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

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Abstract

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

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

Introduction

The brown crab (*Cancer pagurus*) is a decapod crustacean which inhabits sandy and rocky seabeds of northwestern Europe (Edwards, 1979), from the littoral zone, to depths of over 100 m (Shelton and Hall, 1981). Like other crustaceans, the growth of brown crab takes place by moulting the shell, with moult frequency decreasing with age. The species reaches the minimum landing size (MLS) in Scotland of 150 mm carapace width (CW) at an age of around 6 years (Mill *et al.*, 2009). The brown crab is considered to be a slow-growing species with a lifespan of approximately 20 years, reaching an asymptotic size (L∞) of between 220 and 246 mm in Scottish waters (Bennett, 1974; Tallack, 2002; Mill *et al.*, 2009).It is a commercially valuable species with annual landings into Scotland in excess of 10,000 tonnes and a first sale value of £26.8 million in 2018 (Scottish Sea Fisheries Statistics, 2018). Pot fisheries for brown crabs occur along almost the entire length of the British coastline and traditionally these fisheries have been essentially inshore (Eaton *et al.*, 2001). Since the late 1980's, offshore crab fisheries have developed, rapidly becoming the largest pot fisheries both in the North Sea and west coast of Scotland. More recently, the expanded demand for this species from European and emergent Asian markets makes an evaluation of its status more important (Mesquita *et al.*, 2017).

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

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

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

Methods

Study area and sampling

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

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

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

Environmental variables

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

Spatial distribution

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

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

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

Variograms can be used to quantify the mean variability (semi-variance) of a regionalized variable as a function of the distance between any two points (Petitgas *et al.*, 2017). Omnidirectional empirical variograms were computed for the transformed catch rates for both dredge and trawl surveys in each year (2008-2018) using the estimator (Matheron, 1963):

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

where γ is the calculated semi-variance for each dataset, $Z(x_i)$ the catch rate of brown crabs at sampled station x_i, $Z(x_i + h)$ is the catch rate value separated from x_i by a lag distance h (measured as a straight line, in km) and *N(h)* is the number of observation pairs separated by *h*. A distance *h* of 10 km was used for the dredge survey and 25 km for the trawl survey (number of lags = 15) (Table 2).

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

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

Abundance and recruitment indices

To estimate temporal trends and an abundance index of brown crab in the study area, GAMs were applied to the survey data using the catch rate per haul (numbers of crabs caught per square metre) as the response variable. Two sets of models were fitted separately, for the dredge and trawl surveys. Large numbers of zero observations were present in both survey datasets, as no crabs were recorded in many of the sampled stations. To deal with zero observations and considering the response variable was markedly right-skewed, a GAM was applied assuming a Tweedie distribution (Tweedie, 1984; Dunn and Smyth, 2005) with a log link. Tweedie models belong to the exponential family of distributions and include a power mean-variance relationship, $V(\mu) = \mu^p$, where $V()$ is the variance function, μ is the mean of the distribution and p is a parameter ($1<p<2$), where $p=1$ implies a Poisson distribution and $p=2$ a gamma distribution (Dunn and Smyth, 2005). The parameter p was estimated for each survey during the fitting procedure with the *tw* function in the mgcv R package (Wood, 2011).

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

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

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

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

Results

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

Spatial distribution

The spherical model fitted to the dredge surveys gave a range estimate between 59 and 93 km and sills ranging from 0.82 to 0.91 (Table 2). The nuggets varied between 0.53 and 0.76 which is indicative of relatively high variance at short ranges compared with the overall variability at the regional scale (sill). The variograms for all individuals and male crabs were similar with comparable sills and lower estimated nuggets than those found in other scenarios (Figure 2a). For the trawl survey, which only used catch rates for all crabs combined, a linear variogram with a 0.63 nugget (intercept) and a 4.07×10^{-4} slope was estimated as the best fit (Table 2). This implies that the variance in the trawl survey increases without bounds unlike the dredge survey where the variance is bounded at the sill.

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

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

Abundance indices

Selected GAMs to model catch rates of all crabs (abundance index) and juvenile crabs (recruitment index) are summarized in Table 4. As part of the model validation, visual inspection indicated no obvious patterns in the residuals when plotted against each explanatory variable. The deviance explained for the dredge and trawl models was 45.7% and 61.6%, respectively. The Tweedie parameter p was estimated as 1.14 for the dredge survey and 1.02 for the trawl survey. Explanatory variables “year”, “distance to coast”, “depth” and “longitude × latitude” were selected for the dredge and trawl models in the abundance index. The “sediment” (BGS) covariate was found to be not significant in the dredge model (p=0.181) based on the analysis of deviances, while in the trawl model, this variable had a significant effect (p=0.04) (Table 3). The trends of the smooth functions and the BGS parametric term in the trawl model fitted to the catch rates are illustrated in Figure 3. The response variable for both the dredge and trawl surveys showed an approximate gamma distribution (positive values) but also contained a large proportion of zeros (21% in the dredge survey; 78% in the trawl survey) supporting the use of a Tweedie distribution to model the data (Table 4, Figure 3a). The estimated crab catch rates from the dredge survey (1300-3200 animals/km^2) were 1-2 orders of magnitude greater than those from the trawl survey (16-65 animals/km^2) as recorded catches of crabs were much higher in the former (Table 1). The smooth functions fitted for both models showed mostly non-linear responses to the different covariates used. The exception was the covariate "distance to coast" in the trawl model for which a linear (d.f.=1) decrease of catch rates was estimated over the range of distances which were recorded up to 160 km from the coast. The model applied to the dredge data also showed a decrease of catch rates with distance to coast (although non-linear), in particular within 30 km from the coast where most stations were located with data becoming sparser and larger confidence intervals estimated for distances above 40 km up to the maximum value of 67 km (Figure 3c). In both surveys, the abundance of crabs seemed to be affected by depth with lower catch rates found generally at greater depths. Crab catch rates showed a non-linear decrease with depth in the dredge survey where the depth range was 23-84 m. A similar pattern was observed in the trawl surveys (depth range 42-192 m) but only for depths shallower than ~150 m (Figure 3d). Smoothed plots for year effects were also clearly non-linear (Figure 3b). The plot of the effect of BGS sediment (trawl model only) shows that crab catches in the trawl survey increased gradually from softer to harder grounds with catch rates peaking in the "gravel" sediment type (Table 4, Figure 3e). An absolute abundance index was derived from the dredge model and compared with the relative index from the trawl model. These were compared inside the scallop dredge area where the two surveys overlap (Figure 4). The total abundance as estimated by the dredge model varied between 34 and 86 million of crabs in the 2008-2018 period (trawl catch rates ranged between 16 and 65 crabs per square kilometre). The dredge and trawl indices resemble the respective year effects (Figure 3b) and seem to be correlated showing a very similar trend of increasing catch rates in the early years of the time series up to 2016 and a subsequent reduction.

Recruitment index

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

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

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

Discussion

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

Brown crabs have previously been reported to be caught more frequently by scallop dredges than trawls (Kaiser *et al.*, 1996). The different catchabilities of the gears may be related to the different types of operation, including the way these gears interact with the sediment and the towing speed (higher in the trawl survey). The teeth on scallop dredges are able to go deeper in the sediment, capturing crabs that are buried, whereas trawls are more likely to catch only those crabs that are active on the surface of the seabed (Öndes *et al.*, 2016). For example, dredges have been shown to be more efficient than trawls to capture blue crabs (*Callinectes sapidus*) in the western Atlantic given that these species remain inactive and partially buried in the sediment during winter months (Vølstad *et al.*, 2000). Brown crabs are also known to lie in the sediment partially buried (Edwards, 1979; Howard, 1982) making them less available to trawl gears.

Spatial distribution

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

This study clearly demonstrates that juveniles have a strong preference for inshore grounds as catch rates peak at small distances from land and most crabs below 100 mm were recorded within 20 km from the coast. This agrees with previous descriptions of juvenile brown crabs which have been found to live mainly in shallow inshore waters (Bennett, 1974; Bennett, 1995; Robinson and Tully, 2000) indicating selective habitat preferences possibly related to favourable environmental and ecological conditions (Pallas *et al.*, 2006; Pardo *et al.*, 2007; Dickens, 2012). Heterogeneous habitats such as those found inshore may be selected by crabs as a response to the selective pressure of predation. Structurally complex habitats may result in reduced predation rates by the provision of refugia/shelter to juvenile animals or by decreasing the chances of encounters between prey and predators (Harrison and Crespi, 1999).

Abundance indices

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

Depth and location preferences of brown crabs may also be associated with substrata preference. An important difference between the dredge and trawl models was that the latter included sediment type as an explanatory variable. GAM models applied to the trawl data showed that sediment type was a significant variable for explaining crab catch rates, with higher rates found in the harder sediment type (gravel) in comparison with the softer sandy and muddy sediments. This explains the relatively high catch rates predicted in the trawl geostatistical analysis for the areas to the north of the Orkney Islands where gravel sediment is predominant. This contrasts with the results obtained for the dredge survey where sediment was not found to be significant, although the amount of gravel inside the dredge area is restricted to some small patches mostly found in the south of Moray Firth and to the south of Orkney. The limited amount of stations within the gravel sediment in the dredge survey in relation to the other sediment types was perhaps not sufficient for the model to find a significant effect. It is also possible that the physical interaction of dredges and trawls with each substrate is distinct, implying potential differences in catchability by sediment type. Crabs are known to live in a variety of different sediment types (Shelton and Hall, 1981) and habitat preferences may depend on several factors including the migratory and reproductive cycle, which is thought to differ between males and females.

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

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

Recruitment index

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

Future work

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

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

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Table legends

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

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

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

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

Figure legends

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

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

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

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

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

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

Tables

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

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

Table 2

	Dredge				**Trawl**
	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

Table 3

Models	Model type (assumed distribution)	Covariates	Dropped	p-value	Test
Dredge					
Model 1	GAM (Tweedie)	_Year, Distance, Depth, BGS, Lon*Lat_			
Model 2^		_Year, Distance, Depth, Lon*Lat_	_BGS_	0.181	F
Trawl					
Model 3^	GAM (Tweedie)	_Year, Distance, Depth, BGS, Lon*Lat_	-	-	
Recruitment index					
Model 4	Hurdle GAM1 (Binomial) catch rate (0,1)	_Year, Distance, Depth, BGS, Lon*Lat_			
Model 5^		_Year, Distance, Depth, Lon*Lat_	_BGS_	0.254	χ^2
Model 6	Hurdle GAM2 (gamma) catch rate > 0	_Year, Distance, Depth, BGS, Lon*Lat_			
Model 7		_Year, Distance, BGS, Lon*Lat_	_Depth_	0.276	F
Model 8		_Year, Distance, Lon*Lat_	_BGS_	0.277	F
Model 9^		_Year, Lon*Lat_	_Distance_	0.079	F

^ Selected parsimonious model

Lon*Lat includes variables longitude, latitude and an interaction term between these.

Table 4

	Abundance index		Recruitment index	
	Dredge	Trawl	Dredge	
			Hurdle	
Model	GAM	GAM	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
Smoothers												
Year	-	8.7	<0.001	-	3.6	<0.001	-	7.7	<0.001	-	7.5	0.005
Distance	-	6.9	<0.001	-	1	<0.001	-	5.2	<0.001	-	-	-
Depth	-	7.4	<0.001	-	7	<0.001	-	5.3	0.054	-	-	-
Lon*Lat	-	25.3	<0.001	-	28.1	<0.001	-	14.7	0.001	-	13.1	0.012
Parametric terms												
Intercept	-9.084	1	<0.001	-11.78	1	<0.001	-2.859	1	<0.001	-9.487	1	<0.001
BGS												
Gravelly Sand	-	-	-	-1.472	1	0.009	-	-	-	-	-	-
Sand	-	-	-	-1.729	1	0.005	-	-	-	-	-	-
Mud	-	-	-	-1.901	1	0.022	-	-	-	-	-	-

*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 Estimator (UBRE) is used instead (Wood, 2011).

Figures

Figure 1

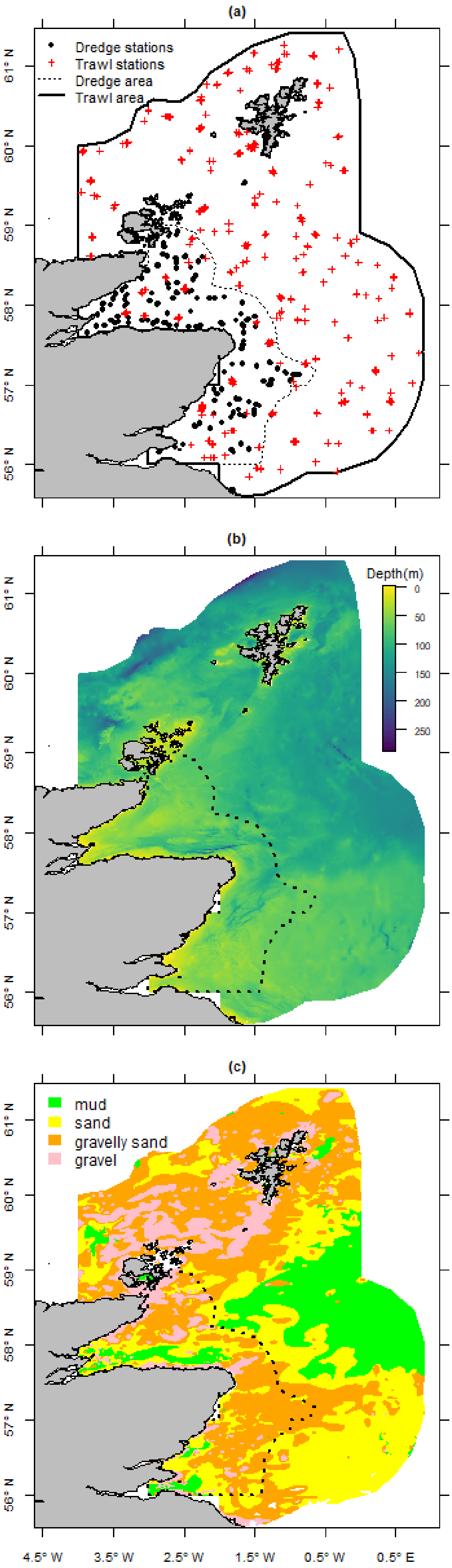


Figure 2

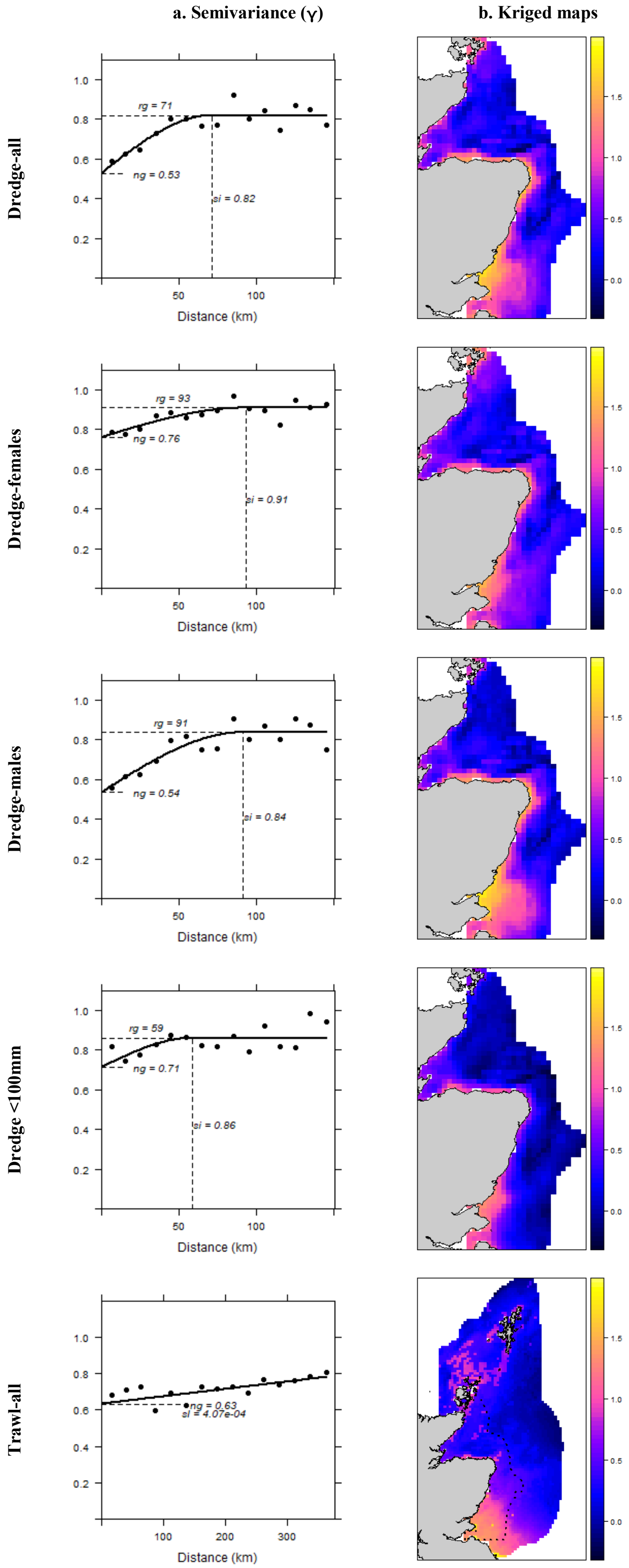

a. Semivariance (γ)
b. Kriged maps
Dredge-all
rg = 71
ng = 0.53
si = 0.82
Dredge-females
rg = 93
ng = 0.76
si = 0.91
Dredge-males
rg = 91
ng = 0.54
si = 0.84
Dredge <100mm
rg = 59
ng = 0.71
si = 0.86
Trawl-all
ng = 0.63
sl = 4.07e-04
1.0
0.8
0.6
0.4
0.2
50
100
200
300
Distance (km)
1.5
1.0
0.5
0.0

Figure 3

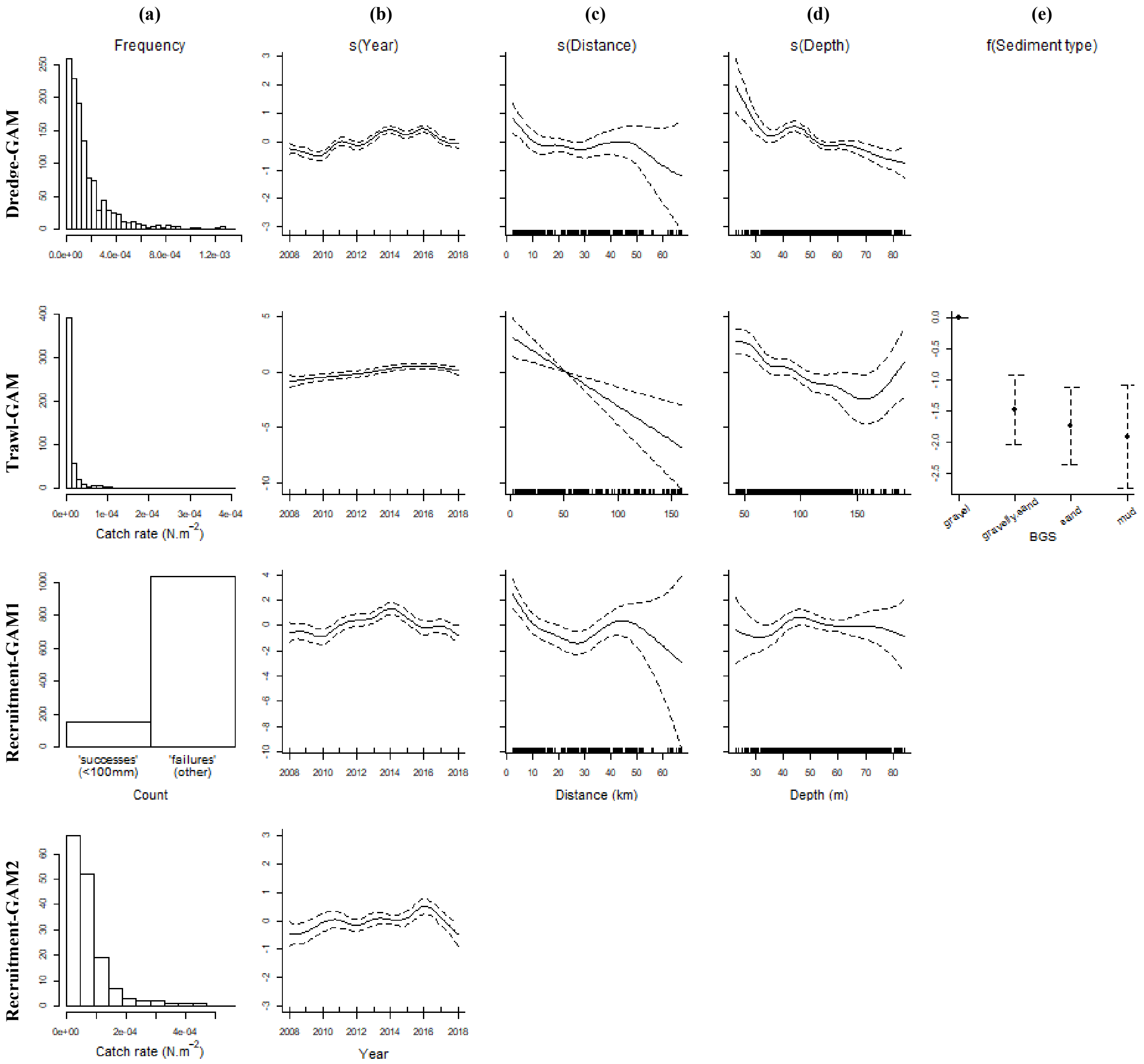
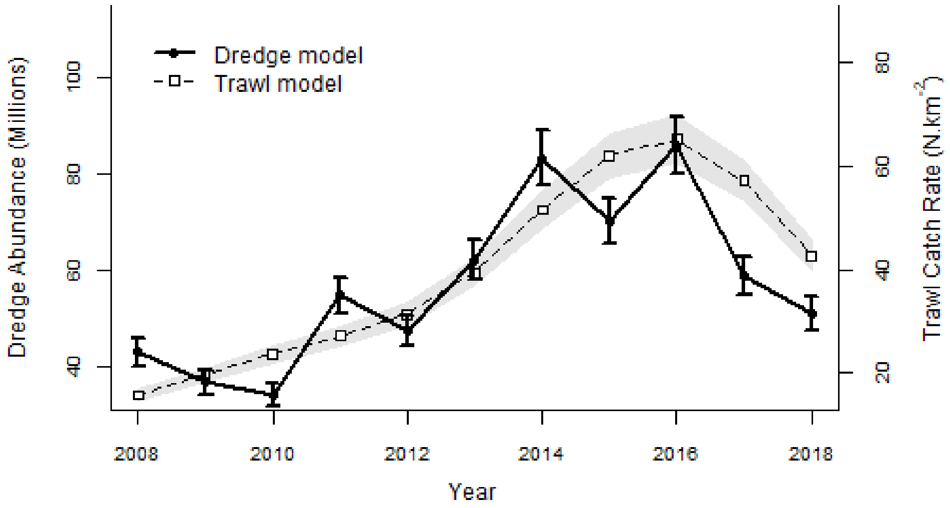
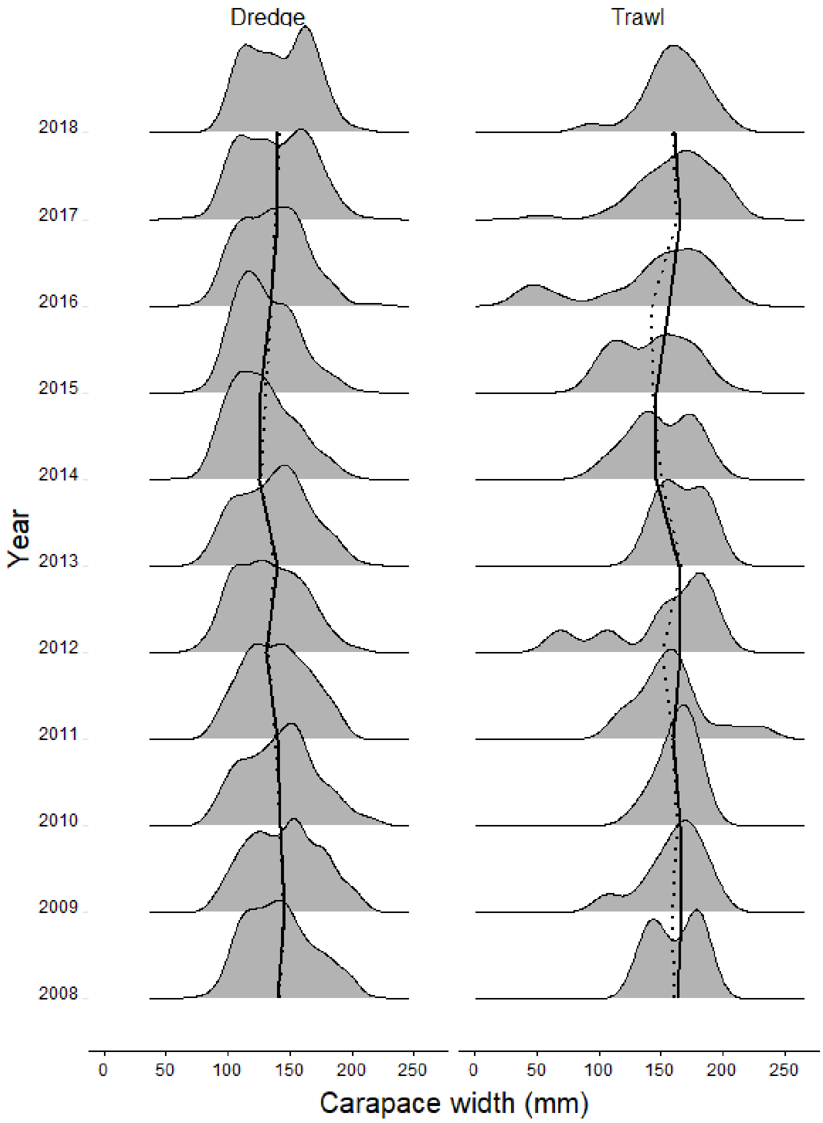

(a)
(b)
(c)
(d)
(e)
Frequency
s(Year)
s(Distance)
s(Depth)
f(Sediment type)
Dredge-GAM
Trawl-GAM
Recruitment-GAM1
Recruitment-GAM2
0.0e+00
4.0e-04
8.0e-04
1.2e-03
0e+00
1e-04
2e-04
3e-04
4e-04
Catch rate (N.m^{-2})
'successes' (<100mm)
'failures' (other)
Count
2e-04
4e-04
Catch rate (N.m^{-2})
2008
2010
2012
2014
2016
2018
Year
Distance (km)
Depth (m)
gravel
gravelly sand
sand
mud
BGS

Figure 4


Dredge model
Trawl model
Dredge Abundance (Millions)
40
60
80
100
Trawl Catch Rate (N.km^{-2})
20
40
60
80
2008
2010
2012
2014
2016
2018
Year

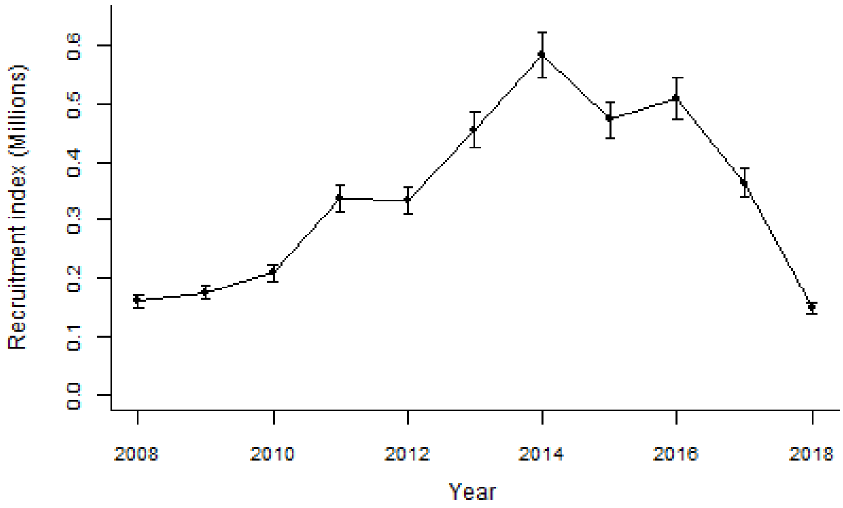
858 Figure 5



859

860

Figure 6


Recruitment index (Millions)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
2008
2010
2012
2014
2016
2018
Year