Predicting Spatial Abundance Of Common Demersal Fish In The Irish Sea

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DECLARATION and STATEMENTS

This work has not previously been accepted in substance for any degree and is not being concurrently submitted for any degree.

This dissertation is being submitted in partial fulfilment of the requirement of M.Sc. Marine Biology.

This dissertation is the result of my own independent work / investigation, except where otherwise stated.

Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

I hereby give consent for my dissertation, if accepted, to be made available for photocopying and for inter-library loan, and the title and summary to be made available to outside organisations.

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Contents

Figures

Tables

Predicting Spatial Abundance Of Common Demersal Fish In The Irish Sea

By Jessica Schop

Abstract

Knowledge of the spatial distribution of marine fish species is an important tool for the development of fisheries management plans. An example of the implementation of such management is the development of marine protected areas. Habitat suitability of species is a key feature in defining the spatial distributions. In this study the habitat suitability of dab (*Limanda limanda*), plaice (*Pleuronectes platessa*), poor cod (*Trisopterus minutus*) and whiting (*Merlangius merlangus*) in the Irish Sea were investigated. Generalised additive mixed models were used to analyse the species response to chlorophyll *a*, shear stress and sediment type. It was hypothesised that all species prefer an area with a high chlorophyll *a* level and a low shear stress. These two factors might be indirectly linked to the food availability, because in general areas with high chlorophyll *a* concentrations tend to attract many marine species, and areas with high shear stress can disturb and even damage benthic invertebrates, which is the main food source the demersal fish. This hypothesis was accepted for *L. limanda*, *P. platessa* and *M. merlangus*, but rejected for *T. minutus*. *T. minutus* preferred areas with a high shear stress and a low concentration of chlorophyll *a*. It was also hypothesised that flatfish (*L. limanda* and *P. platessa*) have a stronger preference for a certain sediment type, compared to the two ganoids species (*T. minutus* and *M. merlangus*), because of their morphological shape and the ability to burry themselves in the sediment. No difference of the abundance of two flatfish was found between the different sediment types, while a preference was found for *T. minutus* and *M. merlangus*. *M. merlangus* preferred fine sediment types and *T. minutus* had a preference for a coarse substrate type.

Introduction

Information on the spatial distribution of fish can provide a better understanding of their niche and role in an ecosystem (Rogers and Ellis, 2000). A good understanding of the marine ecosystems is required for conservation of the marine biodiversity and developing efficient management plans for sustainable fisheries (Link, 2002; Valavanis et al., 2008). Several management plans have been implemented such as a policy of reduction of bycatch (EC, 2007) or the protection of vulnerable habitats (EC, 1992). An improved understanding of the spatial distribution of fish may also be beneficial for the development and design of Marine Protected Areas (MPAs). Improved knowledge of the spatial distribution of fish is essential for the successful implementation of different management plans. Both direct and indirect drivers of the spatial distribution should be taken into account if healthy ecosystems with fish populations are to be maintained.

The spatial distribution of species is dependent on various factors such as habitat suitability, food availability and temporal factors (e.g. seasonality). Ross (1986) reviewed these three factors and found that habitat suitability and food availability are generally most important in defining the distribution of marine species (Ross 1986). Environmental variables, such as sediment type, shear stress, chlorophyll *a*, temperature or salinity can define whether a species prefers a certain area. Other variables such as competition and predator avoidance or diseases are factors that can also contribute in the habitat selection of species (Beutel et al., 1999).

Common dab (*Limanda limanda*), European plaice (*Pleuronectes platessa*), poor cod (*Trisopterus minutus*) and whiting (*Merlangius merlangus*) are abundant and widespread fish species in the waters of the northeast Atlantic (Rogers et al., 1998). In this study these four demersal fish species are studied in the Irish Sea. All four species are important prey and predators of the epi-benthic community (Edwards and Steele, 1968), so a better understanding of their spatial distribution and habitat preferences will contribute to a better understanding of the benthic ecology of the Irish Sea.

L. limanda

L. limanda is a dominant flatfish in United Kingdom waters and is a commonly found from northeast Scandinavia to south France (Rogers et al., 1998). *L. limanda* spawn in areas with a water depth between 20 and 40 m and spawning occurs between January and September (Ortega-Salas, 1980). When the juvenile *L. limanda* hatch, they migrate to shallower water

(Rijnsdorp et al., 1992). The distribution patterns of juvenile *L. limanda* have been well investigated; however, little is known about the distribution of adults (Able et al., 2005). *L. limanda* reach maturity at two years of age, when it reached a length of about 14 cm (Rijnsdorp et al., 1992; Amezcua and Nash, 2001). It has been found that *L. limanda* mainly live on a sandy substrate and tend to migrate to shallow areas to avoid a high shear stress (Martin et al., 2009). In the winter *L. limanda* migrate from shallow areas to deeper water to avoid temperatures below 2.5 degrees Celsius (Rijnsdorp et al., 1992). *L. limanda* is an opportunistic predator that feeds on echinoderms, small crustaceans, bivalve molluscs, polycheates and a few small fish (Kaiser and Ramsay, 1997; Saborowski and Buchholz, 1996; Martin et al., 2009).

P. platessa

P. platessa are distributed on the European continental shelf in northern Scandinavia the Mediterranean and around Iceland (Al-Rashada, 2009). *P. platessa* have a relatively short spawning period, from the end of February to the end of April, that occurs at depths between 20 and 40 m (Rijnsdorp, 1989; Fox et al., 1997; Armstrong et al., 2001). The distribution of juvenile *P. platessa* is similar to juvenile *L. limanda* which is also far better investigated that the distribution of adults (Able et al., 2005). *P. platessa* become migratory after reaching maturity between 2 to 7 years of age and a length between 18 and 35 cm (Dunn and Pawson, 2002). *P. platessa* live in marine and brackish water, prefer sandy substrates and are distributed in water shallower than 200 m (Martin et al., 2009). The diet of adult *P. platessa* consists mainly of polycheates, bivalves molluscs, coelenterates, echinioderms and small fish that live in or on the sea bed (Rijnsdorp and Vingerhoed, 2001). It has been suggested that benthic factors, such as sediment type, are more important for flatfish (*L. limanda* and *P. platessa*) than for other marine fish (Piet et al., 1998) due to their morphological shape and their ability to bury in the sediment (Piet et al., 1998).

T. minutus

T. minutus can be found in the waters of the east Atlantic from Norway until the Portuguese coast. Little is known about the spawning of *T. minutus*; however, it is assumed that it spawns between February and April (Cooper, 1983). It can reach a maximum length of 40 cm; however, a length between 15 and 30 cm is more common. *T. minutus* becomes mature at five years of age when it has reached a length of about 13 cm (Martin et al., 2009). Adult *T. minutus* are found between 20 and 200 m of depth (Persohn et al., 2009). They seem to prefer a temperature range between 11 and 19 degrees Celsius and a salinity range between 34.4 and 35.7 ‰ (Persohn et al., 2009). A sediment preference has not been found for *T. minutus* in the Irish Sea (Froese and Pauly, 2007). The diet of *T. minutus* mainly consists of polycheates, decapods and small fish (Gibson and Ezzi, 1987; Armstrong, 1982). Both *T. minutus* and *M. Merlangus* (which is described below) are species with an important role in the marine food web, as they are an important food source for cetacean and seal species in the Irish Sea (Santos and Pierce, 2003; Santos et al., 2001; Shane et al., 1986; Evans and Hintner, 2010).

M. merlangus

M. merlangus is a common species that lives in small schools in the European waters along the northeast Atlantic, North Sea, around the British Isles, Mediterranean Sea, Black Sea and in the waters around Iceland (Rogers et al., 1998). *M. merlangus* in the Irish Sea spawn between February and June at water depths until 100 m (Nichols et al., 1993; Fox et al., 1997). Larvae have a relatively long pelagic phase and reach five to ten cm before they become demersal (Hislop, 1984). *M. merlangus* becomes sexually mature when it reaches a length between 25 and 50 cm at an age between two and four years (Martin et al., 2009). Adult *M. merlangus* is associated with depths between 10 and 200 m (Zheng et al., 2001; Katsanevakis et al., 2009). A temperature between 10 and 20 degrees Celsius and a salinity range between 33 and 35 ‰ is preferred (Persohn et al., 2009). *M. merlangus* usually distribute over sandy and muddy sediments at inshore areas, but are also found near rocky seabeds (Henderson and Holmes, 1989). However, sediment type has been suggested to be an important variable in defining their spatial distribution, because *M. merlangus* mainly feeds on benthic invertebrates that live in or on fine sediment types (Katsanevakis et al., 2009). *M. merlangus* feeds mainly on polycheates, decapods, molluscs, cephalopods and small fish (Patterson et al., 1985; Rindorf, 2003).

Habitat modelling

The relationships between the abundance of the common demersal fish to four environmental variables were tested in this study. Based on previously described studies, the environmental variables, sediment type, shear stress, depth and chlorophyll *a* were chosen for further investigation. The relationship between the abundance of the four species with chlorophyll *a*, shear stress and sediment types were performed using a Species Distribution Modelling technique (SDM). SDMs are designed to relate the distribution of species to environmental variables. It suggest which species tend to avoid or prefer a certain environmental variable, and these results can used to predict species distributions in areas where samples have not been taken. SDMs are therefore able to deal with information gaps in survey results (Koubbi et al., 2006). A SDM is an important and innovative tool to better understand how species make use of their habitat (Guisan and Zimmermann, 2000). The traditional regression based SDM is the generalised linear model (GLM) (Guisan et al., 2002; Elith and Leathwick, 2009). GLM is based on normal linear regression but the data does not necessary need to be normally distributed. Recently the preference of many scientists shifted to non-linear regression methods, such as generalised additive models (GAM) (Hastie and Tibshirani, 1990; Vanhatalo et al., 2012) which is an extension of GLMs wherein the linear functions are replaced by a smoothing function (Wood, 2006). Advantage of the smoothing function in GAM is that the modelling technique is flexible and can therefore describe the preferred range of a species with respect to an environmental factor (Borchers et al., 1997). It can, for example, specify a temperature range that is favourable, and will better explain a relationship than a linear relationship will. GAMs can be upgraded to a generalised additive mixed model (GAMM), which is useful if observations in space or the timing of the observations are dependent on each other. GAMMs can make the observations more independent (Zuur et al., 2009). In addition to generalised additive (mixed) models, many other approaches exist for relating species abundance to environmental variables. Some examples are boosted regression trees (Leathwick et al., 2006; Friedman, 2002) or multiple adaptive regression splines (Friedman, 1991). The disadvantage of GA(M)M is that smoothers use all data points, which might lead to a wide confidence bands around the smoother while the predictive variable could be highly significant. Also a high variance in the response variable lead to a poor fit of the model. Furthermore it should be noted that models can find more quantifiable relationships than reality. Even though GA(M)M does have disadvantages, it is a common and well developed method that is widely used in fisheries science (Valavanis et al., 2008). No such model has yet been used to determine the distribution of the four common benthic species in the Irish Sea.

Hypotheses

Based on previous knowledge the following two hypotheses were formulated for this study:

1. The four demersal fish species favour areas with high chlorophyll *a* concentrations and low shear stress, because these parameters may be linked to higher food availability.
2. Sediment type is a more important factor in defining the distribution of the two flatfish, *L. limanda* and *P. platessa*, than it is for the ganoids species (*T. minutus* and *M. merlangus*).

The objectives of this study were:

I. To investigate the relationship of *L. limanda*, *P. platessa*, *T. minutus* and *M. merlangus* abundance with chlorophyll *a*, shear stress and between the different sediment types.
II. To investigate if the geographical locations of observations of each species independent.
III. To produce a distribution map in the Irish Sea of each species based on model predictions using chlorophyll *a*, shear stress and the different sediment types?

Material and methods

The distribution of *L. limanda*, *P. platessa*, *T. minutus* and *M. merlangus* in the Irish Sea were investigated based on generalised additive mixed models. These models used three environmental factors along with rectifications of correlated geographical spaced observations. Predictive abundance maps for the *L. limanda*, *P. platessa*, *T. minutus* and *M. merlangus* distribution in the Irish Sea were created from the model predictions.

Study area and survey design

The Irish Sea is located between the west coast of Scotland, England and Wales and the east coast of Ireland and Northern Ireland. It functions as a boundary between the warm temperate Lusitanian fauna and the cold-temperate boreal fauna (Rogers et al., 1998). It has a relatively high species richness compared to nearby areas as the North Sea (Rogers and Millner, 1996). Trawls towed between August and October in ICES divisions VIIa, g and f were selected for this study. However, the study concentrated on a smaller area between 2º W by 7.5º W longitude and 50º N by 55º N latitude (**Figure 1a**), because all trawls were conducted (**Figure 1b**) and all environmental factors were available in this area (**Figure 2**). It is necessary that the environmental factors, or explanatory variables, are available to be able to create species distribution predictions.

Common demersal species are of importance for commercial fisheries and has led to an intensive stock monitoring with routine beam trawl surveys (Van Beek et al., 1989; Gibson and Robb, 1996). R.V. *Corystes* conducted annual surveys in the Irish Sea, which resulted in an excellent database to study the distribution the species. Surveys were carried out at fixed stations in the months of August, September and October between 1993 and 2008. The trawls were towed at a speed of 4 knots for 30 minutes. A four meter beam trawl was used that contained a chain mat, a flip-up rope and a cod-end a liner with a mesh size of 40 mm (ICES, 2009). All trawls were towed during daylight, between 15 minutes after sunrise and 15 minutes before sunset (ICES, 2009). Data from these surveys were available from the International Council for the Exploration of the Sea (www.ices.dk). The fixed stations in the Irish Sea were sampled once a year and the analyses in this study combined all years by calculating the mean abundance for each species per station.

To normalise the data, a subset was made on several trawl characteristics. Firstly, trawls recorded as invalid or sub-sampled were eliminated and to reduce the difference between the trawl durations, trawls that deviated more than 10% from 30 minutes were removed from the dataset. To test whether the locations of the fixed stations deviated between the years, the mean location for each trawl was calculated with mean haul and shoot coordinates. To check whether samples of all stations were taken at the same location each year, the mean station location (calculated by all trawls of that station) was also calculated. A quality check was carried out to eliminate trawls that deviated more than five km from the mean station location. After elimination of these trawls, the mean station numbers and distances were then recalculated to confirm if all trawls were conducted within five km. Furthermore, at 40 stations only one to five trawls were conducted between 1993 and 2008. At four stations three till five trawls were conducted in the period. A mean number of 10 and a median of 11 trawls were conducted per station. This study only included the stations what were sampled more than five times.

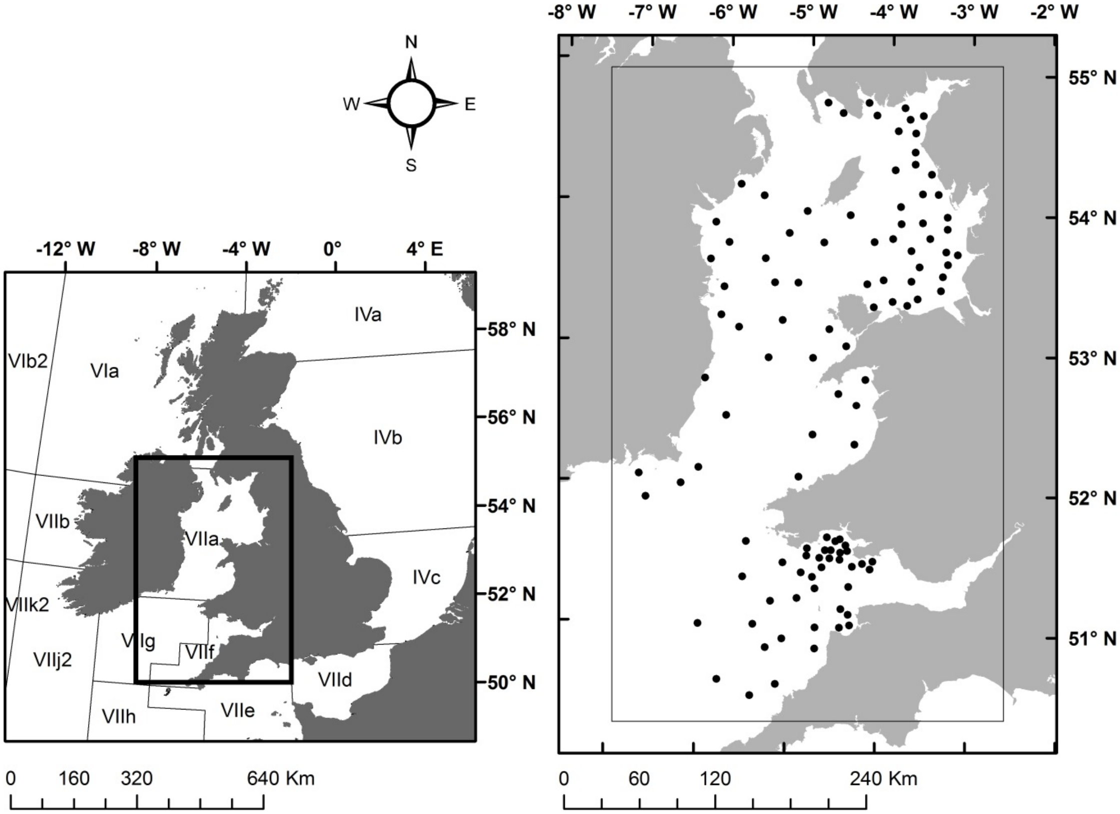

(a) (b)

Figure 1. Map of the location of the Irish Sea (a) and locations of the sample stations (b). Only trawls within ICES divisions VIIa, g and f were selected for this study. A detailed map with the all qualified stations (b) was located in the area between 2 ^{0} W by 7.5 ^{0} W longitude and 50 ^{0} N by 55 ^{0} N latitude, indicated with the square around the stations in figure b.

Environmental predictive variables

Substrate types have previously been associated with distribution of *L. limanda*, *P. platessa*, *T. minutus* and *M. merlangus* (Cohen et al., 1990; Amezcua and Nash, 2001). This indicates that substrate type is likely to be a feature of their habitat and therefore useful for predicting distributions of these species. Sediment type data used in the present study were obtained from the British Geological Survey (2012) that was categorised according to the classification by (Folk et al., 1970) (**Figure 3**). This classification for sediment types was reduced from 14 to 3 categories - gravel, mud and sand (**Figure 3**), to prevent that the models describe noise or random errors rather than the underlying relationship. The distribution of three sediment types in the Irish Sea is patchy (**Figure 2a**). Same areas in the Irish Sea contain another substrate type than gravel, sand or mud. These areas consist mainly of bedrock, but none of the trawls were conducted above areas that were not defined as gravel, sand or mud.

A high bottom shear stress can cause disturbance of benthic invertebrates that live in or on the seabed, which might indicate the distribution of food availability (Evans, 1990; Norkko et al., 2002). Benthic invertebrates are part of the diet for *L. limanda*, *P. platessa*, *T. minutus* and *M. merlangus* (Martin et al., 2009) and shear stress might therefore be an important variable for defining the habitat suitability. Shear stress was defined from the peak bottom stress (N m^{-2}) at the time of mean tides (Hiddink et al., 2009). The resolution of these data was 1/30 degree latitude (3.70 km) by 1/20 degree longitude (3.35 km) (**Figure 2b**). A high shear stress in the Irish Sea can be found mainly in the middle of the Irish Sea and in the Bristol Channel (**Figure 2b**).

Previous studies have related depth to the distribution of *L. limanda*, *P. platessa*, *T. minutus* and *M. merlangus*, and mainly found that distributions over depth gradients were related to the age of the fish (Persohn et al., 2009; Gomelyuk and Shchetkov, 2012). It has also been suggested that depth is the main gradient that defines changes of species distributions (Demestre et al., 2000). Depth records were collected during the trawls and the mean depth per station was used. Depth however was highly correlated to chlorophyll *a* concentration and therefore excluded from further analyses. Predicting habitat suitability with two correlative variables would not contribute as species would react similar to these variables. The variable chlorophyll *a* was preferred to depth, because it was assumed to be more relevant for predicting habitat suitability as it was found before that globally marine fish tend to occur in areas with a high primary production (Hunt and McKinnell, 2006). Chlorophyll *a* is a proxy for primary production (Eppley et al., 1985), hence indirectly linked to food availability of fish. Chlorophyll *a* data were collected by a MODIS sensor using the case 2 ‘chlorophyll *a*’

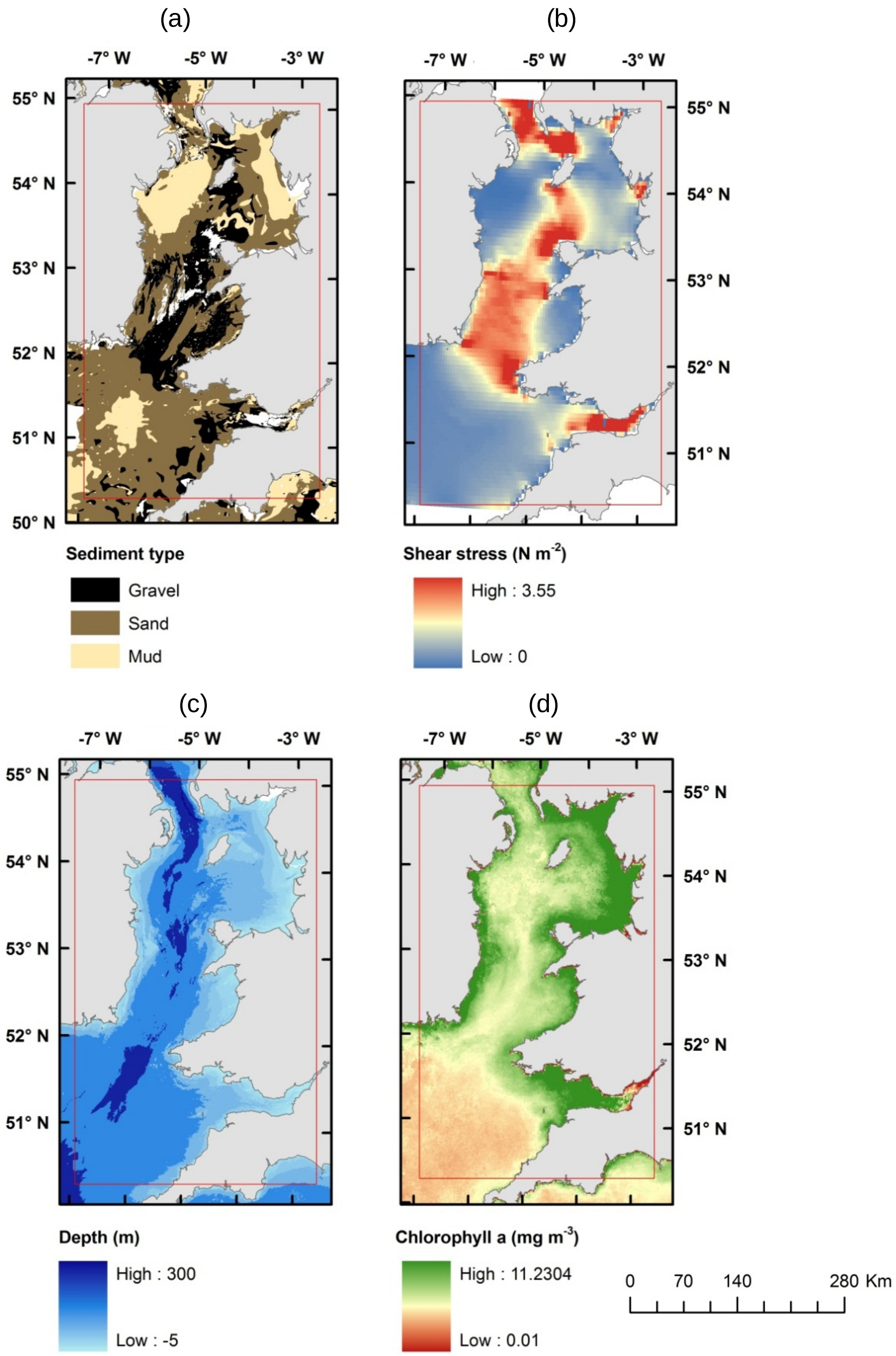


Figure 2. Distribution map of sediment type (a), shear stress (b), depth (c) and chlorophyll *a* (d) in the Irish Sea. The red square indicates the study area wherein all samples were taken and all the environmental factors are known. The sediment map (a) shows some areas without a defined sediment type (white patches). These areas are mainly covered with hard substrata and were not used in this study because none of the surveys were conducted here.

algorithm (OC5) for turbid shelf seas (NEODAAS 2008). Monthly averages from 2008 were obtained and a yearly mean concentration of chlorophyll a of 2008 was calculated by Whiteley (*pers. comm.*). It was not possible to use another year or yearly chlorophyll *a* data because these were not available for this study. The yearly average of chlorophyll *a* concentration of 2008 might not reflect the relationship to fish distribution correctly. The remote sensing chlorophyll *a* levels were measured in mg m^{-3} and the values were extracted from a raster files with a resolution of 1.1 x 1.1 km. In 2008 high chlorophyll *a* concentrations were found mainly along the coastlines of England, Wales and Ireland (**Figure 2a**).

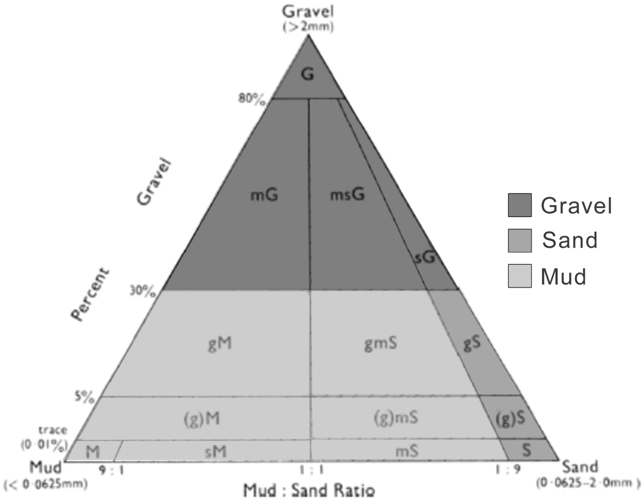


Figure 3. The three categories 'Gravel', 'Sand' and 'Mud' were defined based on (Folk et al., 1970). Gravel was defined by combining 'G' (gravel), 'mG' (muddy gravel), 'msG' (muddy sandy gravel) and 'sG' (sandy gravel). Sand was combined using 'gS' (gravelly sand), '(g)S' (slightly gravelly sand) and 'S' (sand). The remaining 7 categories were combined as mud: 'gM' (gravelly mud); 'gmS' (gravelly muddy sand); '(g)M' (slightly gravelly mud); '(g)mS' (slightly gravelly muddy sand); 'M'(mud); 'sM'(sandy mud) and 'mS'(muddy sand).

Habitat modelling

Generalised additive models (GAM) models were used to investigate the four species using the three explanatory environmental variables. This model was upgraded to a generalised additive mixed model (GAMM) to add a rectification for spatial auto-correlation, which is a method to define dependency of geographical spaced observations. All species were treated similarly with the spatial auto-correlation rectification as the only difference.

R software (R Development Core Team, 2012) was used to carry out all analyses. Firstly, the correlation between the explanatory variables was tested to identify any possible relationship. A high correlation between the explanatory variables can cause unevenness in the final abundance predictions as it responds similar to different variables. Species abundance data were transformed logarithmic + 0.5 transformed to create a more uniform distribution of the abundance to the explanatory variables.

A GAM estimates non-linear relationships between an explanatory and response variable using a smoother function (Wood, 2006). This is useful because in nature not everything is linear. For the smoothing function within the GAMs, Cubic Regression Splines within the "mgcv" R package was used (Wood, 2011). Cubic Regression Splines create these smoothers by dividing an explanatory variable into a certain number of intervals and plotting a polynomial regression type in each (Zuur et al., 2009). The final smooth is then created by attaching the intervals together (Zuur et al., 2009). A normal distribution (or Gaussian distribution) was used, which is an appropriate way to model transformed abundance and spatially distributed data (Vanhatalo et al., 2012; Swartzman et al., 1994).

A GAM model can be specified as:

$$Y(X_i) = \alpha + \sum_{j=1}^{p} \beta_j \times b_j(X_i) + \varepsilon_i$$

in which: $\varepsilon_i \sim N(0, \sigma^2)$

Within the fitted model α represents the intercept, b_j the arbitrary predictive variables and X_i the abundance of a species. A Cubic Spline Regression smoothing function was used to link $Y(X_i)$ with the X_i. The errors (ε_i) are in dependent of X_i and based on the sub-equation. The simulated Y represents the additive effect of the abundance of a species to an environmental variable.

In this study different models were applied using protocols given in Zuur et al. (2009). For defining the best combination of variables to explain habitat suitability, different GAM models were run with all possible combinations of including and excluding all explanatory variables. A smoother was used for both chlorophyll *a* and shear stress. No smoother was used for the sediment type, as this variable was not continuous but categorical.

The most complex fit tested for the model is (s indicates the smoother):

Abundance ~ s(chlorophyll *a*) + s(shear stress) + Sediment

As described in Zuur et al (2009), Akaike's Information Criteria (AIC) was used in the selection process of defining the best model. AIC measures the relative goodness and complexity of model fit by giving it a number (Bozdogan, 1987). By comparing the AIC values of the different GAM models, the model with the lowest AIC value had the best fit and was selected. The combination of explanatory variables from the selected model was used to fit the GAMM.

The residuals of the model were explored for possible spatial auto-correlation. A semi-variogram can be used to analyse such correlation (Zuur et al., 2009). It plots the spatial portioning of the variance of the sample against the defined distance. If the residuals in the semi-variogram are displayed in a horizontal line at near the value one, there is no strong evidence that a spatial auto-correlation is present. If the semi-variogram shows a strong curve, it does indicate that such a correlation is present (Rossi et al., 1992). GAMMs can rectify for spatial auto-correlation using defined correlation types: exponential; Gaussian (normal distribution); linear; rational quadratic or spherical shape. All options were run and the best GAMM was selected by the correlation structure that resulted in the lowest AIC as described before. To check whether the spatial auto-correlation was reduced in the rectified model, another semi-variogram was plotted after.

Mapping predictions

The final habitat suitability maps based on the selected model for each of the species were produced. This was done collecting all environmental variables throughout the Irish Sea at a resolution of 1/30 degree latitude by 1/20 degree longitude. Abundance predictions were made by using the selected model and applying the relationships to the environmental variable throughout the Irish Sea (as described in Valavanis et al., 2008). ArcMap 9.3.1 (Geographical Information System) was used to map the data obtained from the GAMM using a raster size of 1/20 degree longitude and latitude, which is approximately 3.35 km longitude and 5.56 km latitude. This resolution was based on square degrees of latitude and longitude and therefore some resolution was lost from the coarsest resolution of the environmental variable shear stress.

Results

A total number of 1393 trawls at 109 stations in the Irish Sea were selected for the study. The surveys caught a total number of 539,135 specimens of 123 different fish species. The species with the highest abundance were the *L. limanda*, *P. platessa*, solenette (*Buglossidium luteum*), *T. minutus*, common dragonet (*Callionymus lyra*) and *M. merlangus*. Within this study only *L. limanda*, *P. platessa*, *T. minutus* and *M. merlangus* were studied. The total number caught per year is of each of the four species is given in **Table 1**.

Depth was eliminated from the analysis because of the high correlation with chlorophyll *a* (r = -0.8) (**Figure 4**). No strong correlation was found between the remaining variables (r > 0.5). Chlorophyll *a* and shear stress had the lowest correlation (r = 0.1) followed by the relationship between chlorophyll *a* and shear stress (r = 0.2). The correlation coefficient of -0.4 between shear stress and sediment type was not high enough to eliminate one of these variables (**Figure 4**).

Table 1. The numbers of trawls per year and the total number of *L. limanda*, *P. Platessa, T. minutus* and *M. merlangus* caught in these trawls. The number of per species is the total number caught in all trawls in per year

	Number of trawls per year	***L. limanda***	***P. platessa***	***T. minutus***	***M. merlangus***
1993	98	7730	5776	5538	3192
1994	108	10970	5039	2949	1949
1995	105	9169	5070	3639	3573
1996	104	7699	4827	2909	2231
1997	103	10703	6489	3585	3495
1998	96	9708	6274	3834	2322
1999	94	13557	6650	5384	3342
2000	93	12446	7817	4902	1651
2001	94	11314	5969	1675	1428
2002	97	6031	5108	2980	1289
2003	96	8336	5049	7131	1133
2004	53	1581	1710	2163	1247
2005	72	3069	2138	4102	1499
2006	65	2606	1866	3426	918
2007	62	2233	1494	3239	1057
2008	53	2176	1691	2571	1111

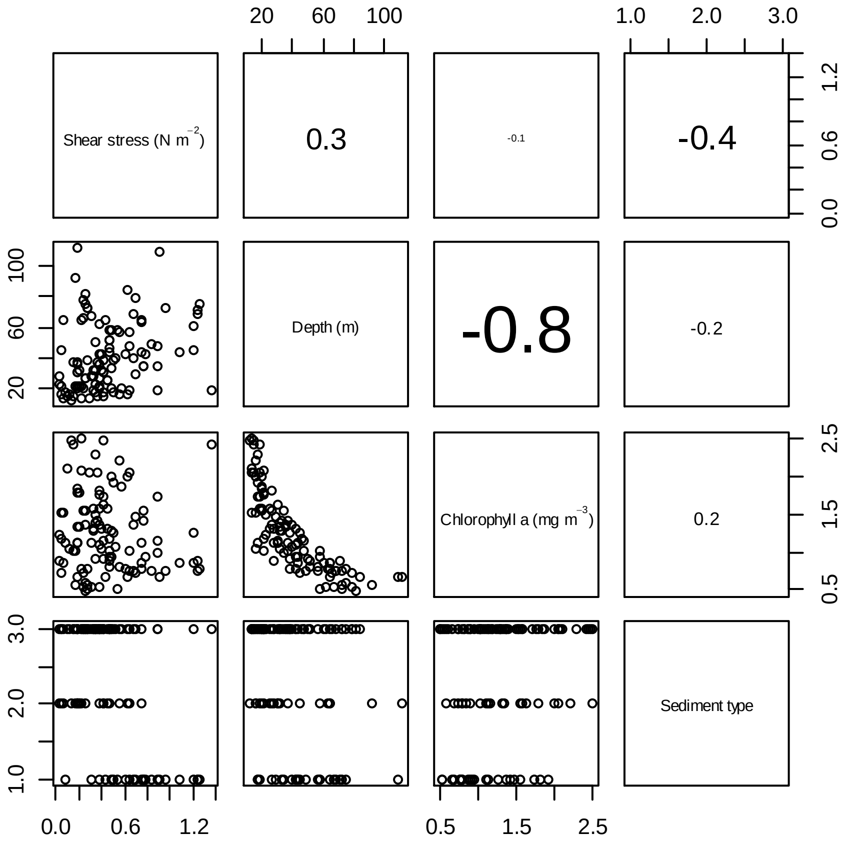


Figure 4. Correlation plot of the four explanatory variables: shear stress, depth chlorophyll *a* and sediment type. The correlation coefficients are given in upper panels on the right. The distributions of the relationships are given in the lower panels on the left side.

L. limanda and *P. platessa*

The relationship between abundance and the environmental variables for *L. limanda* and *P. platessa* were similar and therefore described together. This section shows the found patterns from GAMM models and predictive maps.

For an overview of the response of *L. limanda* and *P. platessa* to the environmental variables, two scatterplots and one boxplot per species are shown in **Figure 5**. Data for both species were log +0.5 transformed to reduce the effect of outliers on the perceived relationship with the environmental variables. A maximum number of 3,247 and a median of 17 *L. limanda* were caught per tow. Not a single *L. limanda* was caught at three of the stations during the period between 1993 and 2008. *P. platessa* was less abundant and a maximal number of 726 with and median of 12 *P. platessa* were caught per tow. *P. platessa* was caught at 101 of the 109 stations.

Semi-variograms of the model residuals detected no major evidence of spatial auto-correlation, as the simulated values of the semi-variograms are close the simulated number one (**Figure 6**). No spatial auto-correlation would be present if all simulated values are close to the value one. However, the best model defined by AIC, contained a rectification for it and thus made the geographically spaced observations more independent from one another (**Figure 6**). The dependency of geographical spaced observations for *L. limanda* abundance was best rectified in the model using a spherical correlation shape. A rational quadratic correlation shape was more suitable to correct the spatial auto-correlation of *P. platessa* abundance. Both models improved independence of the geographical spacing of the station by applying these correlation shapes (**Figure 6**).

According to the selected model the number of caught *L. limanda* and *P. platessa* was mostly driven by levels of chlorophyll *a* (**Table 2**). Higher abundances were found until a chlorophyll *a* concentration up to 2.0 mg m^{-3}. Concentrations higher than 2.0 mg m^{-3} did not seem to influence the densities of *L. limanda* and *P. platessa*. The linear relationship with shear stress indicates that higher densities of *L. limanda* and *P. platessa* are found in areas with low shear stress (**Figure 7**). The abundance of the two species was lower in trawls towed over gravelly sediment compared to sandy or muddy sediment types (**Figure 5**). However, no significant differences between sediment types were found for *L. limanda* or *P. platessa* (**Table 2**).

Based on the GAMM model the distribution was predicted and mapped (**Figure 8**). The distributions of *L. limanda* and *P. platessa* are similar and resemble the distribution of high levels of chlorophyll *a* and a low shear stress. The largest area with high densities of these species is predicted in the northeast Irish Sea. Other areas with a high abundance of both species can be found near the coastlines of Ireland, Scotland, England and Wales (**Figure 8**). The small difference between *L. limanda* and *P. platessa* can be found in the response of shear stress, as *P. platessa* tends to be less influenced by that.

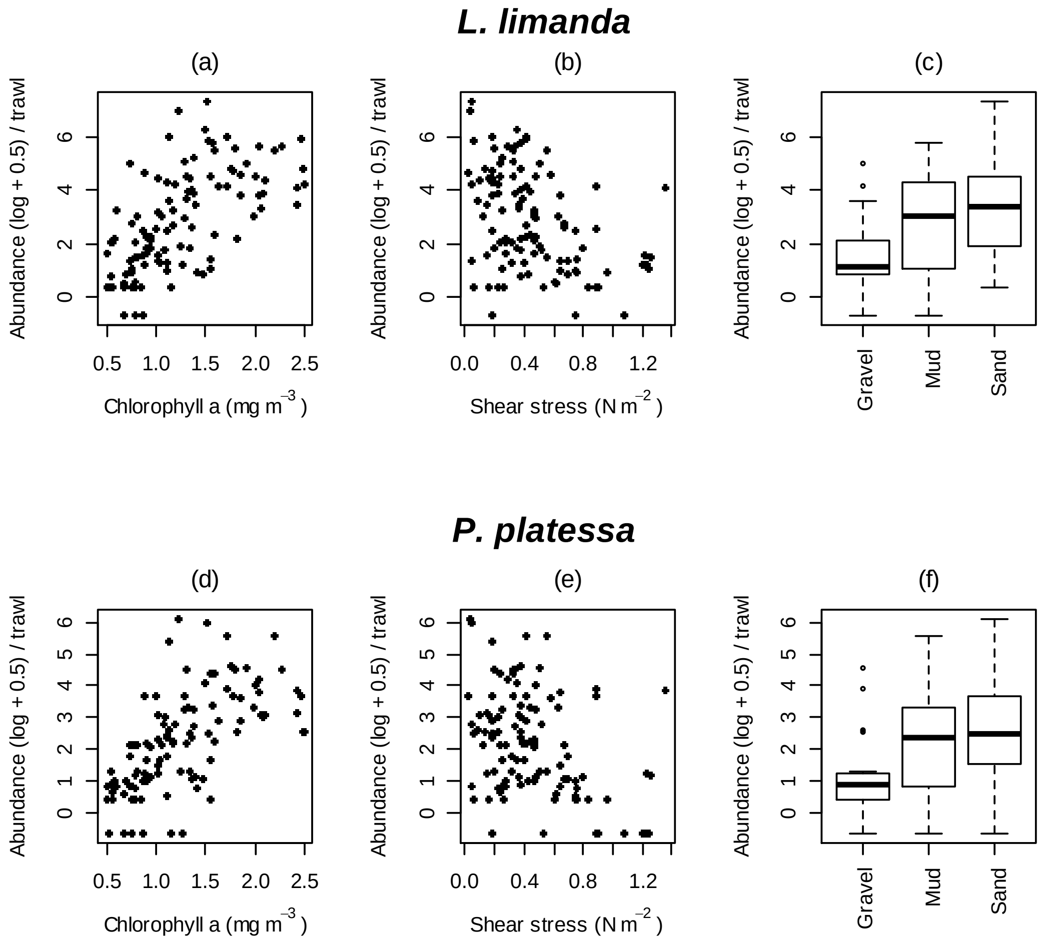


Figure 5. Relationship between the abundance of *L. limanda* (a-c) and *P. platessa* (d-f) to chlorophyll *a* (a and d), shear stress (b and e) and to sediment types (c and f). The variables chlorophyll *a* and shear stress are continuous and therefor presented using scatter plots. Sediment type is presented with a box plot as it more informative for categorical variables.

Table 2. Statistical output of the best generalised additive mixed models for *L. limanda*, *P. platessa*, *T. minutus* and *M. merlangus*. The d.f., F and P values of the chlorophyll *a* and shear stress are approximate significances of the smooth terms. The values for the sediment types are based on parametric coefficients.

	Smoother **chlorophyll *a*** (mg m $^{-3}$)			Smoother **shear stress** (N m $^{-2}$)			**Sediment**					
							(intercept) **gravel**		**mud**		**sand**	
	d.f.	**F**	**P**	**d.f.**	**F**	**P**	**t**	**P**	**t**	**P**	**t**	**P**
L. Limanda	2.67	18.82	< 0.001	1	16.85	< 0.001	7.45	< 0.001	-1.49	0.138	1.4	0.164
P. platessa	3.01	18.59	< 0.001	1.76	7.64	0.001	7.01	< 0.001	-0.87	0.389	1.69	0.094
T. minutus	1.67	8.76	< 0.001	1	20.83	< 0.001	14.82	< 0.001	-2.97	0.004	-1.99	0.05
M. merlangus	3.5	9.71	< 0.001	2.09	1.69	0.188	6.7	< 0.001	3.11	0.002	4.15	< 0.001

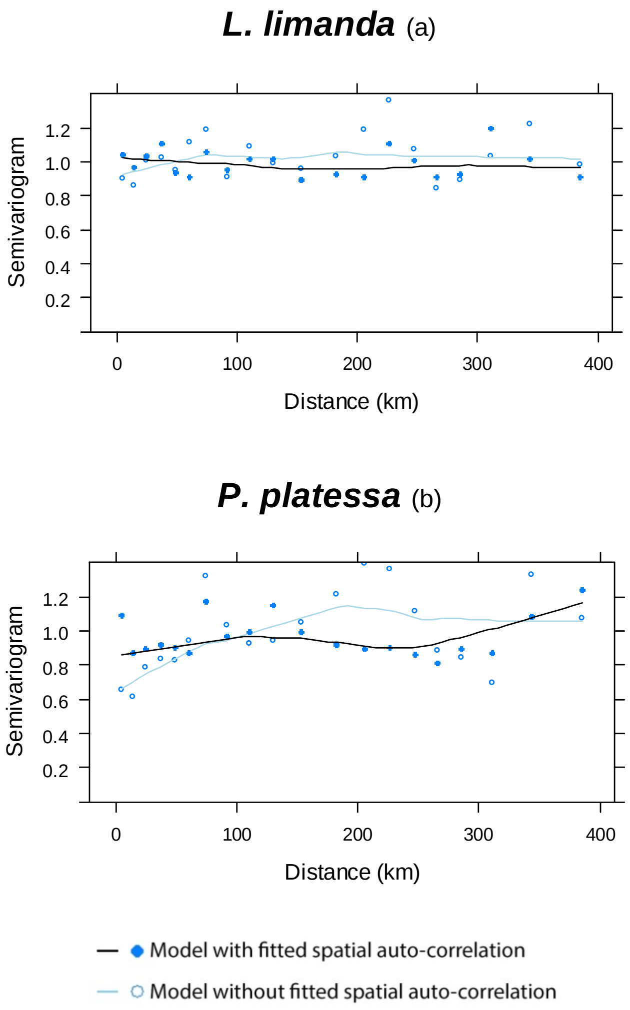


Figure 6. Semi-variogram of the residuals of generalised additive mixed models for *L. limanda* (a) and *P. platessa* (b) to distance between the stations. These figures visualise to which extent spatial auto-correlation is present in a model. The dots are simulated from the standardised residuals and the line shows the theoretical semi-variance with a smoother. If plotted dots are close to 1.0 it indicates that little spatial auto-correlation is present. The more the dots deviate from this value, the more evidence of a spatial auto-correlation will be revealed. The light coloured lines and dots represent the model without a rectification of spatial auto-correlation. The dark line and dots are based on the best model, which is used for further analyses.

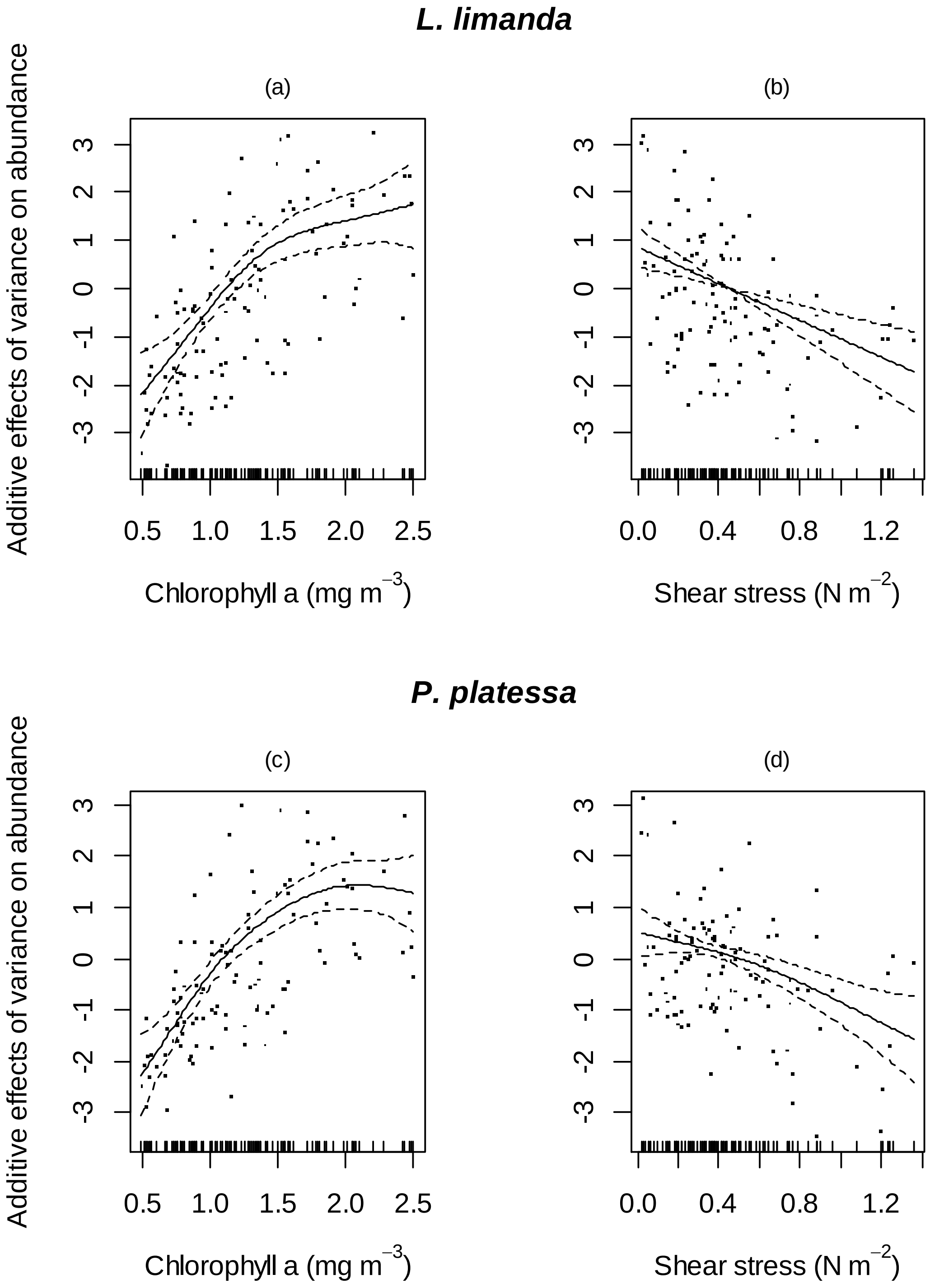


Figure 7. Additive effect of *L. limanda* (a and b) and *P. platessa* (c and d) abundance per tow to chlorophyll *a* (a and c) and shear stress (b and d). The additive effect is the output measure of the generalised additive mixed model as a response on the environmental variables. The solid line, the estimated smoother, is surrounded by the point wise 95 % confidence intervals indicated by the dashed lines. The vertical ticks on the x-axis indicate the observation values of the environmental variables. In this figure, the given points are the normalised residuals of the model.

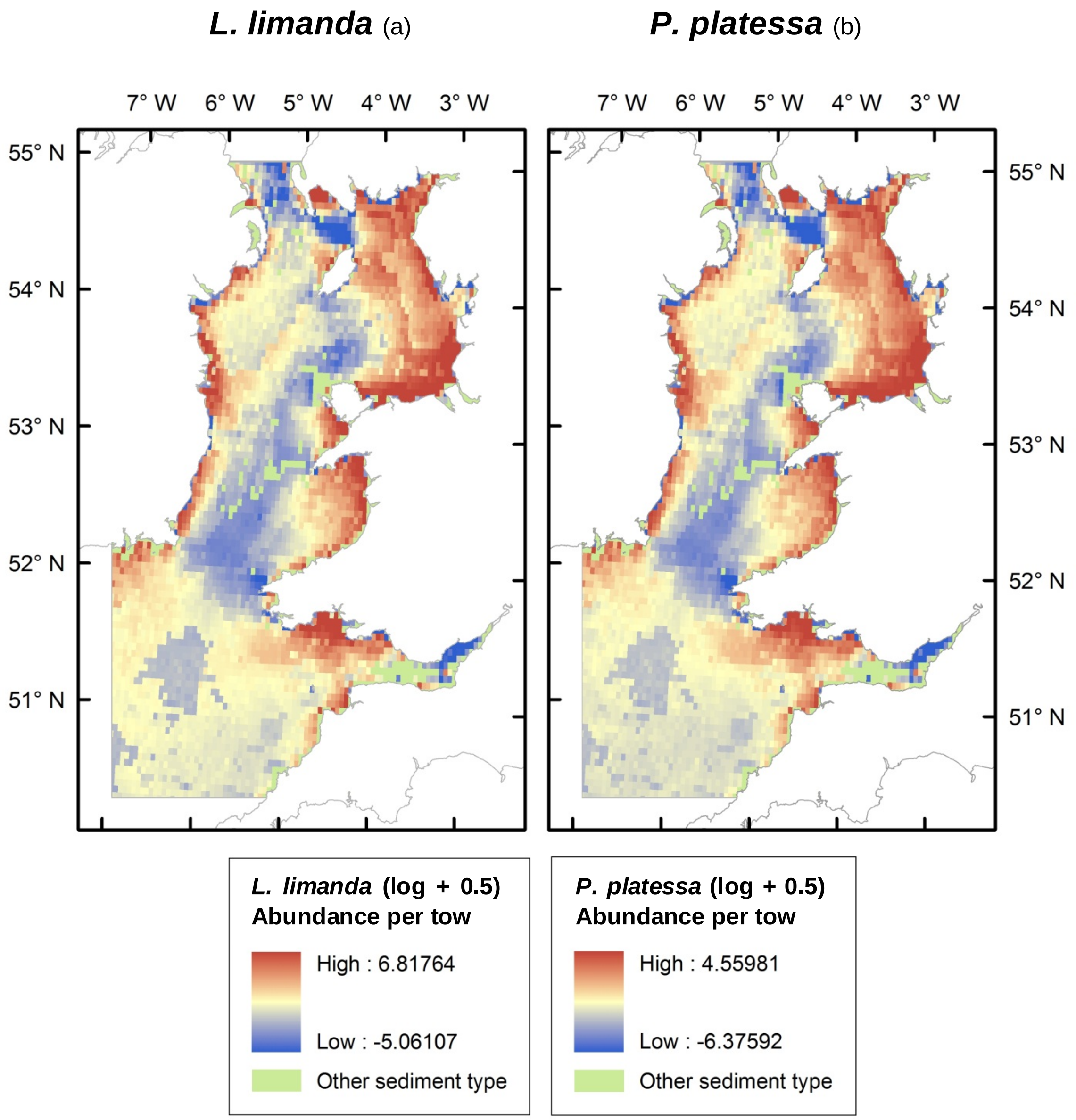


Figure 8. Predicted distribution of *L. limanda* (a) and *P. platessa* (b) from the selected generalised additive mixed model. The predicted abundance is log + 0.5 transformed to reduce the influence of relatively high or low abundances of *L. limanda* and *P. platessa*. Areas without the sediment type gravel, sand or mud were not included in the model, hence no predictions could made here. In this figure those areas are defined with the colour green.

T. minutus

This section describes the relationship found between abundance of *T. minutus* to chlorophyll *a*, shear stress and sediment type. After a description of the patterns obtained, a predictive distribution map based on the best model is given.

A total of 60,027 *T. minutus* were caught at 106 stations. At three stations, none of the trawls caught a single *T. minutus* in 16 years. A maximum number of 1,661 and a median of 29 *T. minutus* were caught per trawl. The abundance of *T. minutus* was log +0.5 transformed to reduce the effect of outliers. The abundance of *T. minutus* to the environmental variables is shown in **Figure 9**.

Semi-variograms of the model residuals detected no major evidence of spatial auto-correlation (**Figure 10**). Therefore a rectification for any spatial auto-correlation was not essential; however, an applied spherical shape correlation shape in the GAMM improved the model slightly according to AIC (**Figure 10**). The selected model, defined by AIC, included all three environmental variables. These three environmental variables all contributed in the explaining the habitat suitability of *T. minutus* significantly (**Table 2**). A high abundance of *T. minutus* was found in areas with a high shear stress, indicated by a linear relationship within the range of shear stress observed at the sample stations (**Figure 11**). *T. minutus* is more abundant in areas with a lower level of chlorophyll *a* (**Figure 11**). The *T. minutus* abundance was significantly higher over coarser sediment types (**Figure 9**, **Table 2**).

From the selected model, a predictive map for *T. minutus* was produced that reflects the distribution of a high shear stress. The highest densities of *T. minutus* are predicted north of the Isle of Man, around the north coast of Anglesey, west of Pembrokeshire, in the Bristol Channel and west of Wigtonshire (southwest Scotland) (**Figure 12**). Another patch of relatively high *T. minutus* density is the area of St. George Channel within the southern Irish Sea.

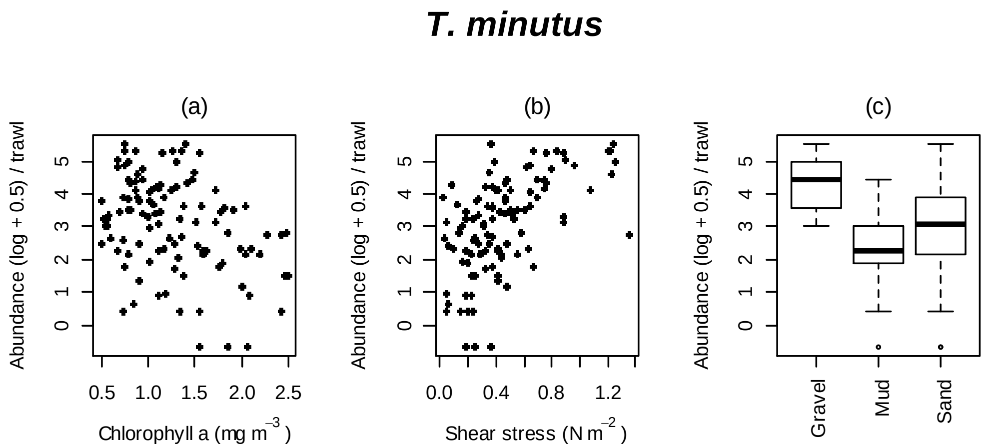


Figure 9. Relationship between the abundance of *T. minutus* to chlorophyll *a* (a), shear stress (b) and the sediment types (c). Chlorophyll *a* and shear stress are continuous variables and therefore presented using scatter plots. A boxplot is used of the categorical sediment types.

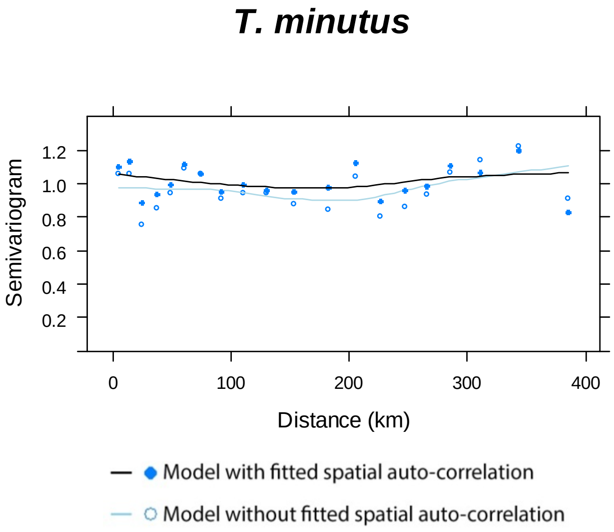


Figure 10. Semi-variogram of the residuals of generalised additive mixed models for *T. Minutus* to distance between the stations. This figure visualise to which extent spatial auto-correlation is present in a model. The dots are simulated from the standardised residuals and the line shows a theoretical semi-variance with a smoother. If plotted dots are close to 1.0 it indicates that little spatial correlation is present. The more dots deviate from this value, the more evidence of a spatial auto-correlation will be revealed. The light coloured lines and dots represent the model without a rectification of spatial auto-correlation. The dark line and dots are based on the best model, which is used for further analyses.

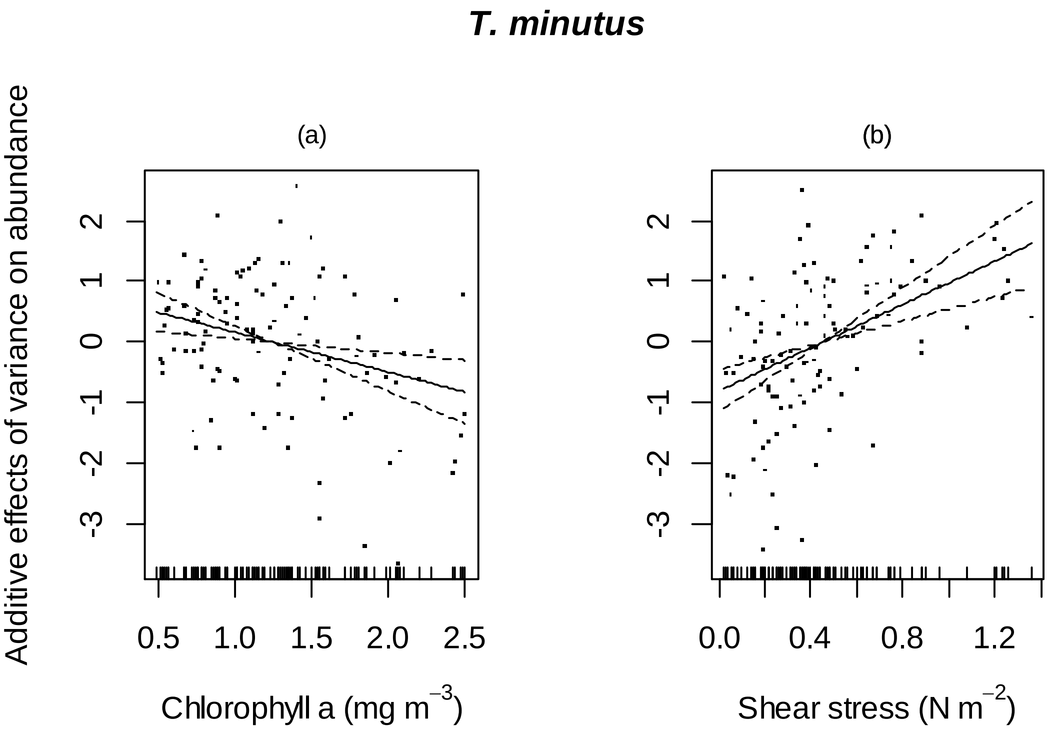
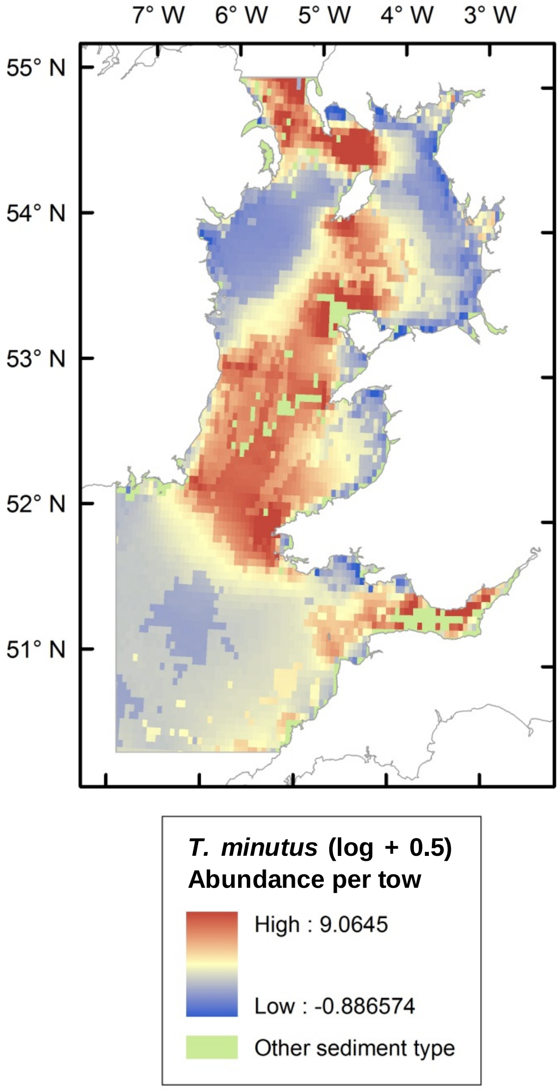


Figure 11. Additive effect of *T. minutus* abundance per tow to chlorophyll *a* (a) and shear stress (b). The additive effect is the output measure of the generalised additive mixed model as a response on the environmental variables. The solid line, the estimated smoother is surrounded by the point wise 95 % confidence intervals indicated by the dashed lines. The vertical ticks on the x-axis indicate the observation values of the environmental variables. The dots represent the normalised residuals of the fitted model.



T. minutus

Figure 12. Predicted distribution of *T. minutus* from the selected generalised additive mixed model. The predicted abundance is log + 0.5 transformed to reduce the influence of relatively high or low abundances of *T. minutus*. Areas without the sediment type gravel, sand or mud were not included in the model, hence no predictions could made here. In this figure those areas are defined with the colour green.

M. merlangus

Over 16 years, a total number of 31,437 *M. merlangus* was caught at 105 stations; however, no trawl towed at four stations contained any *M. merlangus*. The highest number of *M. merlangus* per trawl consisted of 658 individuals and a median of 10 *M. merlangus* per trawl. The abundance of *M. merlangus* was log +0.5 transformed to create a more uniform distribution to the three environmental variables (**Figure 13**).

Possible spatial auto-correlation was investigated using a semi-variogram (**Figure 14**). No major spatial auto-correlation was found; however, a correction using rational quadratic shape in GAMM resulted in a better fit of the model according to the lower AIC value. The semi-variogram of both the final model and the model that did not take spatial auto-correlation into account are plotted in **Figure 14**. The selected model was based on all three environmental variables of which chlorophyll *a* contributed significantly (**Table 2**). Predicted *M. merlangus* abundance is increased with higher levels of chlorophyll *a*. The smoother of chlorophyll *a* increases up to 1.5 mg m^{-3}, then flattens between 1.5 and 2.0 mg m^{-3} (**Figure 15**). Shear stress was not a significant explanatory variable in the model (**Table 2**). The abundance of *M. merlangus* among different sediment types; however, was significantly different (**Table 2**). *M. merlangus* preferred the finer sediment types rather than gravel (**Figure 13**).

A distribution map for *M. merlangus* was produced based on GAMM predictions (**Figure 16**). The map mostly reflects the distribution of chlorophyll *a* in the Irish Sea, and results in some obvious patches in areas with a gravelly substrate. The main densities of *M. merlangus* are predicted in the areas of the northeast Irish Sea, along the whole coast of Ireland and in the mouth of the Bristol Channel.

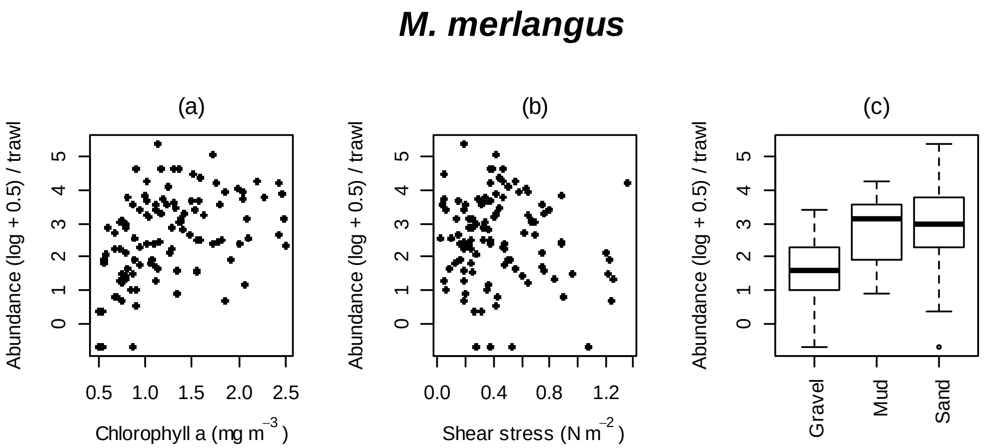


Figure 13. Relationship between the abundance of *M. merlangus* to concentrations of chlorophyll *a* (a), shear stress (b) and the three different sediment types (c). The variables chlorophyll *a* and shear stress are continuous and therefor presented using scatter plots. Sediment type is presented with a box plot as it more informative for categorical variables.

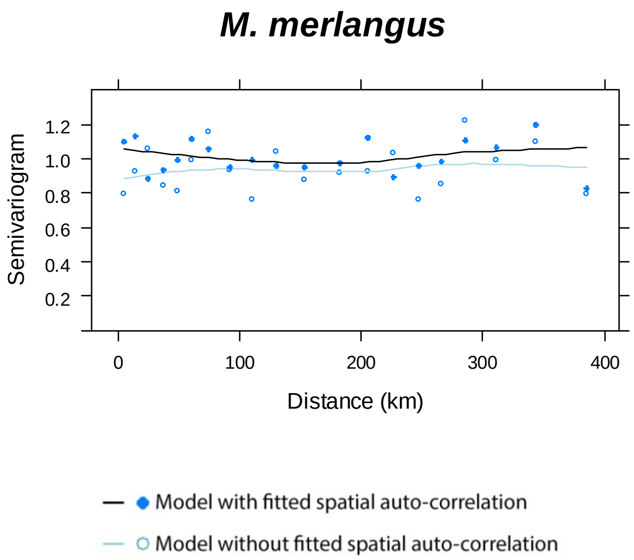


Figure 14. Semi-variogram of the residuals of generalised additive mixed models of *M. merlangus* to distance between the stations. The figure visualise to which extent spatial auto-correlation is present in a model. The dots are simulated from the standardised residuals and the line shows a theoretical semi-variance with a smoother. If plotted dots are close to 1.0 it indicates that little spatial correlation is present. The more dots deviate from this value, the more evidence of a spatial auto correlation will be revealed. The light coloured lines and dots represent the model without a rectification of spatial auto-correlation. The dark line and dots are based on the best model, which is used for further analyses.

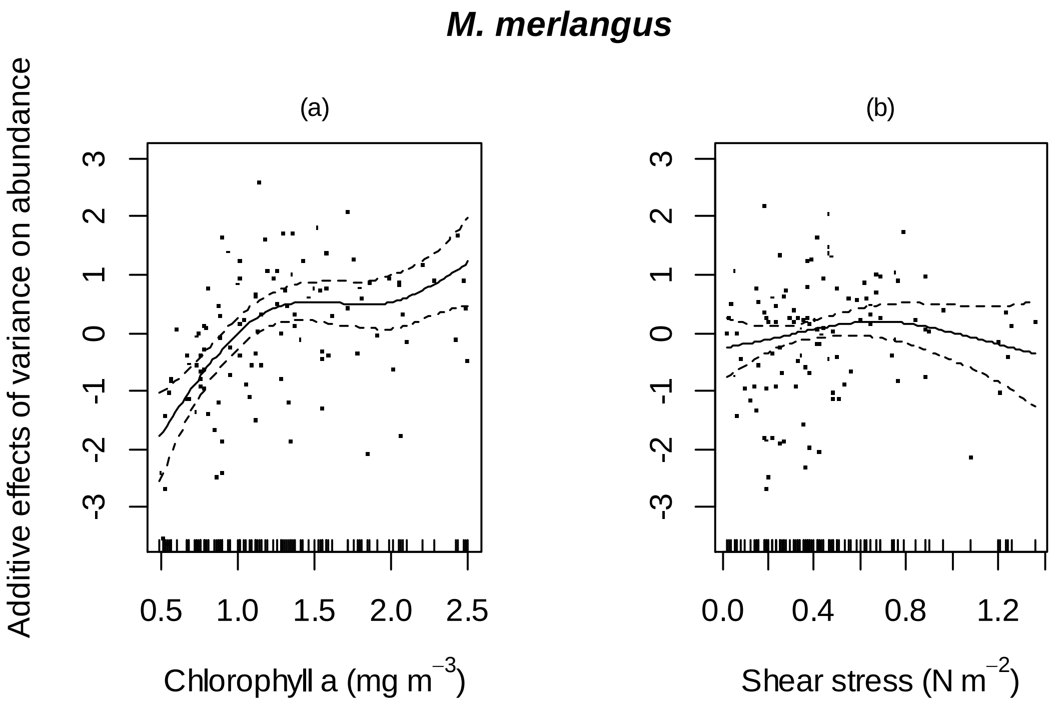


Figure 15. Additive effect of *T. minutus* abundance per tow to chlorophyll *a* (a) and shear stress (b). The additive effect is the output measure of the generalised additive mixed model as a response on the environmental variables. The solid line, the estimated smoother, is surrounded by the point wise 95 % confidence intervals indicated by the dashed lines. The vertical ticks on the x-axis illustrate the observation values of the environmental variables. In this figure, the given points are the normalised residuals of the model.

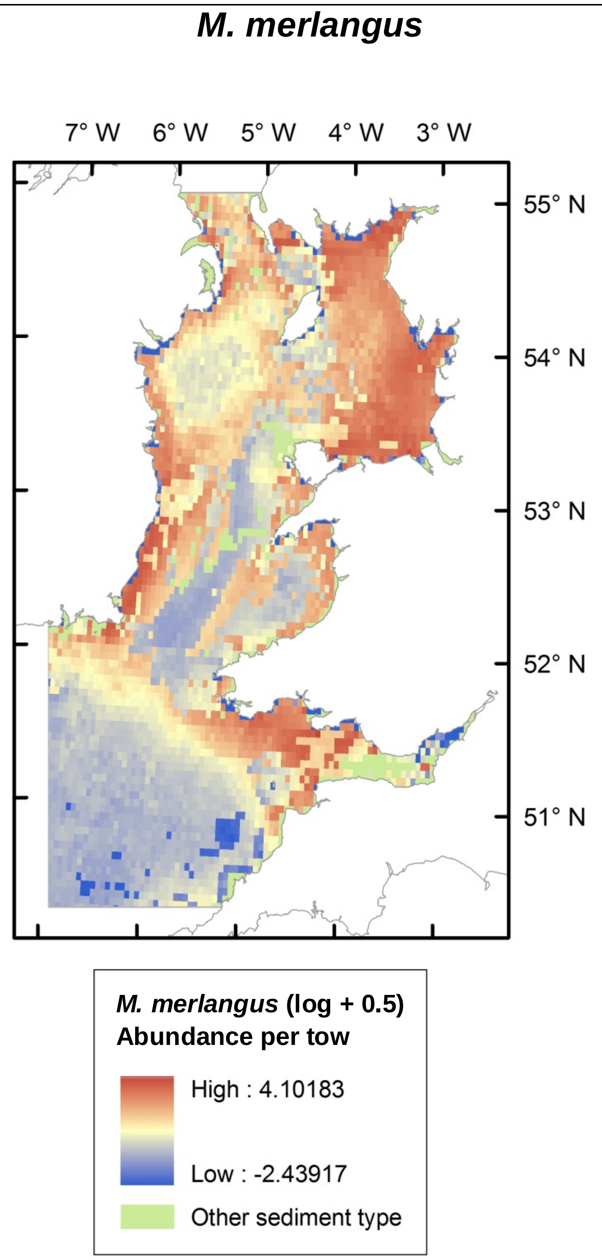

M. merlangus

Figure 16. Predicted distribution of *M. merlangus* from the selected generalised additive mixed model. The predicted abundance is log + 0.5 transformed to reduce the influence of relatively high or low abundances of *M. merlangus*. Areas without the sediment type gravel, sand or mud were not included in the model, hence no predictions could made here. In this figure those areas are defined with the colour green.

Discussion

This section will first summarise the main conclusions of the study followed by a separate discussion addressing each species. Furthermore, the applied methods are discussed and finally some recommendations are given.

The first hypothesis was that the four demersal species will be attracted to areas with a high chlorophyll *a* concentration and a low shear stress, due to potential higher food availability in these areas (Martin et al., 2009). The results show that chlorophyll *a* and shear stress do indeed influence the distribution of all fish species, with the exception of *M. merlangus*, where no significant effect of shear stress was found. *L. limanda* and *P. platessa* were most abundant in areas with a high chlorophyll *a* concentration and a low shear stress. *T. minutus*, however, preferred areas of high shear stress and tended to avoid areas with a high chlorophyll *a* concentration. In conclusion, chlorophyll *a* might indicate areas of food availability for *L. limanda*, *P. platessa* and *M. merlangus*, and shear stress might do the same for *L. limanda* and *P. platessa*. The hypothesis that the four species prefer area with a high chlorophyll *a* concentration and a low shear stress was therefore rejected for *T. minutus*.

The second hypothesis was that sediment type is more important for flatfish compared to gadoids because of their morphological shape that offers the possibility to burry themselves. This study did not support this hypothesis as no differences were found between the density of *P. platessa* and *L. limanda* over different sediment types, while differences between sediment types were significant for *T. minutus* and *M. merlangus*. In conclusion, it cannot be said that flatfish have a greater need for a specific sediment type compared to other marine fish. This therefore contradicts the study by Gibson and Robb (1992) and Amezcue and Nash (2001) who found that flatfish mainly distribute over a sandy sediment type. However, it should be noted that the fish in the Irish Sea were caught between August and October. Different timing of sampling, areas or life stages may result in different conclusions. For example, it was found that the relationship between distribution and depth of all demersal fish species studied is related to the age of fish (Gomelyuk and Shchetkov, 2012; Persohn et al., 2009).

L. limanda

L. limanda tends to be distributed in areas with high chlorophyll *a* concentrations. Chlorophyll *a* is a measure of primary production (Eppley et al., 1985) and areas with a high primary production tend to attract many marine species because of the high food availability (Hunt and McKinnell, 2006). It has been found previously that *L. limanda* favours productive areas (Rogers and Millner, 1996). No other studies have related chlorophyll *a* concentrations to the abundance of *L. limanda*; however, previous studies have related *L. limanda* distribution to depth and found that they prefer shallow areas (Rogers and Millner, 1996; Martin et al., 2009), which in the Irish Sea have higher chlorophyll *a* concentrations. Dissolved oxygen, on the other hand, was also found to be more important in defining the distribution of *L. limanda* (Maes et al., 2004). However, that study was conducted at a time when water quality was poor and therefore the overall dissolved oxygen might have been low. It is plausible that any fish living in poor quality water, distributes itself in areas with high oxygen levels as respiration is necessary for survival. This earlier finding does indicate that other variables such as water quality might be more important than the chlorophyll *a* concentration.

A high abundance of *L. limanda* was found in areas with lower shear stress. Similar relationships with tidal stress, have been found for flatfish in the eastern English Channel (Lauria et al., 2011). Lauria (2011) found that sediment types were a more important factor than shear stress (Lauria et al., 2011); however, another study described an avoidance of shear stress as more important than a sediment type preference (Martin et al., 2009). In the present study, no differences were found between the abundance of *L. limanda* on different sediment types. There are many papers that have found that juvenile flatfish tend to prefer finer sediment types (Gibson and Robb, 1992; Gibson, 1994). It is assumed that the preference for a finer sediment type is due to greater food availability and the possibility to bury themselves as a defensive mechanism against predators (Burke et al., 1991; Gibson and Robb, 1992). However, far less work on sediment preferences has been undertaken on adult *L. limanda*. A study in the northern Irish Sea found that adult flatfish have a preference for sandy substrates and tend to avoid gravel substrates (Amezcua and Nash, 2001). Although the differences between the sediment types in the present study were not significant, similar patterns were found, with lowest densities over a gravelly substrate. The additional environmental variables, chlorophyll *a* and shear stress, were better predictors of the abundance of *L. limanda* in the Irish Sea at least in the period between August and October.

P. platessa

The responses to the three environmental variables for *P. platessa* were similar to the responses of *L. limanda*. This section will highlight any differences and relate the findings for *P. platessa* to previous studies.

The distribution of *P. platessa* in Irish Sea showed that high densities are found in areas with a high chlorophyll *a* concentration, which may attract many fish species as it indirectly indicates food availability (Hunt and McKinnell, 2006). Few studies have used chlorophyll *a* as a variable to relate the habitat suitability of *P. platessa*. However, different studies found that *P. platessa* tend to appear in shallow areas (Amezcua and Nash, 2001; Martin et al., 2009) which in the Irish Sea is intercorrelated with chlorophyll *a*. *P. platessa* was less abundant in areas with high shear stress in the months between August and October, as was also the case in the English Channel (Lauria et al., 2011). On the other hand, another study found that adult *P. platessa* in July favoured areas with a relatively high shear stress offshore whilst in October they were distributed more in inshore areas but that still contained a high shear stress (Martin et al., 2009). Contrary to expectations, no differences were found in the abundance of *P. platessa* between the three main sediment types. This is in contradiction to a study between July and August in the English Channel that found that sediment type was the main explanatory variable for *P. platessa* abundance (Lauria et al., 2011). Other previous studies have described that in March during spawning, *P. platessa* in the Irish Sea preferred sandy substrate types while they were distributed over other sediment types in October (Fox et al., 1999; Amezcua and Nash, 2001). Thus a preference for a particular sediment type might be different between the timing of spawning and non-spawning.

T. minutus

Shear stress was found to be the most important environmental variable driving distribution for *T. minutus*. *T. minutus* mainly feed on decapods and small fish (Armstrong, 1982; Gibson and Ezzi, 1987). It has been suggested that shear stress is advantageous for the growth of many calcareous benthic organisms as a higher shear stress prevents settlement of fine sediments (Pehlivanoglou, 2001). It was found that *T. minutus* selected their food based upon the size of the prey (Armstrong, 1982), which might indicate why *T. minutus* favours areas with higher shear stress. Another study, however, in the English Channel, contradicted the present findings with *T. minutus* being more abundant in areas with lower shear stress (Martin et al., 2009).

This study found that *T. minutus* prefer a coarser sediment type, which coincides with the findings of at least one other study (Katsanevakis et al., 2009). *T. minutus* is considered to be a bentho-pelagic species less dependent on substrate type (Gaertner et al., 1999). *T. minutus* tended to avoid areas with high chlorophyll *a* concentrations. The species feeds in deep water (Armstrong, 1982), where chlorophyll *a* concentrations in the Irish Sea were low. It might be that another ecologically based correlation variable besides depth and chlorophyll *a* defines the habitat suitability of *T. minutus*. Predicting and understanding the distribution drivers for *T. minutus* is difficult and complex compared with flatfish because the species inhabits the pelagic zone to a large extent (Rogers et al., 1998; Gaertner et al., 1999; Ellis et al., 2000).

M. merlangus

The response of *M. merlangus* abundance to chlorophyll *a* was significant. However, the pattern of this relationship indicates that chlorophyll *a* is not the controlling variable, as no distinguishable pattern of the GAMM smoother was found. There do not appear to be any previous papers that study the relationship between *M. merlangus* and chlorophyll *a* concentrations. Nevertheless, it has been found that *M. merlangus* are distributed in relative shallow waters in between 90 and 120 m depths (Stelzenmüller et al., 2005), and Zheng et al. (2002) found that the optimum depth range for the species was around 80 m. This contradicts the findings in the present study, where no pattern was found with the correlation variable. The relationship between *M. merlangus* abundance and shear stress was not found to be a significant. *M. merlangus* prefer finer sediment types over gravelly sediment types, which coincides with previous studies that also stated that sediment type is an important feature for characterising the spatial distribution of *M. merlangus* (Katsanevakis et al., 2009). The reason for a preference for fine sediment might be because of higher food availability. Even though *M. merlangus* feeds on benthic species that will be related to a particular substrate type (Katsanevakis et al., 2009), the species mainly feeds on small fish that are not directly related to a certain sediment type (Patterson et al., 1985; Rindorf, 2003). Caution in interpretation of the results for *M. merlangus* should therefore be shown as *M. merlangus* is a bentho-pelagic species that is relatively independent of benthic macrofauna (Gaertner et al., 1999). Life in the pelagic zone is less stable due to absence of the influence of physical variables such as substrate. It is therefore more difficult to relate pelagic species abundance to environmental factors (Hislop, 1984), which might be better explained using variables such as temperature (Kaiser et al., 1999).

Limitations

Living organisms require many different environmental variables, of which some are more important than others (Warwick and Uncles, 1980). Other factors such as temperature, conductivity or human interactions with the environment, that were not included in this study, may be more important drivers for species distribution. For example, *L. limanda* abundance increases significantly until 48 hours after trawling activity (Kaiser and Spencer, 1994; Kaiser and Ramsay, 1997). It would also be worthwhile to investigate different life phases or sexes as species distributions have previously been found to differ between male and females (Rijnsdorp et al., 1992). These additional variables should ideally be included when the habitat preferences are studied. In addition, the niche of a certain species cannot completely be described by using species distribution models (SDM) as these models use only a subset of possible explanatory variables (Warren, 2012). More appropriate methods for estimating a niche still need to be developed (Warren, 2012), and should ideally be based on direct measures on life history advantage such as survivorship or growth (Beutel et al., 1999). Only three environmental variables were used in this study. Sediment type and shear stress are relatively stable in a natural system where environmental factors are changing constantly. Factors such as water temperature, water quality and human disturbance are more variable and these may play a more important role in defining species distributions (Gibson, 1997; Kaiser and Ramsay, 1997). Since none of these additional factors were included in this study, the results may be defining incorrect relationships or describe incorrect correlation variables.

Chlorophyll *a* revealed a clear relationship with the abundance of *L. limanda*, *P. platessa* and *T. minutus*; however, it would be more correct to investigate the relationship to chlorophyll *a* levels in more detail. In this study, a yearly mean concentration of the year 2008 was used, and the assumption was made that chlorophyll *a* levels are relatively consistent between years. This was not tested and it is plausible that chlorophyll *a* concentrations between different years do not correlate with each other, as they are dependent on variables such as nutrient level and light intensity (Dugdale and Goering, 1967). Variation in primary production can lead to bottom-up and top-down effects in the food chain, which in turn affects fish abundances and distribution (Hunt and McKinnell, 2006). In addition, remote sensing by satellite is only able to provide an indication of the chlorophyll *a* level, because it records only the top layer of the euphotic zone (Smith, 1981) and does not record the vertical distribution of chlorophyll *a*, which is rarely uniform (Cullen, 1982). This might lead to possible incorrectly inferred relationships.

Although all models in the present study were checked and corrected for dependence within the geographically spaced sampling scheme, no correction was made for the survey timing within the temporal range between August and October, or between the years 1993 and 2008. Habitat preferences are likely to change throughout the year as species will spawn in specific areas, for example (Gibson, 1997), while outside the spawning season, these marine fish species will maintain themselves in an area that is beneficial for survival and growth (Gibson, 1997). The study was based on four months of sampling from outside the spawning season of the four demersal species. The abundance of the fish species may fluctuate between the sampled years (Greenstreet and Hall, 1996). It is known, for example, that *M. merlangus* became less abundant in the North Sea over the 20th century and that in the same period, *P. platessa* became more abundant in the Irish Sea (Ellis et al., 2000). For the present study, data from 16 years were combined to provide a mean abundance per station. Within this period, environmental factors might have changed, including higher fishing pressure in certain areas, or the establishment of marine protected areas.

Recommendations

The Irish Sea is only a small area within the geographical range of the four species. It would be of interest to focus on the entire range or to divide this into subareas for the analyses. These can then be compared and might show if relationships are dependent upon geographical area. It has been suggested that environmental impacts might have a greater impact if they are investigated on the edges of the geographical distribution (Brunel and Boucher, 2006). More research would be useful to define the role of seasonality, sex, or age on the habitat preferences of different fish species. Seasonal variability, for example, might be dependent on temperature or feeding activity. It is also known that that the feeding activity of female *L. limanda* is constant throughout the year, whereas this varies in males between summer and winter. This phenomenon is suggested to be due to energy requirements of the gonad development of *L. limanda* (Saborowski and Buchholz, 1996). Finally,all lengths and year classes were combined in this study; however, it might have been more accurate to eliminate fish under a certain length or age.

The results and predicted distributions of *L. limanda*, *P. platessa*, *T. minutus* and *M. merlangus* can be used in the development of several management plans for sustainable fisheries, such as the selection and establishment of marine protected areas. Therefore a good understanding of the marine ecosystems is required (Link, 2002; Valavanis et al., 2008). A management plan with an ecosystem approach should take direct and indirect impacts of the environment into account to maintain a lively ecosystem with healthy fish populations.

Understanding the distribution of marine fish and what drives their distribution patterns, can assist in creating suitable conservation management plans including fisheries management. Implementing ecological management plans requires a good knowledge about species spatial distributions, and the relationship to environmental variables. The findings in this study can additionally be applied to several other ecological objectives. Defining direct relationships between the distributions of different predators, such as cetaceans, is one example. It is often suggested that food availability is likely to drive predator distributions (Evans, 1990; Northridge et al., 1995). However, due to a lack of data, such a relationship has never been utilized before with the species studied here. This study can be used to assess such relationships, although it should be noted that the predicted distributions are responding to only three variables, which predict the distribution rather than show the distribution in reality.

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