of explanatory variables (depth, distance to coast, sediment type  
26 and year). Brown crab catch rates were higher in coastal areas. The male and female crab  
27 distribution was relatively similar and juvenile crabs (<100 mm) showed a very clear inshore  
28 distribution along the shoreline up to 20 km from the coast. The total abundance as estimated from  
29 the dredge survey varied between years, from 34 to 86 million crabs from the dredge survey. The  
30 annual trawl catch rate, which provides an index of relative abundance, ranged between 16 and 65  
31 animals/km<sup>2</sup>. The dredge and trawl indices were correlated, showing a similar trend of increasing  
32 catch rates in the early years of the time series up to 2016, and a subsequent reduction. A  
33 recruitment index was also estimated, showing a gradual increase in captured juvenile crabs up to  
34 2014, followed by a steep decrease with the lowest estimated value being reached in 2018. The  
35 advantages and limitations of using active fishing methods rather than passive gears such as traps  
36 for obtaining standardized catch rates are discussed. The results obtained provide baseline  
37 information on abundance, distribution and habitat for a widely distributed species and could be  
38 used in future stock assessments, informing the management of this important species.

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41 **Keywords:** brown crab, geostatistics, survey, fishery-independent data, dredge, trawl, spatial  
42 distribution, creel fisheries, Scotland

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45 **Introduction**

46

47 The brown crab (*Cancer pagurus*) is a decapod crustacean which inhabits sandy and rocky  
48 seabeds of northwestern Europe (Edwards, 1979), from the littoral zone, to depths of over 100 m  
49 (Shelton and Hall, 1981). Like other crustaceans, the growth of brown crab takes place by moulting  
50 the shell, with moult frequency decreasing with age. The species reaches the minimum landing size  
51 (MLS) in Scotland of 150 mm carapace width (CW) at an age of around 6 years (Mill *et al.*, 2009).  
52 The brown crab is considered to be a slow-growing species with a lifespan of approximately 20

53 years, reaching an asymptotic size ( $L_{\infty}$ ) of between 220 and 246 mm in Scottish waters (Bennett,  
54 1974; Tallack, 2002; Mill *et al.*, 2009). It is a commercially valuable species with annual landings  
55 into Scotland in excess of 10,000 tonnes and a first sale value of £26.8 million in 2018 (Scottish  
56 Sea Fisheries Statistics, 2018). Pot fisheries for brown crabs occur along almost the entire length  
57 of the British coastline and traditionally these fisheries have been essentially inshore (Eaton *et al.*,  
58 2001). Since the late 1980's, offshore crab fisheries have developed, rapidly becoming the largest  
59 pot fisheries both in the North Sea and west coast of Scotland. More recently, the expanded  
60 demand for this species from European and emergent Asian markets makes an evaluation of its  
61 status more important (Mesquita *et al.*, 2017).

62 Concerns about increased landings and uncertainty over the level of exploitation have  
63 highlighted gaps in the current understanding of brown crab stocks (Bennett, 1995; Smith and  
64 Addison, 2003). Information on spatial distribution is important for understanding the population  
65 structure and dynamics of commercially valuable marine resources (Hunter *et al.*, 2013), but there  
66 have been very few studies documenting habitat preferences of brown crab. Juveniles from  
67 different crab species prefer nursery habitats close to the shore, presumably to avoid predation  
68 before moving to different habitats, potentially representing a major source of recruitment for  
69 offshore fisheries (Edwards, 1979; Robinson and Tully, 2000; Beck *et al.*, 2001). Brown crabs are  
70 known to be associated with rocky substrates but also inhabit mixed coarse, sand and soft  
71 sediments, particularly offshore where they dig into mud in search of food, or bury themselves to  
72 avoid strong currents (Hall *et al.*, 1993).

73 Abundance indices are generally lacking for decapod crustaceans in European waters.  
74 Fisheries-dependent data obtained from vessels using pots are difficult to interpret due to problems  
75 in standardizing catch rates, which are affected by, for example, pot design, gear saturation, soak-  
76 time and types of bait (Miller, 1990). The problems with commercial catch data can be avoided by  
77 using fisheries-independent research surveys which provide estimates of abundance and catch  
78 composition across the geographic range of a species (Hilborn and Walters, 1992). Given the  
79 occurrence of brown crabs in a wide variety of sediment types, the species is often found in the  
80 same habitat as other commercial species such as scallops and demersal fish (Jenkins *et al.*, 2004;  
81 Öndes *et al.*, 2016). Many nations have long-term scientific research surveys which contribute to  
82 fisheries assessment and management (Jouffre *et al.*, 2009). The brown crab is not currently  
83 targeted by any specific fishery-independent survey and there are currently no estimates available  
84 of abundance or recruitment for populations around Scotland. Despite this, catches of brown crab  
85 are routinely recorded during a number of fisheries surveys conducted by Marine Scotland Science  
86 (MSS). There are no studies documenting brown crab catch rates from surveys using mobile gears  
87 such as dredges or trawls. It is expected that analysing catch rates from these surveys may contain  
88 relevant information on habitat preferences of the species, for example in relation to substrate type,  
89 depth distribution or distance to coast.

90 This study provides an analysis of catch rates of brown crab between 2008 and 2018 in two  
91 fisheries-independent surveys taking place in the North Sea: a dredge survey directed at the main  
92 king scallop fishing grounds (Dobby *et al.*, 2017); and the International Bottom Trawl Survey  
93 (IBTS) developed for demersal fish species (ICES, 2018). The aims of this study were to: (i)  
94 determine the spatial distribution of brown crab by size and sex; (ii) model crab catch rates in  
95 relation to explanatory variables (depth, distance to coast, sediment type and year); (iii) derive  
96 abundance and recruitment indices for brown crab. The work represents the first study directed at  
97 understanding the abundance, distribution and important habitat features of brown crab in the North  
98 Sea using fisheries-independent data.

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## 101 **Methods**

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### 103 Study area and sampling

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105 The study area was located in the western North Sea, off the east coast of Scotland. Brown  
106 crab data were collected during 11 dredge surveys and 11 trawl surveys (2008-2018, Table 1). The  
107 surveys were carried out by MSS in summer (between May and September) on-board the Scottish  
108 research vessels FRV “Alba na Mara” (dredge) and FRV “Scotia” (trawl) covering fishing stations  
109 around the east coast of Scotland (Figure 1a).

110 The scallop dredge survey was directed at king scallop stocks and took place at fixed  
111 stations. The dredge gear consisted of a mixture of standard commercial dredges (9 tooth bar, 80  
112 mm internal diameter belly rings) and smaller dredges (11 tooth bar, 60 mm internal diameter belly  
113 rings) aimed at capturing smaller scallops (Dobby *et al.*, 2017). The North Sea IBTS quarter 3 (Q3)  
114 is an internationally coordinated survey carried out in August each year to collect data on a range  
115 of demersal species in ICES Division 3a and Subarea 4 (ICES, 2018). The fishing gear consisted of  
116 a GOV (Grand Ouverture Vertical) bottom trawl with standard ground gear as described in ICES  
117 (2018). The survey followed a repeat station survey design based on an initial stratified-random  
118 allocation, with at least two stations in each ICES statistical rectangle (1 degree longitude  $\times$  0.5  
119 degree latitude).

120 At each station, the fishing gear was towed for approximately 30 minutes at a speed of 2.5  
121 knots (dredge) or 4 knots (trawl) and any identified brown crabs were counted, sexed and measured  
122 to the nearest millimetre below. Catch rates were standardized for gear size and tow length by  
123 calculating a swept area for each station, i.e. the product of the tow length and the gear width. In  
124 the dredge survey, gear size was measured as the total dredge width. For the trawl survey, the  
125 horizontal opening of the mouth of the net (wingspread) was used as a measure of the gear width.  
126 Catch rates were calculated for each station as numbers of crabs caught per square metre ( $N.m^{-2}$ ).

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130 Environmental variables

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132 Bathymetry datasets for the areas considered were obtained from the UK Hydrographic  
133 Office and supplied to MSS by OceanWise Ltd at a resolution of 6 arc second (OceanWise, 2015)  
134 (Figure 1b). The sediment layers were obtained from the British Geological Survey (BGS) (Cooper  
135 *et al.*, 2013) based on the Folk sediment classification (Folk, 1954). Four sediment strata covering  
136 the survey areas were considered: mud, sand, gravelly sand and gravel (Figure 1c). At each station,  
137 the geodesic distance to the nearest point in the UK coast (including islands) was computed (in  
138 km), referenced to the World Geodetic System 1984 (WGS84).

139

140 Spatial distribution

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142 To examine the spatial structure of brown crab distribution, geostatistics (Rivoirard *et al.*,  
143 2000) were applied to analyse catch rates in the dredge and trawl surveys (2008-2018). The  
144 analysis focused on all brown crabs caught on both dredge and trawl surveys. For the dredge  
145 surveys, where a higher number of stations were completed and larger numbers of crabs were  
146 sampled (Table 1), the analysis was performed separately for females, males, and juvenile crabs  
147 under 100 mm CW. Due to the skewed nature of crab catch rates in both surveys, with many zeros  
148 (no crabs caught during a haul), and to reduce the influence of the largest values (Petitgas *et al.*,  
149 2017), a logarithmic transformation was performed on the data as follows:

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$$151 \quad C_{ij} = \log\left(\frac{r_{ij}}{\bar{r}_j} + 1\right),$$

152

153 where  $C_{ij}$  is the log transformed catch rate (response variable),  $r_{ij}$  is the catch rate in station  $i$  and  
154 year  $j$  and  $\bar{r}_j$  is the mean catch rate in year  $j$ . Given that the analysis combines several years,  
155 dividing the catch rate by  $\bar{r}_j$  ensures the data are mean standardized by year.

156 Variograms can be used to quantify the mean variability (semi-variance) of a regionalized  
157 variable as a function of the distance between any two points (Petitgas *et al.*, 2017).

158 Omnidirectional empirical variograms were computed for the transformed catch rates for both  
159 dredge and trawl surveys in each year (2008-2018) using the estimator (Matheron, 1963):

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$$161 \quad \gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [Z(x_i) - Z(x_i + h)]^2,$$

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163 where  $\gamma$  is the calculated semi-variance for each dataset,  $Z(x_i)$  the catch rate of brown crabs at  
164 sampled station  $x_i$ ,  $Z(x_i + h)$  is the catch rate value separated from  $x_i$  by a lag distance  $h$  (measured

165 as a straight line, in km) and  $N(h)$  is the number of observation pairs separated by  $h$ . A distance  $h$  of  
166 10 km was used for the dredge survey and 25 km for the trawl survey (number of lags = 15) (Table  
167 2).

168 The variograms for each survey/year were combined to obtain an experimental mean  
169 variogram standardized by the yearly sample variance following the approach proposed by  
170 Rivoirard *et al.* (2000). Four mean variograms were obtained from the 11 years of data for the  
171 dredge survey (all crabs, females, males, juveniles) and one mean variogram for the trawl (all  
172 crabs) survey. Visual inspection of the resulting mean variograms (Figure 2a) suggested that  
173 spherical models provided a good fit for the dredge data and a linear model was appropriate for the  
174 trawl data. Spherical models were fitted to the variograms using a non-linear regression to obtain  
175 model parameters, resulting in estimates of a sill, range and nugget (Bivand *et al.*, 2008). The range  
176 is the distance at which the semi variance (sill) becomes asymptotic. The nugget is the  
177 discontinuity from the origin at a distance of zero, due to measurement error and small scale  
178 variability (Rivoirard *et al.*, 2000; Petitgas *et al.*, 2017). For the trawl data, a nested model  
179 consisting of a nugget and a linear model, weighted by the number of observation points in each  
180 lag, was fitted using ordinary least squares (Pebesma, 2004). The estimated variogram models  
181 were used to interpolate the data by kriging (Matheron, 1963; Rivoirard *et al.*, 2000; Bivand *et al.*,  
182 2008).

183 A number of predictor variables for the study area were available (distance to coast, depth  
184 and BGS sediment type), allowing the application of kriging with external drift whereby some of  
185 the variance of the data is attributed to the variable in question (Rivoirard *et al.*, 2000; Oliver and  
186 Webster, 2014). Data exploration of crab catch rates, in relation to different predictor variables, led  
187 to the selection of depth and distance to coast as important variables to explain the spatial  
188 distribution of crabs in the dredge surveys. The same variables were used for the trawl surveys with  
189 the addition of BGS sediment type, which was found to have an effect in the trawl-caught catch  
190 rates. The interpolated catch rate predictions were computed onto an equally spaced grid (3 nautical  
191 miles resolution) of the survey area and two-dimensional density maps were generated for each  
192 dataset on both surveys. The validity of the variogram models and kriging interpolations was  
193 evaluated using a leave-one-out cross-validation procedure (Bivand *et al.*, 2008). A routine was  
194 implemented whereby each point was removed from the dataset, using the remaining data to  
195 predict the omitted density value and the residuals were computed and spatially plotted for  
196 inspection and validation of the model applied to each dataset.

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199 Abundance and recruitment indices

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201 To estimate temporal trends and an abundance index of brown crab in the study area, GAMs  
202 were applied to the survey data using the catch rate per haul (numbers of crabs caught per square

203 metre) as the response variable. Two sets of models were fitted separately, for the dredge and trawl  
204 surveys. Large numbers of zero observations were present in both survey datasets, as no crabs were  
205 recorded in many of the sampled stations. To deal with zero observations and considering the  
206 response variable was markedly right-skewed, a GAM was applied assuming a Tweedie  
207 distribution (Tweedie, 1984; Dunn and Smyth, 2005) with a log link. Tweedie models belong to the  
208 exponential family of distributions and include a power mean-variance relationship,  $V(\mu) = \mu^p$ ,  
209 where  $V()$  is the variance function,  $\mu$  is the mean of the distribution and  $p$  is a parameter ( $1 < p < 2$ ),  
210 where  $p=1$  implies a Poisson distribution and  $p=2$  a gamma distribution (Dunn and Smyth, 2005).  
211 The parameter  $p$  was estimated for each survey during the fitting procedure with the *tw* function in  
212 the *mgcv* R package (Wood, 2011).

213 The size data available for brown crabs caught in the dredge and trawl surveys were  
214 compared to develop a recruitment index for the east of Scotland. A size of 100 mm CW was  
215 chosen as a cut-off point to separate juvenile crabs from mature adults, based on the lowest  
216 estimates of gonadal size at maturity in Europe (Haig *et al.*, 2016). A preliminary analysis of the  
217 length information showed that very few crabs below 100 mm CW were captured in the trawl  
218 surveys. Consequently, the recruitment analysis in the study area was focused only on data from  
219 the dredge survey, during which smaller crabs were frequently caught. The response variable was  
220 the catch rate of crabs ( $N.m^{-2}$ ) under 100 mm CW. GAM models assuming a Tweedie distribution  
221 were fitted to the defined recruitment index but model diagnostics based on the residuals showed  
222 generally a poor fit. Therefore, a two-part hurdle model (Mullahy, 1986; Zeileis *et al.*, 2008; Zuur  
223 *et al.*, 2009) was used to model the recruitment index of juvenile crabs. In the first part, a binomial  
224 GAM (logit link) was used to model the probability that a zero is observed in each sampled station.  
225 Positive recruitment index values were plotted and compared with several distributions (Delignette-  
226 Muller and Dutang, 2015) and shown to follow a gamma distribution. Therefore, in the second part  
227 of the model, non-zero values were modelled with a GAM using a gamma distribution with a log  
228 link.

229 The explanatory variables considered for the two abundance models and for the recruitment  
230 hurdle model (both parts) were: sediment type (BGS data, categorical variable with 4 levels),  
231 depth, distance to coast, year (2008-2018) and geographical position (latitude and longitude plus an  
232 interaction term between these) at each sampling station. A backwards stepwise model selection  
233 was used to build the GAMs starting with a full model containing all explanatory variables and  
234 removing non-significant variables one at a time. The degrees of freedom of each smooth function  
235 in the GAM models were not constrained and the convergence of the smoothness selection  
236 optimization was inspected for each model. Testing of the fitted models was based on analysis of  
237 deviance. Marginal F-tests (Wood, 2006) were used to compare nested GAM models, and chi-  
238 squared tests (Chambers and Hastie, 1992) applied to compare nested binomial models, selecting  
239 the simpler model if no differences were found (at a significance level of  $\alpha=0.05$ ). The model  
240 selection procedure is summarized in Table 3.

241 Model validation was performed by visually inspecting the residuals obtained for each model  
242 which were plotted against each explanatory variable to assess the presence of patterns. The final  
243 selected models were used to estimate the abundance and recruitment indices by year. For the  
244 hurdle model, estimates of the part 1 binomial GAM (probability of a non-zero event) were  
245 multiplied by estimates of the zero-truncated part 2 (gamma GAM) to obtain a final combined  
246 estimate. Predictions were made for each grid cell within a 3×3 nautical mile grid and averaged for  
247 each survey year over the scallop survey area (Figure 1a). The relative abundance indices derived  
248 from the dredge model ( $N.m^{-2}$ ) were raised to the total dredge area (26,600  $km^2$ ) to generate an  
249 absolute index of abundance and recruitment. The trawl model was used to produce a relative index  
250 of abundance ( $N.m^{-2}$ ) estimated inside the dredge area and this was compared with the dredge  
251 absolute abundance index for the period 2008-2018.

252 All statistical analysis was implemented in the R statistical programming environment (R  
253 Core Team, 2018). The computing of variograms, model fitting, kriging and cross validation were  
254 performed with the gstat package v. 1.1-6 (Pebesma, 2004). GAM models were fitted with R  
255 package mgcv v. 1.8-23 (Wood, 2011). The probability distribution of survey catch rates was  
256 evaluated using functions provided by package fitdistrplus v. 1.0-11 (Delignette-Muller and  
257 Dutang, 2015).

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259

## 260 **Results**

261

262 The two surveys considered in the study are part of MSS research vessel program where the  
263 east coast of Scotland dredge survey is generally carried out one month before the IBTS Q3 trawl  
264 survey. The same vessels were involved in the data collection for each survey with consistent gear  
265 and sampling procedures. The mean number of stations sampled in each year inside the study area  
266 was 108 stations in the dredge surveys and 46 stations in the trawl surveys (Table 1). The dredge  
267 survey area, where sampling effort is higher (1 station per 248  $km^2$ ) is approximately 22% of the  
268 larger trawl area where sampling was sparser (1 station per 2609  $km^2$ ).

269

### 270 Spatial distribution

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272 The spherical model fitted to the dredge surveys gave a range estimate between 59 and 93  
273 km and sills ranging from 0.82 to 0.91 (Table 2). The nuggets varied between 0.53 and 0.76 which  
274 is indicative of relatively high variance at short ranges compared with the overall variability at the  
275 regional scale (sill). The variograms for all individuals and male crabs were similar with  
276 comparable sills and lower estimated nuggets than those found in other scenarios (Figure 2a). For  
277 the trawl survey, which only used catch rates for all crabs combined, a linear variogram with a 0.63  
278 nugget (intercept) and a  $4.07 \times 10^{-4}$  slope was estimated as the best fit (Table 2). This implies that



279 the variance in the trawl survey increases without bounds unlike the dredge survey where the  
280 variance is bounded at the sill.

281 The predicted catch rate for all crabs in the dredge survey was higher in coastal areas  
282 particularly in the south of the Moray Firth and along the south east coast towards the Firth of Forth  
283 (Figure 2b). In the southern area off the Firths of Forth and Tay, the higher predicted catch rates  
284 extended further offshore to the east. Catch rates from the trawl survey had a similar distribution  
285 pattern to that found for the dredge survey, although the prediction area of the former was larger.  
286 Trawl catch rates showed that the high density area in the south found in the dredge survey may  
287 have extended further to the southeast and, in addition, showed a region of medium to high  
288 densities estimated to the north of the Orkney Islands corresponding mostly to gravel grounds  
289 (Figure 1c). The male and female distribution (derived from the dredge survey) were found to be  
290 relatively similar, the main difference being the fact that females were more often found in the  
291 inshore waters south of Orkney and to the east side of the survey area. Juvenile crabs <100mm CW  
292 showed a very clear inshore distribution along the shoreline up to ~20 km from the coast, except in  
293 the north of the survey area where catch rates were low both inshore and offshore.

294 The kriging prediction variances on the five scenarios presented were lowest at and around  
295 the observation points and highest in areas where the number of stations was low. Higher predicted  
296 mean variances were estimated for the female (0.81) and juvenile (0.78) models in relation to the  
297 males and all crabs models (0.61 and 0.62 respectively) (Table 2). Cross-validation analysis  
298 performed to verify the validity of spherical and linear variogram fits and kriging predictions  
299 supported the suitability of the models used. Spatial plots of the residuals for each scenario showed  
300 no spatial patterns in the data.

301

#### 302 Abundance indices

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304 Selected GAMs to model catch rates of all crabs (abundance index) and juvenile crabs  
305 (recruitment index) are summarized in Table 4. As part of the model validation, visual inspection  
306 indicated no obvious patterns in the residuals when plotted against each explanatory variable. The  
307 deviance explained for the dredge and trawl models was 45.7% and 61.6%, respectively. The  
308 Tweedie parameter  $p$  was estimated as 1.14 for the dredge survey and 1.02 for the trawl survey.  
309 Explanatory variables “year”, “distance to coast”, “depth” and “longitude  $\times$  latitude” were selected  
310 for the dredge and trawl models in the abundance index. The “sediment” (BGS) covariate was  
311 found to be not significant in the dredge model ( $p=0.181$ ) based on the analysis of deviances, while  
312 in the trawl model, this variable had a significant effect ( $p=0.04$ ) (Table 3). The trends of the  
313 smooth functions and the BGS parametric term in the trawl model fitted to the catch rates are  
314 illustrated in Figure 3. The response variable for both the dredge and trawl surveys showed an  
315 approximate gamma distribution (positive values) but also contained a large proportion of zeros  
316 (21% in the dredge survey; 78% in the trawl survey) supporting the use of a Tweedie distribution to

317 model the data (Table 4, Figure 3a). The estimated crab catch rates from the dredge survey (1300-  
318 3200 animals/km<sup>2</sup>) were 1-2 orders of magnitude greater than those from the trawl survey (16-65  
319 animals/km<sup>2</sup>) as recorded catches of crabs were much higher in the former (Table 1). The smooth  
320 functions fitted for both models showed mostly non-linear responses to the different covariates  
321 used. The exception was the covariate “distance to coast” in the trawl model for which a linear  
322 (d.f.=1) decrease of catch rates was estimated over the range of distances which were recorded up  
323 to 160 km from the coast. The model applied to the dredge data also showed a decrease of catch  
324 rates with distance to coast (although non-linear), in particular within 30 km from the coast where  
325 most stations were located with data becoming sparser and larger confidence intervals estimated for  
326 distances above 40 km up to the maximum value of 67 km (Figure 3c). In both surveys, the  
327 abundance of crabs seemed to be affected by depth with lower catch rates found generally at  
328 greater depths. Crab catch rates showed a non-linear decrease with depth in the dredge survey  
329 where the depth range was 23-84 m. A similar pattern was observed in the trawl surveys (depth  
330 range 42-192 m) but only for depths shallower than ~150 m (Figure 3d). Smoothed plots for year  
331 effects were also clearly non-linear (Figure 3b). The plot of the effect of BGS sediment (trawl  
332 model only) shows that crab catches in the trawl survey increased gradually from softer to harder  
333 grounds with catch rates peaking in the “gravel” sediment type (Table 4, Figure 3e). An absolute  
334 abundance index was derived from the dredge model and compared with the relative index from  
335 the trawl model. These were compared inside the scallop dredge area where the two surveys  
336 overlap (Figure 4). The total abundance as estimated by the dredge model varied between 34 and  
337 86 million of crabs in the 2008-2018 period (trawl catch rates ranged between 16 and 65 crabs per  
338 square kilometre). The dredge and trawl indices resemble the respective year effects (Figure 3b)  
339 and seem to be correlated showing a very similar trend of increasing catch rates in the early years  
340 of the time series up to 2016 and a subsequent reduction.

341

342 Recruitment index

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344 The dredge survey captured smaller crabs (median=134 mm, mean=135.9 mm) than the  
345 trawl survey (median=160 mm, mean=154.5). The median size per year was found to be  
346 significantly correlated (Pearson correlation=0.83, p=0.002) in the two surveys, but fluctuated with  
347 no trend throughout the study period (Figure 5). Because animals below 100 mm were seldom  
348 caught in trawl surveys, the recruitment index was based on dredge data and was modelled with a  
349 two-part hurdle model. The results from the first part of the model (binomial GAM) showed that  
350 the variables year, distance to coast and geographical position were significant (p<0.05) for  
351 explaining the probability of juvenile crabs being captured in the dredge survey (Table 4). The  
352 depth smoother was borderline insignificant (p=0.054, also included in the model) implying a  
353 slightly lower likelihood of finding juvenile crabs away from the coast and in depths greater than

354 50 m. A  $\chi^2$  test showed that including the type of sediment ( $p=0.254$ ) as an explanatory variable did  
355 not improve the model significantly and this was not included in the final model (Table 3).

356 The second part of the hurdle model used a GAM assuming a gamma distribution of the  
357 response variable, i.e. the catch rate of juvenile crabs caught in each dredge station where juveniles  
358 were recorded (positive catch rates). The results from this model showed that only variables “year”  
359 and geographical position were significant ( $p<0.05$ ) (Table 4). Juvenile crabs in the dredge survey  
360 were mostly found in stations close to the coast in shallow waters, as shown by the geostatistical  
361 analysis (Figure 2a). The variables depth ( $p=0.276$ ), sediment ( $p=0.277$ ) and distance to coast  
362 ( $p=0.079$ ) did not significantly improve the second part of the model and were excluded during the  
363 stepwise selection (Table 3). A predicted recruitment index obtained from combining the two  
364 model parts in the dredge survey area is shown in Figure 6. The recruitment index shows a gradual  
365 increase in juvenile crabs up to 2014 (0.58 million crabs), followed by a recent steep decrease with  
366 the lowest value estimated (0.15 million) observed in 2018.

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368

## 369 **Discussion**

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371 There is an increasing demand from fisheries managers and stakeholders to obtain  
372 information on stock status of exploited marine species. Detailed information on the distribution  
373 patterns of species is often missing in fisheries science. Mapping is an important tool to identify  
374 habitats and the distribution range of important marine resources. Fishery-independent surveys at  
375 sea provide high quality data, as sampling and collection are scientifically designed and  
376 standardized (Pennino *et al.*, 2016). Despite the fact that the two surveys analysed in this study  
377 were aimed at other species such as scallops (dredge) and demersal fish (trawl), data collected on  
378 the distribution of brown crab was informative and useful abundance estimates were derived.  
379 Hilborn and Walters (1992) list a number of limitations of fisheries surveys that may lead to  
380 unrepresentative sampling, including the location of sampling stations in relation to the target  
381 species and the timing of the survey and its relation to the seasonal cycle. The dredge survey  
382 analysed is mostly carried out around the coast, following the scallop fishing distribution in the  
383 East of Scotland which often overlaps with the inshore crab and lobster fishery (Öndes *et al.*,  
384 2016). The trawl survey includes the area of the dredge survey but also extends further offshore to  
385 the east and northern North Sea. The dredge survey has a much higher sampling effort resulting,  
386 not only in more stations per area, but also in much higher catch rates than the trawl surveys, given  
387 that brown crabs are mostly found in the inshore grounds of the North Sea. The timing of the  
388 dredge and trawl surveys is similar as both take place in summer, making the two surveys  
389 comparable.

390 Brown crabs have previously been reported to be caught more frequently by scallop dredges  
391 than trawls (Kaiser *et al.*, 1996). The different catchabilities of the gears may be related to the  
392 different types of operation, including the way these gears interact with the sediment and the

393 towing speed (higher in the trawl survey). The teeth on scallop dredges are able to go deeper in the  
394 sediment, capturing crabs that are buried, whereas trawls are more likely to catch only those crabs  
395 that are active on the surface of the seabed (Öndes *et al.*, 2016). For example, dredges have been  
396 shown to be more efficient than trawls to capture blue crabs (*Callinectes sapidus*) in the western  
397 Atlantic given that these species remain inactive and partially buried in the sediment during winter  
398 months (Vølstad *et al.*, 2000). Brown crabs are also known to lie in the sediment partially buried  
399 (Edwards, 1979; Howard, 1982) making them less available to trawl gears.

400

#### 401 Spatial distribution

402

403 Geostatistics were used to describe the patterns of spatial distribution of brown crab in the  
404 North Sea around the East coast of Scotland. Kriging with external drift is a common way to handle  
405 a trend in non-stationary geostatistics, taking advantage of auxiliary variables that are known across  
406 the study area including the sampling stations (Petitgas *et al.*, 2017). In this study, the predictors  
407 used in the kriging analysis included depth and distance to coast (dredge and trawl), and BGS  
408 sediment type (trawl model only). Results of variographic analyses of the dredge survey suggest  
409 that in the four scenarios (all crabs, females, males, and juveniles) the underlying covariate  
410 function is represented by a spherical model, showing that there is spatial autocorrelation in crab  
411 density estimates at stations located within small distances of each other. The spherical model has  
412 been widely used in fisheries geostatistics given its properties of linear behaviour at the origin  
413 stabilizing on a sill, implying the model is bounded and, therefore, associated with stationary  
414 covariance (Rivoirard *et al.*, 2000; Petitgas *et al.*, 2017). For the trawl data (which uses all crabs)  
415 the nugget effect is higher than for the dredge survey (all crabs scenario) and the semivariance  
416 increases linearly with distance, corresponding to non-stationary covariance, which implies a trend  
417 in the distribution. The spatial distributions of males and female crabs in the dredge survey were  
418 found to be quite similar but there is some evidence of higher female catch rates in the north of the  
419 survey area. Several studies based on tagging provide evidence that female brown crabs move more  
420 frequently and over longer distances than male crabs e.g. in the North Sea (Edwards, 1979),  
421 English Channel (Bennett and Brown, 1983; Hunter *et al.*, 2013), Bay of Biscay (Latrouite and Le  
422 Foll, 1989), Sweden (Ungfors *et al.*, 2007) and north of Scotland (Jones *et al.*, 2010; Coleman and  
423 Rodrigues, 2016). Edwards (1979) describes an inshore movement of crabs in spring for hatching,  
424 moulting and mating, and an offshore movement in the autumn (in particular females) for  
425 spawning. The sediment type may also play a role during spawning as female crabs seem to prefer  
426 softer substratum (more likely found offshore) in order to scoop out a hollow to rest the lower  
427 abdomen and ensure attachment of the eggs to the pleopods (Brown and Bennett, 1980).

428 This study clearly demonstrates that juveniles have a strong preference for inshore grounds  
429 as catch rates peak at small distances from land and most crabs below 100 mm were recorded  
430 within 20 km from the coast. This agrees with previous descriptions of juvenile brown crabs which

431 have been found to live mainly in shallow inshore waters (Bennett, 1974; Bennett, 1995; Robinson  
432 and Tully, 2000) indicating selective habitat preferences possibly related to favourable  
433 environmental and ecological conditions (Pallas *et al.*, 2006; Pardo *et al.*, 2007; Dickens, 2012).  
434 Heterogeneous habitats such as those found inshore may be selected by crabs as a response to the  
435 selective pressure of predation. Structurally complex habitats may result in reduced predation rates  
436 by the provision of refugia/shelter to juvenile animals or by decreasing the chances of encounters  
437 between prey and predators (Harrison and Crespi, 1999).

438

439 Abundance indices

440

441 Abundance indices were estimated from the survey data using GAM models assuming a  
442 Tweedie distribution. Tweedie models are natural candidates for modelling continuous non-  
443 negative variables where many zeros are present in the data (Dunn and Smyth, 2008). Tweedie  
444 distributions have been used as a modelling approach in a diverse range of fields including fisheries  
445 (Candy, 2004; Shono, 2008; Arcuti *et al.*, 2013). In this study, a value of between 1 and 2 was used  
446 for the  $p$  parameter as the Tweedie model was represented by a mix of distributions with a positive  
447 mass around zero, given the high number of stations where no crabs were captured. Results from  
448 the GAM models applied to the dredge and trawl survey data showed a significant effect of  
449 covariates depth and distance to coast in predicting brown crab catch rates. These effects (with the  
450 exception of distance to coast in the trawl survey) were non-linear but reflected a general decrease  
451 in catch rates at greater depths and away from the coast. This study represents a first insight into  
452 the distributional pattern and potential effects of depth and distance to coast on the distribution of  
453 brown crab in the North Sea during the summer. However, these results may not be applicable to other  
454 times of year or other stocks because the distribution of brown crab varies with season and locality,  
455 and the trawl surveys in the present study included few hauls at depths greater than 150 m (while  
456 the dredge survey was restricted to areas of <100 m depth). For example, female brown crabs  
457 support a large fishery in offshore grounds to the north and west of Scotland at depths between 100  
458 and 200 m (Mesquita *et al.*, 2017). More recently, numerous individuals of adult brown crab were  
459 observed at more than 400 m depth (well over the depths normally reported for the species) on the  
460 coast of Norway using video transects (Bakke *et al.*, 2019). In the English Channel, larger adult  
461 crabs tend to be caught in the fishery at greater depths while juveniles and smaller crabs were  
462 mostly reported inshore (as described in this study) but no standardized catch rates were available  
463 (Brown and Bennett, 1980). A study in the Isle of Man found that the catch per unit of effort of  
464 brown crab caught in traps increased with depth but the study was limited to a small inshore area  
465 with depths up to 65 m (Öndes *et al.*, 2019).

466

467 Depth and location preferences of brown crabs may also be associated with substrate  
468 preference. An important difference between the dredge and trawl models was that the latter  
469 included sediment type as an explanatory variable. GAM models applied to the trawl data showed

469 that sediment type was a significant variable for explaining crab catch rates, with higher rates found  
470 in the harder sediment type (gravel) in comparison with the softer sandy and muddy sediments.  
471 This explains the relatively high catch rates predicted in the trawl geostatistical analysis for the  
472 areas to the north of the Orkney Islands where gravel sediment is predominant. This contrasts with  
473 the results obtained for the dredge survey where sediment was not found to be significant, although  
474 the amount of gravel inside the dredge area is restricted to some small patches mostly found in the  
475 south of Moray Firth and to the south of Orkney. The limited amount of stations within the gravel  
476 sediment in the dredge survey in relation to the other sediment types was perhaps not sufficient for  
477 the model to find a significant effect. It is also possible that the physical interaction of dredges and  
478 trawls with each substrate is distinct, implying potential differences in catchability by sediment  
479 type. Crabs are known to live in a variety of different sediment types (Shelton and Hall, 1981) and  
480 habitat preferences may depend on several factors including the migratory and reproductive cycle,  
481 which is thought to differ between males and females.

482 The GAM models for both dredge and trawl catch rate included a significant year effect,  
483 which was used to estimate abundance indices for both gears inside the scallop dredge area. It was  
484 clear that the dredge survey is more efficient at catching brown crabs than the trawl survey and for  
485 this reason we propose a (minimum) absolute abundance estimate for the dredge survey and a  
486 relative abundance index for the trawl survey (used for comparison). Different biases may arise  
487 from the proposed catch rates in the two surveys. The dredge survey only covers an inshore area off  
488 Scotland, although its station density is relatively high. The trawl survey covers a larger area than  
489 the dredge survey but has a lower station density and also a catch rate bias (given its lower  
490 catchability). An absolute abundance estimate for the whole area could potentially be extrapolated  
491 from the dredge survey but caution is needed when interpreting the results, given the absence of  
492 dredge data in the offshore areas.

493 Estimation of absolute abundance from surveys is difficult because it typically requires  
494 assumptions about gear efficiency (Miller *et al.*, 2018). An absolute abundance estimate implies,  
495 for example, assumptions that crabs are not able to swim over the dredge/nets and that no herding  
496 takes place. Crabs of both sexes are known to converge for the reproductive season to facilitate  
497 mating encounters (Edwards, 1979; Orensanz and Gallucci, 1988) but there is no evidence of large  
498 mating aggregations (Hartnoll, 1969), implying that the assumption of no herding is reasonable.  
499 Catch rates estimated from the dredge survey in this study ranged between 1300 and 3200  
500 animals/km<sup>2</sup>. These estimates are comparable to the catch rate for the same species, of 2100  
501 animals  $\geq 70$  mm/km<sup>2</sup>, estimated from a mark-recapture model applied to a population of crabs in  
502 the east coast of England (Bell *et al.*, 2003). There is a very clear similarity in the crab abundance  
503 signal estimated from the two surveys in the present study. The fact that the surveys show the same  
504 signal in terms of crab abundance trends indicates that active gear surveys can be used to estimate  
505 the distribution of brown crabs, even though dredging/trawling are not the main methods employed  
506 by the fishery to capture the species.

507

508 Recruitment index

509

510 The median size of crabs caught during the study period was shown to be correlated in the  
511 two surveys. No crabs below 35 mm were caught by any of the surveys. This is not surprising,  
512 given the habitat preferences of smaller crabs, which are mainly found very close to shore and  
513 outside the areas covered by the surveys. The dredge survey generally captured smaller individuals  
514 than the trawl survey, including juvenile animals below 100 mm CW, suggesting that small crabs  
515 are also more likely to escape trawling and the dredge survey is a better choice to detect  
516 recruitment pulses. Brown crab recruitment estimates were produced for the dredge study area  
517 using a two-part hurdle model. The difficulties associated with fitting a Tweedie model to the  
518 recruitment data may be explained by the high percentage of zeros (87%) in the dredge data, i.e.  
519 individuals below 100 mm CW were only caught in a small percentage of sampled stations. Some  
520 authors have described a poor performance of Tweedie models in handling extremely unbalanced  
521 zero data (around 90% or more zeros), in which case, hurdle models are considered reliable  
522 alternatives to analyse the data (Shono, 2008; Zhou *et al.*, 2018). Two-part GAMs (first part:  
523 presence and absence; second part: catch rates given presence) have been used in fisheries and  
524 ecology studies to describe trends in abundance and geographic distribution in fisheries  
525 (Maravelias, 1997; Murase *et al.*, 2009; Goetz *et al.*, 2012). The hurdle model applied to the  
526 recruitment data showed that several covariates (year, depth, distance to coast) were important in  
527 determining juvenile crab presence (part 1) while only year was significant for juvenile crab catch  
528 rates (given presence) (part 2), although this may be at least in part an artefact of the much smaller  
529 sample size for presence records. From the first part of the model, there was a greater probability of  
530 juvenile crabs being present close to the coast between 40 and 50 m depth, as previously shown by  
531 the geostatistical analysis. When considering only the stations where juveniles were present in the  
532 second part of the model (shallow areas closer to the coast), there was not enough contrast in the  
533 data to detect an effect of depth or distance to coast. The combination of the two parts of the hurdle  
534 model results in a recruitment index peaking in 2014. The highest recruitment estimate was  
535 detected two years before the abundance peak of 2016 on both the dredge and trawl surveys  
536 suggesting that the higher recruitment signal detected in 2014 may have contributed to the higher  
537 estimates two years later. The low recruitment estimated in 2018 suggests that the abundance  
538 decline recently observed is likely to continue in the coming years. Growth studies based on  
539 tagging in the North Sea suggest that it takes around 2 years for a 70 mm crab to reach 115 mm  
540 (Edwards, 1979), although growth may vary with the frequency of moult increments, which is  
541 likely to be related with temperature and may be subject to interannual variability.

542

543

544

545 Future work

546

547 This study demonstrated that spatial modelling may be used to create brown crab distribution  
548 maps and abundance indices from fisheries survey data, allowing for the detection of trends in the  
549 crab fishery. The deviance explained by the GAM models (33- 62%) could be improved by the  
550 inclusion of other potentially influential variables not considered in this study, e.g., bottom water  
551 temperature or current strength. These abiotic factors related to environmental and oceanographic  
552 conditions are strongly associated with the spatial distribution of crustacean assemblages (Basford  
553 *et al.*, 1989; Fariña *et al.*, 1997).

554 One advantage of using dredge and/or trawl gears instead of passive gears such as traps for  
555 obtaining standardized catch rates, is that the catchability of the former is not affected by factors  
556 such as season, bait, current strength/direction (affecting the spread of the bait plume) and soak  
557 time. Additionally, catch rates calculated from mobile gears eliminate issues related with animals  
558 which avoid traps, such as berried females (Howard, 1982), and are not affected by saturation  
559 effects related to the behaviour of the first animals entering the traps. The main limitation  
560 associated with the use of active gear surveys applied to benthic crustaceans is that towed nets or  
561 dredges are limited to trawlable seabed, which may introduce some biases considering that  
562 crustaceans may also live in rocky habitats (Smith and Tremblay, 2003). For this reason, the  
563 abundance estimates provided in this study should be interpreted with caution given the  
564 assumptions (no herding and crabs unable to escape by swimming over the nets/dredge) and should  
565 be regarded as a minimum estimate. Abundance data may be used in stock assessment models and  
566 when combined with other sources of data such as effort, landings and catch composition (e.g.  
567 length) may be able to provide information on the dynamics of the stock (Maunder and Piner,  
568 2014). There have previously been no abundance indices available for the Scottish brown crab  
569 fisheries. The methodology developed here was applied to the North Sea but could potentially be  
570 extended to other areas in Europe covered by scallop and dredge surveys. This approach has the  
571 potential to be used in stock assessment to determine stock status and provide future advice on  
572 sustainable levels of catches, contributing to the management of the brown crab fisheries around  
573 Scotland and elsewhere.

574

575

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577

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582



583

584

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773 **Table legends**

774

775 Table 1. Summary information for dredge and trawl surveys in the present study: vessel used, year,  
776 month, numbers of stations and crabs sampled.

777

778 Table 2. Variogram models fitted to the dredge and trawl surveys including type of model (Sph-  
779 spherical, Lin-linear), lag distance information, model parameters (range, sill, nugget and slope),  
780 goodness of fit (RSS-residual sum of squares) and mean predicted variance.

781

782 Table 3. Variable selection for the abundance (dredge and trawl) and recruitment index models  
783 using a backwards stepwise approach. Hypothesis testing was performed with marginal F-tests  
784 (GAMs) and  $\chi^2$  tests (binomial GAMs).

785

786 Table 4. Selected models for estimating abundance (dredge and trawl GAMs) and recruitment  
787 (hurdle). For the BGS sediment effect (trawl model only), gravel is used as the reference type. The  
788 significance of parametric model terms was tested with t-tests. The p-values associated with the  
789 GAM smothers for each model term were derived from Wald tests (Wood, 2012).

790

791 **Figure legends**

792

793 Figure 1. (a) Study region on the east coast of Scotland with the dredge and trawl survey areas and  
794 stations sampled (2008-2018). (b) Bathymetry map of the study area (depth in metres). (c)  
795 Distribution of marine sediments in the study area from the British Geological Survey (Cooper *et*  
796 *al.*, 2013).

797

798 Figure 2. (a) Variograms estimating semivariance ( $\gamma$ ) with spherical (parameters: range-*rg*, sill-*si*,  
799 nugget-*ng*) and linear (parameters: intercept/nugget-*ng*, slope-*sl*) models. (b) Kriged maps showing  
800 predicted catch rates (in the transformed log scale). The five analysis scenarios considered are  
801 displayed from top to bottom: 1.all crabs (dredge), 2.females (dredge), 3.males (dredge),  
802 4.juveniles (dredge) and 5.all crabs (trawl).

803

804 Figure 3. Results for the abundance and recruitment indices derived from the dredge model (top  
805 panel), trawl model (second panel) and hurdle models (third and bottom panels) applied to brown  
806 crab catch rates. (a) Distribution of the response variable; (b) partial effect of “year”; (c) partial  
807 effect of “distance to coast”; (d) partial effect of “depth”; (e) parametric effect of BGS sediment  
808 type (trawl model only; gravel is used as the reference type). The dashed lines give the standard  
809 errors around the parametric and smooth effects (shown in the scale of the linear predictor).

810

811 Figure 4. Brown crab abundance indices by year estimated from GAMs applied to dredge (solid  
812 line, left vertical axis) and trawl (dashed line, right vertical axis) surveys (2008-2018) with 95%  
813 confidence intervals. The abundance index for the dredge model is an absolute estimate (millions  
814 of individuals) while the trawl index is relative ( $N.m^{-2}$ ). Predictions are averaged for grid cells  
815 within the dredge survey area (Figure 1a).

816

817 Figure 5. Length frequency distribution of brown crabs captured in the dredge and trawl surveys  
818 (2008-2018). The medians and means in each year are represented by the full and dotted vertical  
819 lines respectively.

820

821 Figure 6. Brown crab recruitment index by year with 95% confidence intervals. The recruitment  
822 index is an absolute estimate calculated as the number (millions) of juvenile crabs <100mm CW.  
823 Recruitment estimates were derived from a hurdle model applied to dredge surveys (2008-2018).  
824 Predictions are averaged for all grid cells within the dredge survey area (Figure 1a).

825

826

827 **Tables**

828

829 **Table 1**

Survey	Vessel	Year	Month	N stations*	N crabs*
Dredge	FRV Alba na Mara	2008	Jun-Jul	92	241
Trawl	FRV Scotia	2008	Aug	38	7
Dredge	FRV Alba na Mara	2009	Jul	99	176
Trawl	FRV Scotia	2009	Aug	41	11
Dredge	FRV Alba na Mara	2010	Jun-Jul	114	261
Trawl	FRV Scotia	2010	Aug-Sep	46	14
Dredge	FRV Alba na Mara	2011	Jun-Jul	113	272
Trawl	FRV Scotia	2011	Jul-Aug	43	14
Dredge	FRV Alba na Mara	2012	May-Jun	117	404
Trawl	FRV Scotia	2012	Jul-Aug	40	8
Dredge	FRV Alba na Mara	2013	Jul	116	324
Trawl	FRV Scotia	2013	Jul-Aug	38	12
Dredge	FRV Alba na Mara	2014	Jun	107	610
Trawl	FRV Scotia	2014	Jul-Aug	41	19
Dredge	FRV Alba na Mara	2015	May-Jun	90	327
Trawl	FRV Scotia	2015	Jul-Aug	51	39
Dredge	FRV Alba na Mara	2016	May-Jun	115	544
Trawl	FRV Scotia	2016	Aug	57	35
Dredge	FRV Alba na mara	2017	Jun	119	345
Trawl	FRV Scotia	2017	Aug	50	42
Dredge	FRV Alba na Mara	2018	Jul	109	284
Trawl	FRV Scotia	2018	Jul-Aug	56	20

830 \*Number of stations and crabs sampled during each survey within the dredge and trawl  
 831 areas used for this study shown in Figure 1a

832

833

834 **Table 2**

	<b>Dredge</b>				<b>Trawl</b>
	All	Females	Males	<100mm	All
Model	Sph	Sph	Sph	Sph	Lin
Lag distance (km)	10	10	10	10	25
Range (km)	71	93	91	59	-
Sill	0.82	0.91	0.84	0.86	-
Nugget	0.53	0.76	0.54	0.71	0.63
Slope	-	-	-	-	4.07e-04
RSS	8.61	4.62	10.29	11.32	1.45
Mean variance	0.62	0.81	0.61	0.78	0.66

835

836

837 Table 3

Models	Model type (assumed distribution)	Covariates	Dropped	p-value	Test
<b>Dredge</b>					
Model 1	GAM (Tweedie)	<i>Year, Distance, Depth, BGS, Lon*Lat</i>			
Model 2 <sup>^</sup>		<i>Year, Distance, Depth, Lon*Lat</i>	<i>BGS</i>	0.181	F
<b>Trawl</b>					
Model 3 <sup>^</sup>	GAM (Tweedie)	<i>Year, Distance, Depth, BGS, Lon*Lat</i>	-	-	
<b>Recruitment index</b>					
Model 4	Hurdle GAM1 (Binomial) catch rate (0,1)	<i>Year, Distance, Depth, BGS, Lon*Lat</i>			
Model 5 <sup>^</sup>		<i>Year, Distance, Depth, Lon*Lat</i>	<i>BGS</i>	0.254	$\chi^2$
Model 6		<i>Year, Distance, Depth, BGS, Lon*Lat</i>			
Model 7	Hurdle GAM2 (gamma) catch rate > 0	<i>Year, Distance, BGS, Lon*Lat</i>	<i>Depth</i>	0.276	F
Model 8		<i>Year, Distance, Lon*Lat</i>	<i>BGS</i>	0.277	F
Model 9 <sup>^</sup>		<i>Year, Lon*Lat</i>	<i>Distance</i>	0.079	F

838 <sup>^</sup> Selected parsimonious model  
 839 Lon\*Lat includes variables longitude, latitude and an interaction term between these.

840

841

842 Table 4

843

Model	Abundance index						Recruitment index					
	Dredge			Trawl			Dredge					
	GAM			GAM			Hurdle			GAM2		
							GAM1			GAM2		
N	1191			501			1191			155		
Perc. zeros (%)	20.9			77.8			87.0			0		
Family	Tweedie			Tweedie			Binomial			Gamma		
Link function	log			log			logit			log		
P	1.14			1.02			-			-		
Dev. explained (%)	45.7			61.6			32.5			41.6		
GVC/UBRE score	3.606e-04			1.957e-05			-0421*			0.323		
Model terms	Est.	d.f.	p-val	Est.	d.f.	p-val	Est.	d.f.	p-val	Est.	d.f.	p-val
<b>Smoothers</b>												
<i>Year</i>	-	8.7	<0.001	-	3.6	<0.001	-	7.7	<0.001	-	7.5	0.005
<i>Distance</i>	-	6.9	<0.001	-	1	<0.001	-	5.2	<0.001	-	-	-
<i>Depth</i>	-	7.4	<0.001	-	7	<0.001	-	5.3	0.054	-	-	-
<i>Lon*Lat</i>	-	25.3	<0.001	-	28.1	<0.001	-	14.7	0.001	-	13.1	0.012
<b>Parametric terms</b>												
<i>Intercept</i>	-9.084	1	<0.001	-11.78	1	<0.001	-2.859	1	<0.001	-9.487	1	<0.001
<b>BGS</b>												
<i>Gravelly Sand</i>	-	-	-	-1.472	1	0.009	-	-	-	-	-	-
<i>Sand</i>	-	-	-	-1.729	1	0.005	-	-	-	-	-	-
<i>Mud</i>	-	-	-	-1.901	1	0.022	-	-	-	-	-	-

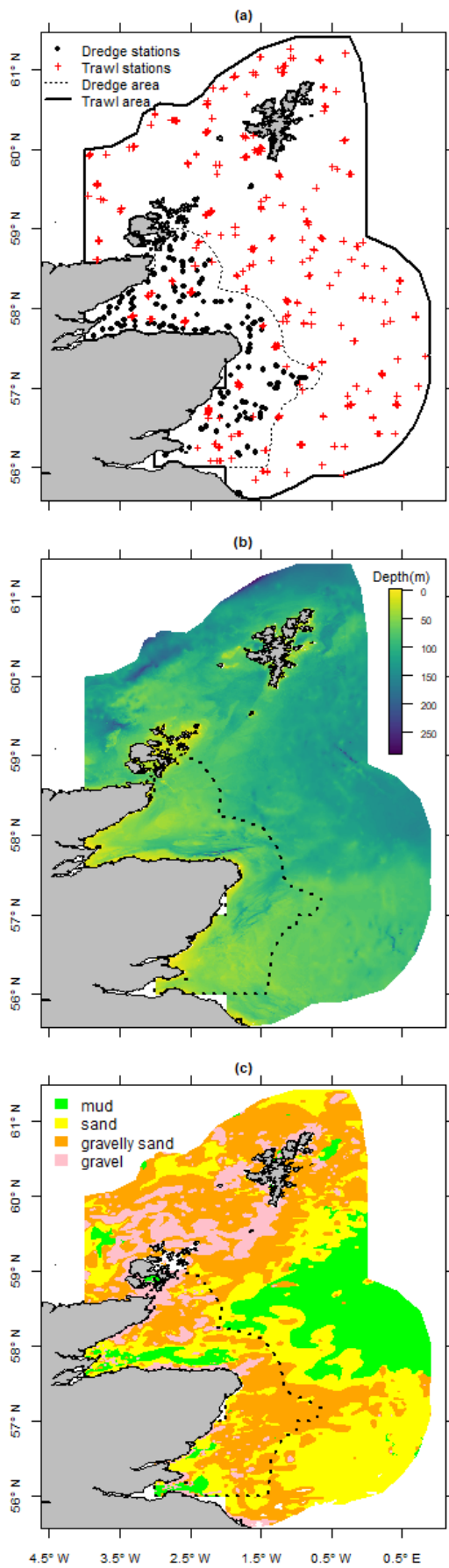
844 \*GCV was used as the prediction error criteria for all models except the binomial GAM where the scale parameter is known and an Un-Biased Risk  
 845 Estimator (UBRE) is used instead (Wood, 2011).

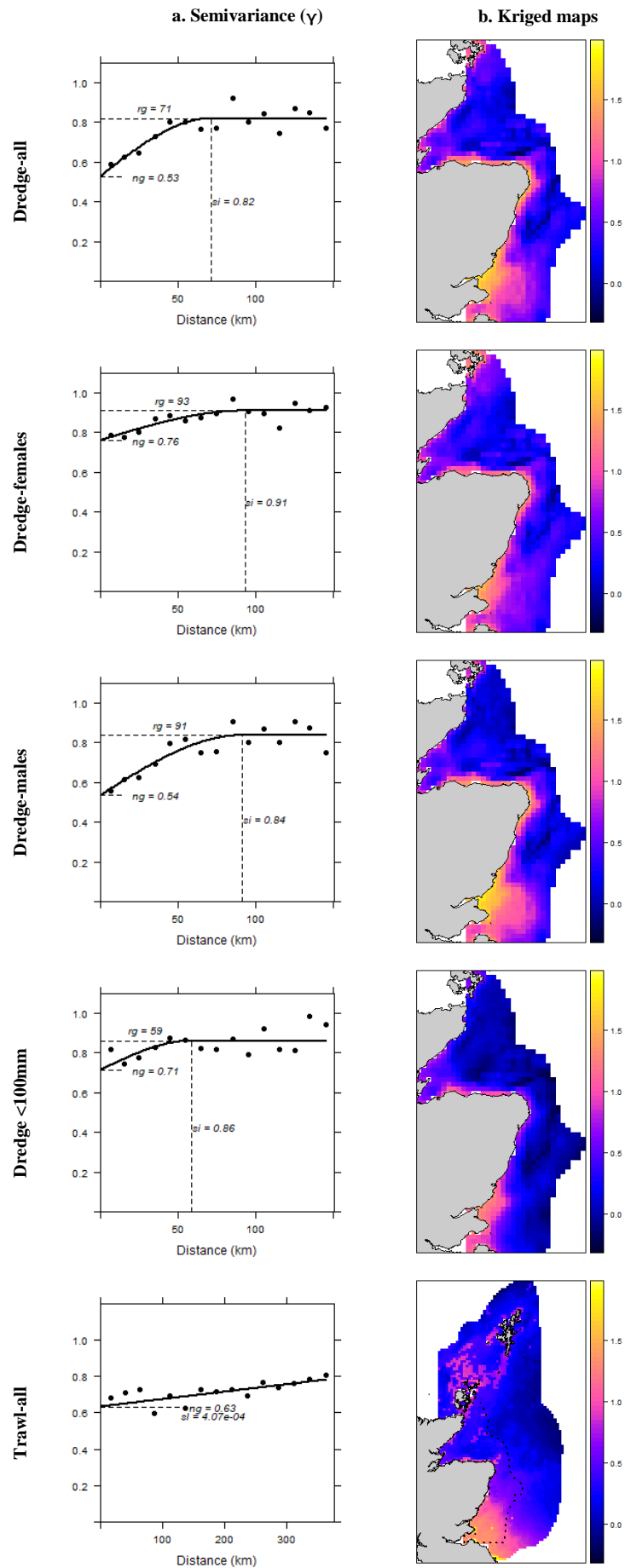
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847 **Figures**

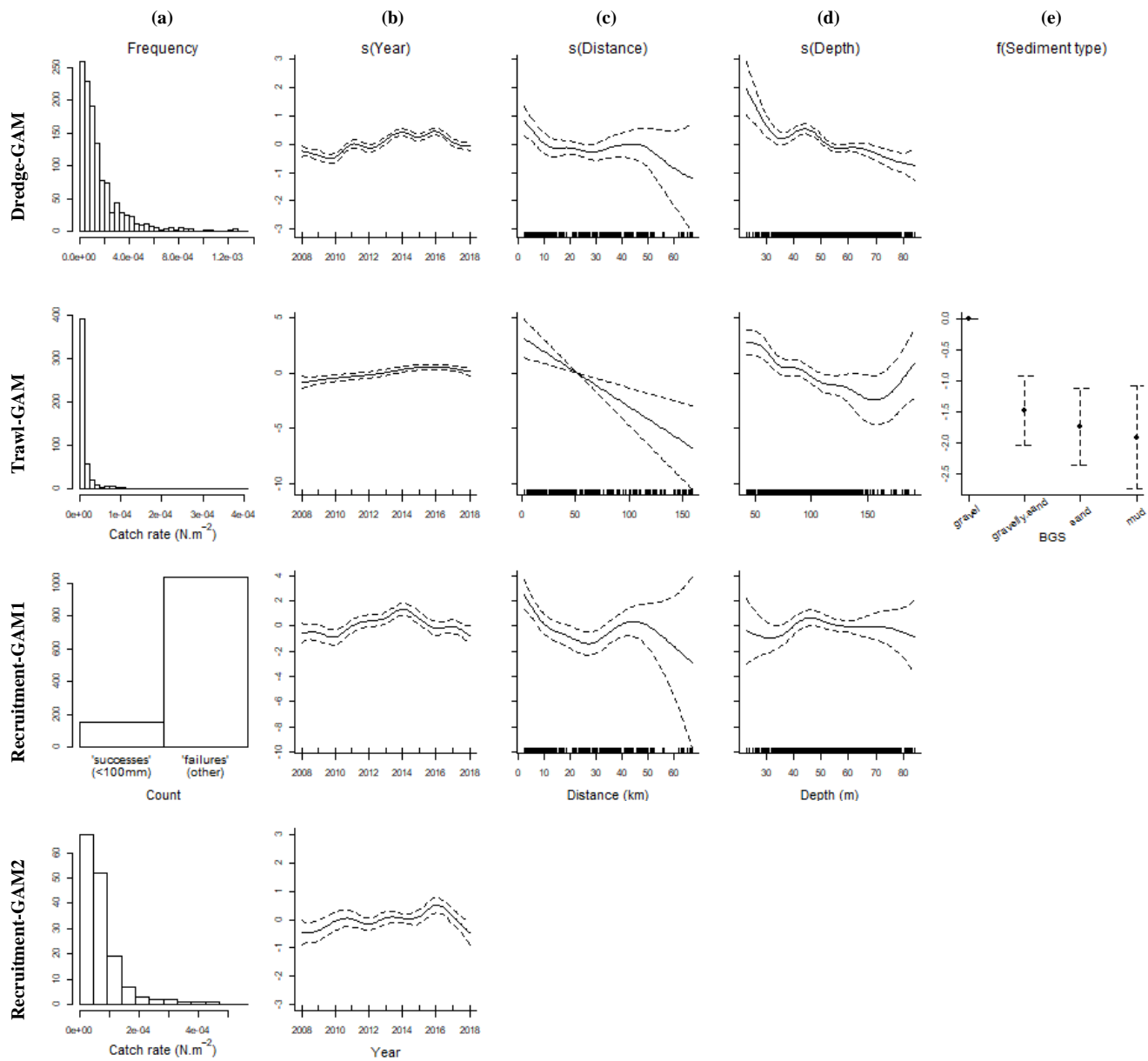
848 **Figure 1**





851 Figure 3

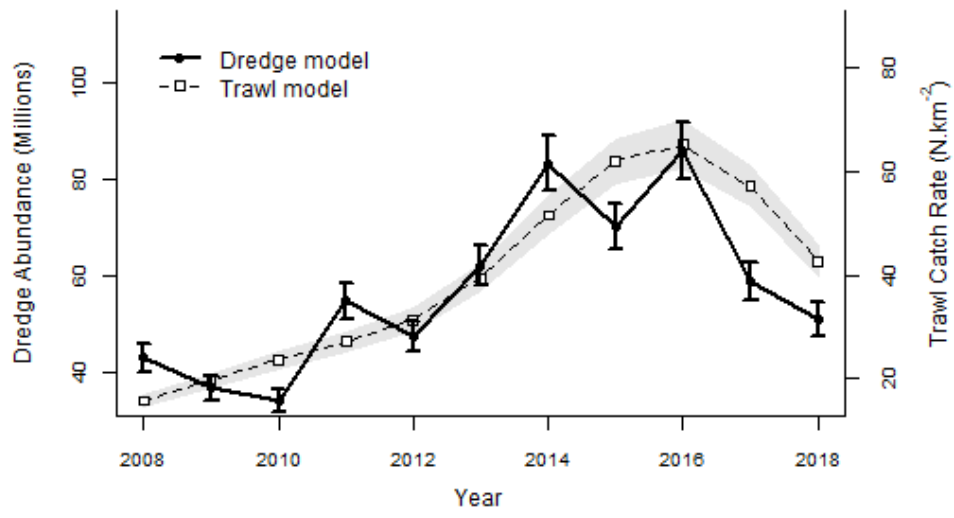
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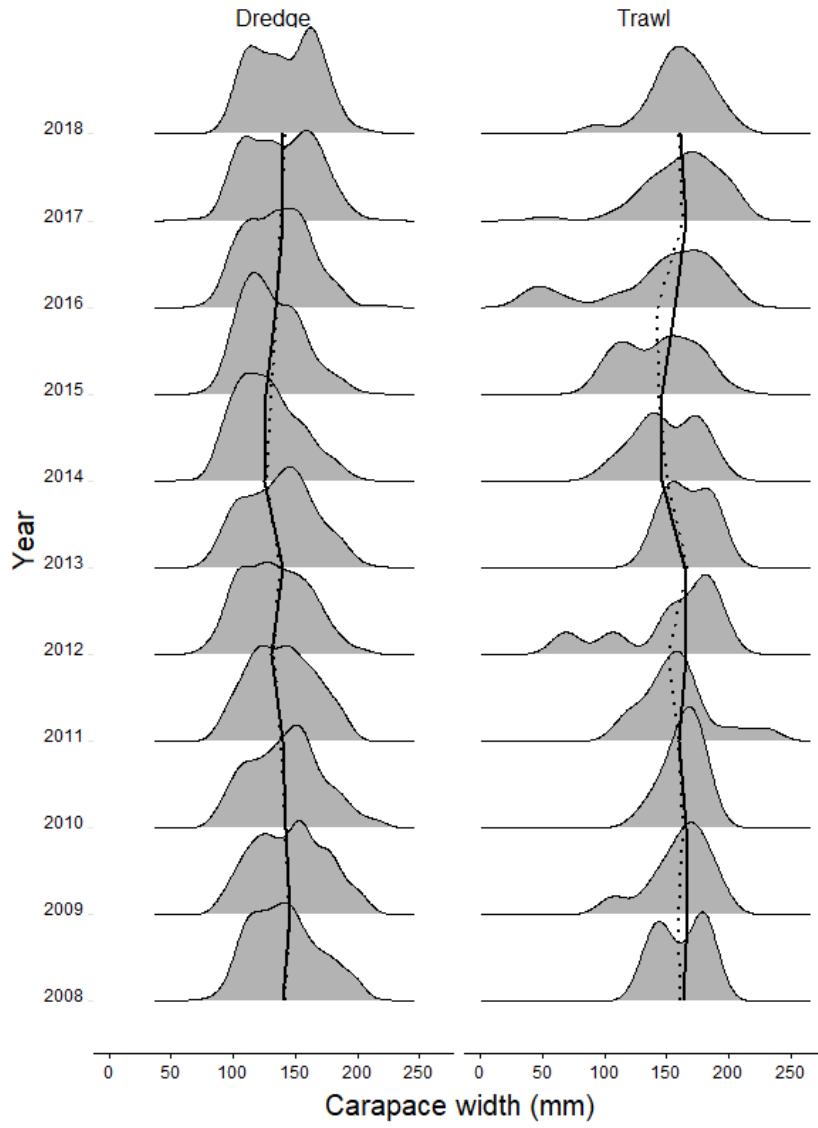
855 Figure 4



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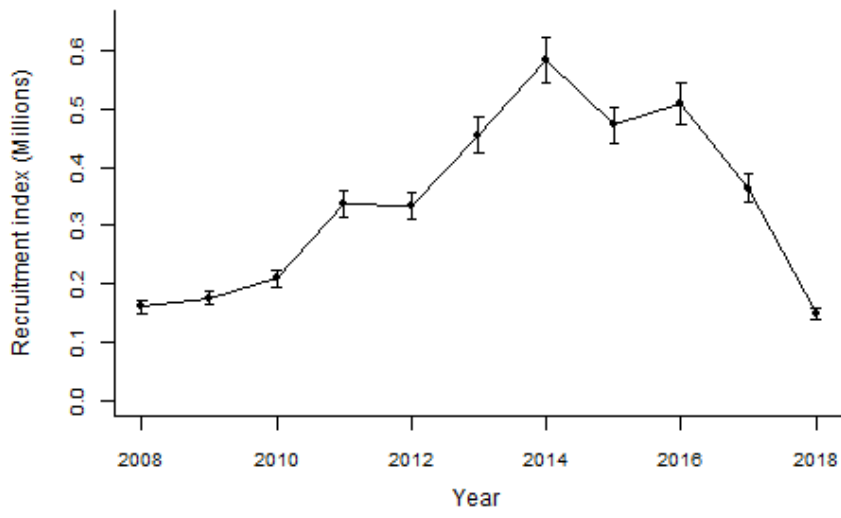
858 Figure 5



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860

861 Figure 6



862

863