

# Suitable habitats of fish species in the Barents Sea

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## Funding information

Arktis 2030, Grant/Award Number: QZA-15/0137

## Abstract

Many marine species exhibit poleward migrations following climate change. The Barents Sea, a doorstep to the fast-warming Arctic, is experiencing large scale changes in its environment and its communities. Tracking and anticipating changes for management and conservation purposes at the scale of the ecosystem necessitate quantitative knowledge on individual species distribution drivers. This paper aims at identifying the factors controlling demersal habitats in the Barents Sea, investigating for which species we can predict current and future habitats and inferring those most likely to respond to climate change. We used non-linear quantile regressions (QGAM) to model the upper quantile of the biomass response of 33 fish species to 10 environmental gradients and revealed three environmental niche typologies. Four main predictors seem to be limiting species habitat: bottom and surface temperature, salinity, and depth. We highlighted three cases of present and future habitat predictability: (a) Habitats of widespread species are not likely to be limited by the existing conditions within the Barents Sea. (b) Habitats limited by a single factor are predictable and could shift if impacted by climate change. If the factor is depth, the habitat may stagnate or shrink if the environment becomes unsuitable. (c) Habitats limited by several factors are also predictable but need to be predicted from QGAM applied on projected environmental maps. These modeled suitable habitats can serve as input to species distribution forecasts and end-to-end models, and inform fisheries and conservation management.

## KEYWORDS

climate change, environmental niche, generalized additive models, habitat suitability models, limiting factors, quantile regression, species distribution

## 1 | INTRODUCTION

There is growing evidence of spatial shifts of species distribution correlated with climate change (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Hickling, Roy, Hill, Fox, & Thomas, 2006; Lenoir et al., 2020; Parmesan & Yohe, 2003; Thomas, 2010). The Arctic is warming fast (IPCC, 2014), and could experience higher species

turnover rates due to invasion and local extinction than anywhere on the globe (Cheung et al., 2009). The Barents Sea is a subarctic, shelf sea under the influence of two water masses flowing from the warm, saline Atlantic in the southwest and the cold, less saline Arctic in the northeast (Loeng, 1991). Communities associated with those two water masses differ in terms of fish species composition (e.g., Fossheim et al., 2015; Johannesen, Høines, Dolgov, & Fossheim, 2012), traits (Certain, Dormann, & Planque, 2014;

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Frainer et al., 2017), and trophic structure (Kortsch, Primicerio, Fossheim, Dolgov, & Aschan, 2015). During past decades, the Barents Sea has been experiencing an increase in Atlantic water inflow and coinciding heat content in the water column, as well as loss of sea ice in the northeast (Årthun, Eldevik, Smedsrud, Skagseth, & Ingvaldsen, 2012; Dalpadado et al., 2012; Lind, Ingvaldsen, & Furevik, 2018). In the meantime, the distribution of demersal fish has been altered with a general displacement of boreal communities and retraction of arctic communities toward the northeast (Fossheim et al., 2015). Many of those are important commercial species (e.g., Atlantic cod, *Gadus morhua*, Atlanto-scandic herring, *Clupea harengus*, and capelin, *Mallotus villosus*). In the current context of increasing efforts toward the implementation of an ecosystem approach to fisheries management, knowledge about species distribution patterns and their main drivers is of crucial importance to anticipate species range shifts and the associated changes in key ecosystem processes and services.

Unfortunately, studies in Arctic and subarctic waters have sometimes suffered from a lack of appropriate data to provide robust conclusions about changes in individual species biogeography (Ingvaldsen et al., 2015). Several studies have investigated the past responses of some commercial fish to climatic signals (Hamre, 1994; Matishov et al., 2012), and few have focused on the non-commercial species of the Barents Sea (e.g., Chambault et al., 2018). Regarding climate-induced shift range, only expert-based predictions are available (Hollowed, Planque, & Loeng, 2013). Hence, extending the number of species for which such information is quantitatively available is a pressing need for the Barents Sea.

Most species distribution models (SDM) aim at reproducing the expected average probability of presence or abundance of a species according to observed environmental conditions. An alternative approach is to explicitly focus on how those conditions may limit species habitats by predicting the maximum (or at least a high quantile) of the species response instead of the mean. Quantile regressions (QR) are specifically designed to predict quantiles of a response variable from a set of covariates (Cade & Noon, 2003; Cade, Terrell, & Schroeder, 1999). When applied to a high quantile of observed species density (e.g., >0.9), for a set of environment conditions, it is possible to determine the most limiting factor by considering successively several single-covariate models and identifying the one that predicts the lowest response (Austin, 2007). This approach inherits from the Sprengel–Liebig law of the minimum (van der Ploeg, Böhm, & Kirkham, 1999), which considers that a response variable can only be as high as allowed by the most limiting factor.

Quantile regression originated in economics (Koenker & Bassett, 1978) but has also been used in ecology for various applications (e.g., Bethea, Buckel, & Carlson, 2004; Knight & Ackerly, 2002; Planque & Buffaz, 2008). Review papers have highlighted its utility for the prediction of suitable habitats (Austin, 2007; Elith & Leathwick, 2009; Hegel, Cushman, Evans, & Huettmann, 2010), as it would describe an approximation of the potential niche (Cade, Noon, & Flather, 2005; Jiménez-Valverde et al., 2008). It has already several applications for terrestrial (e.g., Cade et al., 1999; Carrascal,

Villén-Pérez, & Palomino, 2016) and aquatic (e.g., Ateweberhan, McClanahan, Maina, & Sheppard, 2018; Lancaster & Belyea, 2006; Vaz et al., 2008) species linear response to environmental gradient. However, based on theoretical considerations, the species response to an environmental factor is expected to be bell-shaped (Hutchinson, 1957; Whittaker, 1967), so other studies have accordingly applied non-linear quantile regression models (e.g., Cozzoli et al., 2013; Dunham, Cade, & Terrell, 2002; Schröder, Andersen, & Kiehl, 2005).

The aim of the present work is to (a) quantify the limiting effect of the environmental factors that impact the spatial distribution of a large number of fish species in the Barents Sea, (b) assess the predictability of future geographical distributions based on currently available information, and (c) identify which species are most likely to respond to future environmental changes and which do not have predictable habitats at the scale of the Barents Sea. For this purpose, we developed QR non-linear models for all combinations of 33 species and 10 environmental factors from the autumn ecosystem survey in the Barents Sea.

## 2 | MATERIAL AND METHODS

### 2.1 | Data

#### 2.1.1 | Fish biomass by species

Fishes were caught by a Campelen 1,800 bottom trawl during the autumn IMR-PINRO joint ecosystem survey between 2004 and 2017 (Eriksen et al., 2018). The spatial extent of the study area (~1.6 million km<sup>2</sup>) has been covered by 278 stations per year in average, depending on the sea ice extent in the northeastern part of the sea. The sampling scheme consists of a regular grid with knots separated by 35 nautical miles. The same stations are visited each year, with a few exceptions due to technical, time, or climatic difficulties. The bulk of the catch is composed of demersal species, together with some bathy-pelagic and pelagic species which were also kept in the analyses. Estimated species biomasses were standardized by trawling distance. Only the trawls towed between 50 and 500 m depth in 15 to 60 min were kept. Towing speed was about 3 knots. In total, data comprised 3,827 stations and 78 species over the 14 years. Taxa that were absent in more than 95% of the stations were removed, reducing the number of studied species to 33.

#### 2.1.2 | Environmental predictors

Eleven variables reflecting the environmental conditions of fish habitat were included in the analysis. During the ecosystem survey, CTD were deployed at each station to measure surface (10 m) and bottom temperature (°C, T.surf and T.bottom) and salinity (S.surf and S.bottom). Two stratification variables were calculated from the temperature and salinity profiles following Planque, Lazure, and

Jegou (2006). The surface mixed layer depth (SML, m) was calculated from a double layer model, and the potential energy anomaly (PotEnAno,  $\text{kg}\cdot\text{m}^{-1}\cdot\text{s}^{-1}$ , Simpson & Bowers, 1981) was estimated as the energy required to mix vertically the entire water column.

Bathymetry (m) and slope (degrees) were extracted from NOAA raster for the Barents Sea (Jakobsson et al., 2012). Sediment type was defined by extraction of seafloor description by Norway's geological survey (NGU) (Contains data under the Norwegian license for public data NLOD). Among the 16 sediment classes described for the Barents Sea, many were only present in a tiny portion of our study area. Hence, they were aggregated in seven coarser classes following the EUNIS sediment hierarchical classification (Davies et al., 2004). Chlorophyll a (Chla,  $\text{mg}/\text{m}^3$ ) average concentrations between March and July of each year were extracted, as estimated by the NASA from ocean color (NASA OBPG, 2018). A number of days with ice cover (daysofice) were counted from daily sea ice extent maps from the NOAA (Cavalieri, Parkinson, Gloersen, & Zwally, 1996). For all those variables, values were extracted at each bottom trawl station location.

Correlation analysis (described in Appendix S1-1) showed a high correlation of potential energy anomaly with depth, but as depth is a well-known strong structuring factor of demersal habitats, the former was removed from the analysis. Therefore, 10 environmental variables were kept for the study, 3 being static through time (bathymetry, slope, and sediment).

## 2.2 | Analysis

### 2.2.1 | Species response to environmental predictors

Prior to the regression analysis, species biomass data were  $\log + d$ -transformed, where  $d$  is half the lowest biomass of the species and is added to avoid 0s before applying the log. It is then removed from the predictions to avoid an overestimation of the biomass. All quantitative environmental parameters were discretized in 20 categories of equal frequency to facilitate the model fitting process, except for days of ice which was 0-inflated and for which the first category comprised all the 0s while the 19 others were spread equiprobably over the rest of the distribution.

One quantile generalized additive model (QGAM) was fitted for each pair of species-predictor (330 models) using the *qgam* package in R (Fasiolo, Goude, Nedellec, & Wood, 2017) and setting the quantile level at 99%. QGAMs allows for non-linear relationship between the predictor and the species response and as such is able to capture bell-shaped responses, or responses that reach a plateau for high or low levels of the predictor. Further considerations about the strengths and weaknesses of the method are briefly described in Appendix S1-2. To avoid regressions with complex and ecologically meaningless shapes, the number of degrees of freedom in the QGAMs was limited to 3. For the qualitative variable (sediment), linear QR was applied to fit the 99<sup>th</sup>

quantile within each sediment category. The *quantreg* package in R (Koenker, 2018) was used.

For each species-predictor model, we calculated two descriptors: the mode is the maximum of the modeled response to the predictor; the range is calculated as the ratio of the difference between the range (max-min) of predictor values where the species has been found to the range of the same predictor over all the sampled stations of the Barents Sea. To identify niche typologies among the species, we used the R packages *FactoMineR* (Le, Josse, & Husson, 2008) and *factoextra* (Kassambara & Mundt, 2020) to perform a hierarchical clustering analysis based on the principal component analysis (PCA) of the two categories of niche descriptors. The number of clusters selected is based on the maximum relative loss of inertia.

To test the predictive power of each model, all were fitted using observations for years 2004 to 2013. They were then evaluated on observations for years 2014–2017. The evaluation was based on two metrics. The first metric is the proportion of observations in the evaluation dataset that were below the predicted 99<sup>th</sup> quantile. It is expected that 99% of the observations should fall below model predictions. If the observed proportion is higher, this means that the model is overestimating the maximum biomass (i.e., underestimating the limiting effect of the predictor). If the observed proportion is lower, too many observations in the evaluation dataset are higher than the expected maximum value, so the model is underestimating the maximum biomass (i.e., overestimating the limiting effect of the predictor). We categorized the variation from the 99<sup>th</sup> quantile into a “slight” (98.5% to 99.5% of data below the predictions) and a “strong” (less than 98.5% or more 99.5%) over/underestimation of the maximum biomass. We estimated that a model had a good predictive power if the predictions showed a slight deviation from the 99<sup>th</sup> quantile.

The second metric, termed “contrast,” is measured for each model on the predicted values, by the difference between minimum and maximum relative to the maximum. High (close to one) contrast occurs when the expected response of the species varies greatly across the environmental gradient. The predictor influences the species biomass, and has a limiting effect when biomasses are low. Low (close to zero) contrast occurs when there are little variations in the predicted species biomass along the environmental gradient. The predictor has a low effect on the species and is not limiting in the range of the Barents Sea. In the case of the sediment type, three of the seven classes (“Compacted sediments or sedimentary bedrock,” “Sand, gravel and pebbles,” and “Thin or discontinuous sediment on bedrock”) were associated with less than 1% of all the samples (Appendix S1-3). Those sediment types are ignored for the calculation of the contrast to ensure that the metric is built on sediment categories that carry enough information.

### 2.2.2 | Spatial prediction of suitable habitats

For each year, it is possible to construct maps of habitat suitability for each species. Each station is associated with a set of predictor

values. For a given species, each model predicts a 99th quantile of biomass in response to that set of predictor values. The most limiting factor is the one leading to the lowest 99% quantile. From here on, we use the term “most limiting” factor as defined by this criterion, whether the predictors can have a direct (like bottom temperature and depth) or indirect limiting effect (like chlorophyll *a*, which is not in direct link with the species habitat, but is an indicator of primary production that can indirectly affect bottom species). The maximum (99th quantile) biomass predicted based on the local environmental conditions is a local measure of habitat suitability. We applied this process to every location sampled each year.

This process results in two maps per year and per species: a habitat suitability map and a limiting factor map. The habitat suitability map displays the spatial distribution of the expected maximum biomass. The limiting factor map simply shows the most limiting factor at each location. However, when the biomasses are high, no factor can be considered limiting. In the limiting factor maps, wherever the maximum biomass predicted by the model of the most limiting factor is superior to 25% of the species-predictor model maximum, we estimated the factor to have a “weak limiting effect” on the species at the station. We thus used three categories to describe the limiting factors: fixed, dynamic, and weakly limiting (which can be a dynamic or fixed predictor).

### 2.2.3 | Predictability of future suitable habitats

To be able to identify and predict a species suitable habitats in the Barents Sea using QGAMs, it is necessary that (a) at least one selected predictor, dynamic or fixed, has an impact on the taxon response, that is, the species-predictor model has a high contrast, (b) the value of the predictor(s) for which the species biomass is strongly limited occurs within the study area and at the temporal scale of the study. Once those two conditions are met, the quality of the prediction depends on the robustness of the model to new conditions (i.e., predicted maximum quantile on the evaluation dataset should be close to the 99th).

To identify typologies of suitable habitat predictability, we performed a second hierarchical clustering analysis of habitat predictability indicators produced in the previous analyses.

## 3 | RESULTS

### 3.1 | Limits to the distribution of three species of the Barents Sea

Three species with contrasting suitable habitat, the Norway pout (*Trisopterus esmarkii*), the Thorny skate (*Amblyraja radiata*), and the Atlantic poacher (*Leptagonus decagonus*), are used to illustrate the detailed results of the quantile regressions of their biomass to three predictors: two that are associated with a high and a low contrast in the species response and one qualitative predictor. Habitat suitability maps are shown only for 2013, which was the year with the

widest spatial coverage. To avoid repetitions, we present results regarding the niche typologies and the predictability of suitable habitats in the second part of the results.

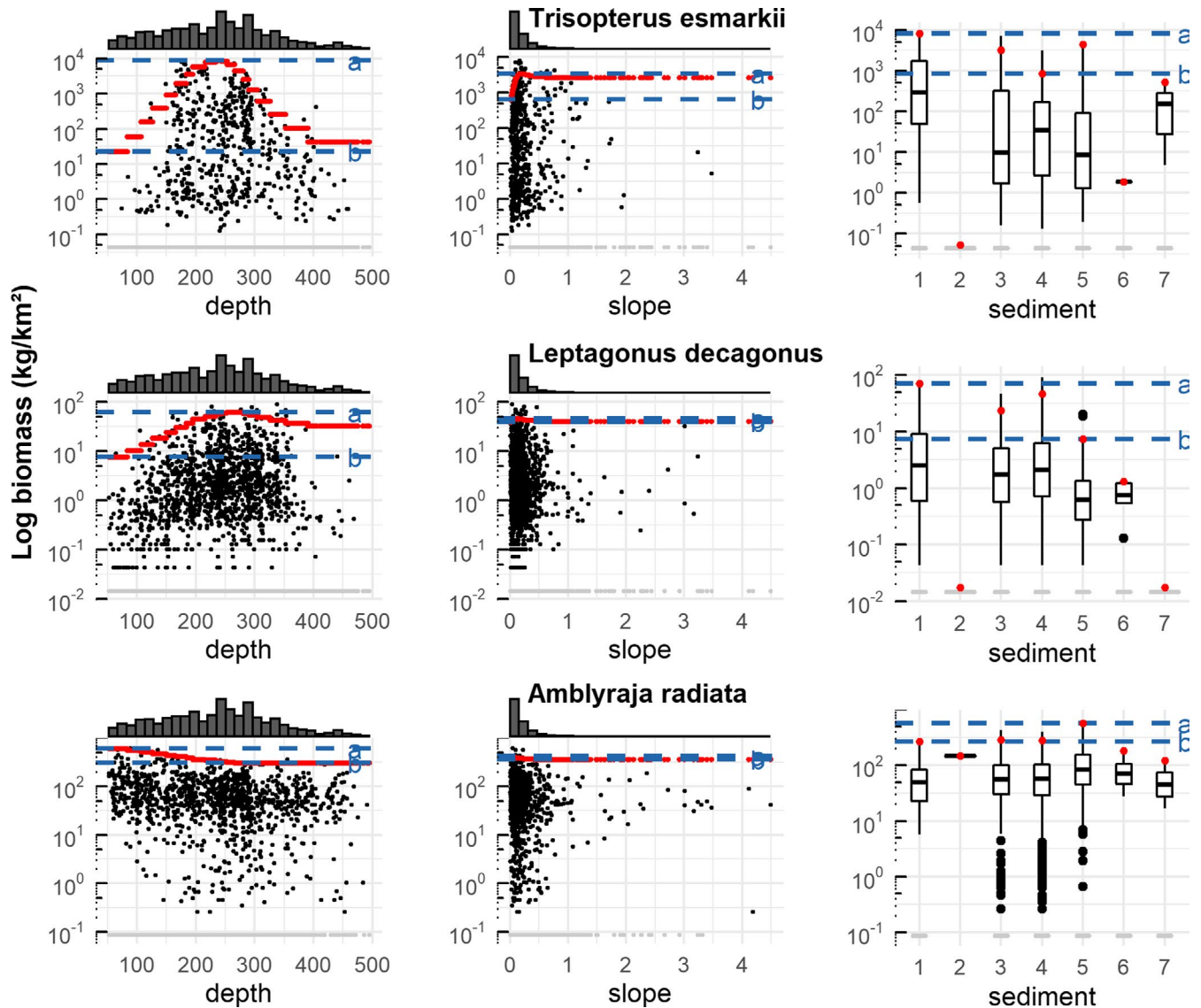
#### 3.1.1 | Species responses to environmental predictors

Convergence and predicted quantiles: Modeled responses to depth, slope, and sediment converged successfully for the three species (Figure 1). For *Trisopterus esmarkii* and *Leptagonus decagonus*, between 99.0% and 99.2% of the observations were below the modeled response to depth, slope, and sediment, which is close to the desired 99<sup>th</sup> quantile. *Amblyraja radiata* models weakly fitted to the data as both depth and slope models were above more than 99.5% of the data. When the same models were applied to the testing dataset, depth, and slope models slightly overestimated the maximum biomass of *Trisopterus esmarkii* and *Leptagonus decagonus* (testing percentile between 99.0% and 99.5%) while *Amblyraja radiata* biomasses were strongly overestimated. This means the model is likely to be less precise when applied to new conditions. For sediment, on the contrary, the model strongly overestimated the maximum biomass for *Trisopterus esmarkii*, and slightly overestimated and underestimated it for *Leptagonus decagonus* and *Amblyraja radiata*, respectively.

Model contrast: The contrast in the response was the highest for the *Trisopterus esmarkii*–depth model (contrast 0.997) and tied second highest for *Trisopterus esmarkii* and *Leptagonus decagonus*–sediment model (contrast: 0.897). Such high values indicate that the sampling includes environmental conditions that are very limiting for the species. The response of *Leptagonus decagonus* to slope showed the lowest contrast (0.131).

#### 3.1.2 | Habitat suitability mapping

When applying the models to the environmental conditions of 2013, predictions were rather low (i.e., some factors were very limiting) in most of the Barents Sea for *Trisopterus esmarkii* (Figure 2). Bottom temperature was most limiting in the majority (60.9%) of the stations. Depth and surface temperature were the most limiting in 12.8% and 9.0% of the stations in 2013, respectively. Only 2.5% of the stations were associated with weakly limiting conditions. For *Leptagonus decagonus*, there was not a single most limiting predictor in the majority of the stations, but several predictors that limited an equivalent portion of the samples: bottom and surface temperature (24% and 15% of the stations, respectively), depth (14%), bottom salinity (12%), sediment (11%), and days of ice (10%). All other predictors were limiting in less than 10% of the stations. For this species, 55% of the stations were weakly limiting. For *Amblyraja radiata*, sediment, bottom temperature, and days of ice were the most frequent most limiting factor, but only ice and bottom temperature predicted strong limitation of the biomass in 3.3% of the stations. The 96.7%



**FIGURE 1** Modeled  $\log_{10}$  responses of three Barents Sea species to three environmental predictors: depth, slope, and sediment type. Depth and slope: black dotted scatterplot of the log of non-null biomasses observed in response to the predictor. Gray dots indicate sampled environmental conditions where the species biomass is null. Red dots indicate modeled log of maximum biomass predictions. The “stair” pattern in the model predictions results from the discretization of the predictors prior to fitting. On top of the scatterplot, the marginal density shows the distribution of samples conditional to the predictor values. Sediment: boxplot of response to the sediment. The model prediction is the 99th quantile for each sediment class: 1 = coarse sediment; 2 = compacted sediment or sedimentary bedrock; 3 = mixed sediment; 4 = mud, clay, and sandy mud; 5 = sand and muddy sand; 6 = sand, gravel, and pebbles; and 7 = thin or discontinuous sediment on bedrock. All panels: blue dashed lines indicate references for the calculation of the contrast: a: max predicted maximum biomass, b: min predicted maximum biomass. Contrast =  $(a-b)/a$  [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

other stations were weakly limited (i.e., the predicted biomasses were above 25% of the model's predictions maximum).

### 3.2 | Limits to the distribution of 33 fish species

Individual species-predictor models are provided for all 33 species in Appendix S1-4. Tables summarizing and clustering the species models descriptors (i.e., niches typologies) are in Appendix S1-5. Some figures use abbreviated species names. The correspondence

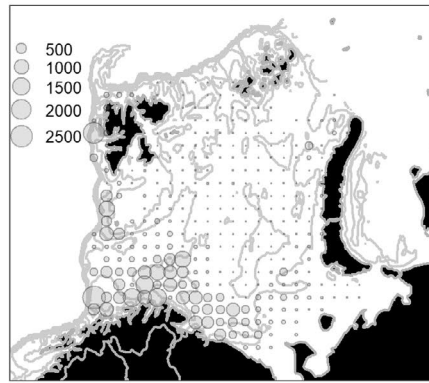
between abbreviated and full names is provided in Appendix S1-5. Maps for all the species are presented in Appendix S1-6.

#### 3.2.1 | Species responses to environmental predictors

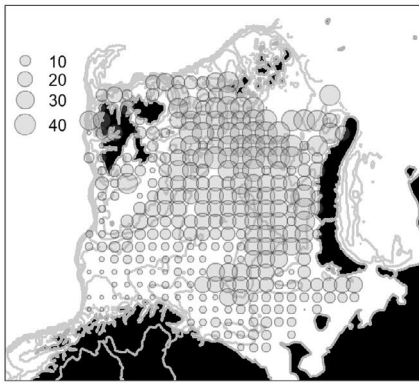
Convergence and predicted quantiles: All models successfully converged. The training and testing sets performed quite differently on predicting the 99<sup>th</sup> quantile (Figure 3). When fitted on the training

**Trisopterus esmarkii**

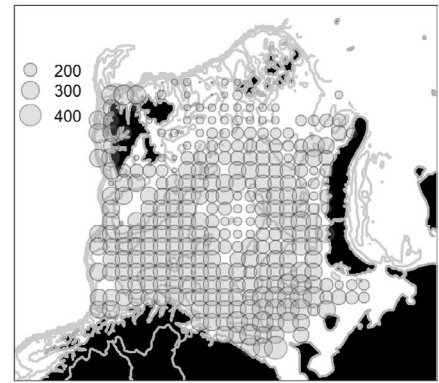
Predicted maximum (99%) biomass (kg/km<sup>2</sup>)



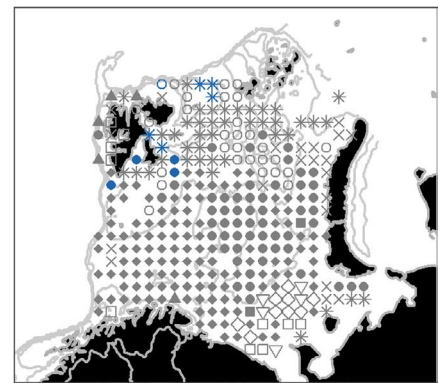
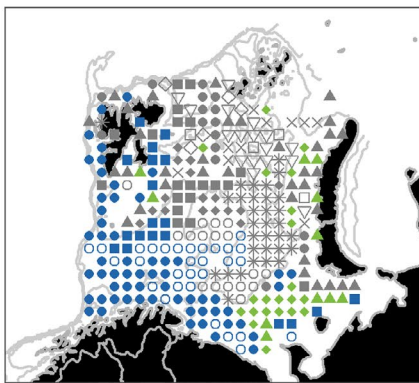
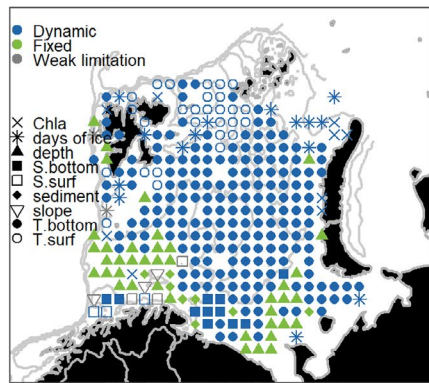
**Leptagonus decagonus**



**Amblyraja radiata**



Most limiting factor



**FIGURE 2** Spatial predictions in 2013 of *Trisopterus esmarkii*, *Leptagonus decagonus*, and *Amblyraja radiata*. Top: suitable habitat (maximum biomass); bottom: most limiting predictor. Color indicates the predictor's category: fixed (sediment, depth, and slope), dynamic (all the others) or not weakly limiting (predicted biomass >25% of the model maximum). [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

set, most of the models (94%) were above between 98.5% and 99.5% of the data. Only 6% strongly overestimated the maximum biomass (i.e., were above more than 99.5% of the data). None of them strongly underestimated the maximum biomass.

The models performed less well at predicting the 99<sup>th</sup> quantile when applied to the testing dataset, as only 50% of the models were above between 98.5% and 99.5% of the data; 38% strongly overestimated the maximum biomass, and 11% strongly underestimated it. One model is an outlier, performing very poorly in the testing set: *Arctozenus risso* response to sediment. This may be because this species biomass peaked in 2016, at levels absent from the training set.

Model contrast: Most of the models showed relatively high level of contrast: 45% had high contrast (>0.90), and 37% had an intermediate contrast (0.50 to 0.90). Slope has the lowest mean contrast (0.44) across the 33 species, followed by surface mixed layer depth (0.58). Surface salinity and chlorophyll a are associated with similar contrast in the species response (~0.75). Following predictors display high average contrasts: sediment (0.83), ice cover (0.85), bottom salinity (0.86), and bottom temperature (0.87). Depth and surface temperature models are the most contrasted with an average of 0.90.

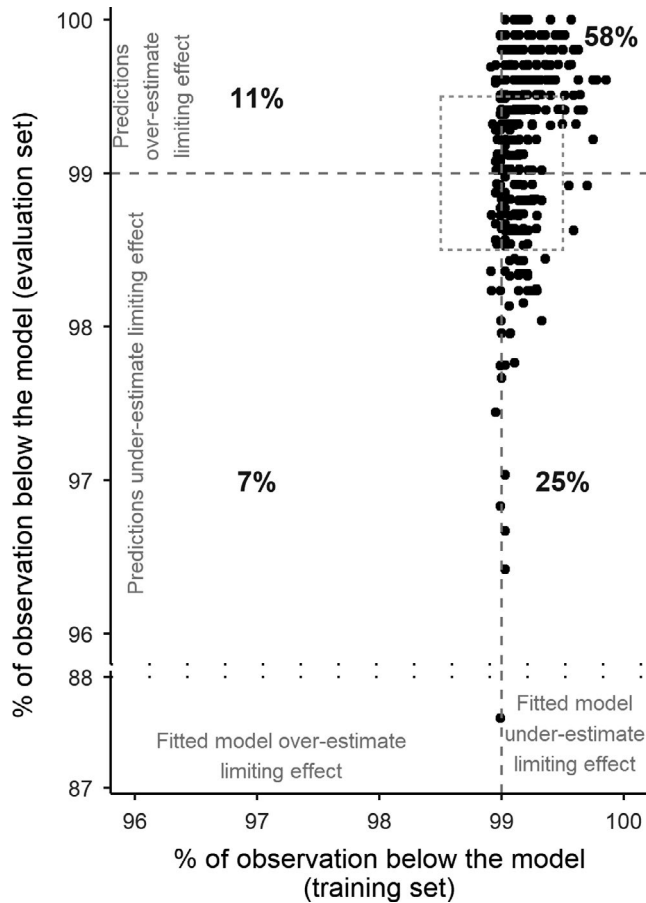
Among temporally fixed predictors, the most contrasted responses were to depth (24 of the 33 species), sediment (8 species), and slope (1 species). Bottom and surface temperature caused the

highest contrast among dynamic predictors for 12 and 13 species, respectively, ice cover for 5 and bottom salinity for 3.

Niche shapes: The shape of the model approximates the potential niche of the species. Most model shapes can be interpreted as a complete or a partial bell, with large differences in amplitude, from very contrasted to very flat models. Occasionally, species response models to surface or bottom salinity or ice coverage would take a v shape.

The PCA using the niche descriptors (Table A5.1 and A5.2 in Appendix S1) described 55% of the variability of niche profiles among the species. The first axis (37.7% of the variability) opposed the species according to the ranges of all their models, except that to bottom temperature and bottom salinity. The second axis (17.3%) opposed species with high mode values for bottom salinity, depth, days of ice, and slope to those with high values of chlorophyll a concentrations, surface temperature, and large ranges of bottom temperature.

The hierarchical clustering distinguished 3 clusters (Figure 4). The first cluster is mainly characterized by short ranges for all predictors (v test from -1.9 to -4.4, with p values from 4.6.10<sup>-2</sup> to 1.2.10<sup>-5</sup>), low mode value of days of ice (v test=-2.8; p value = 5.7.10<sup>-3</sup>), and high mode values of surface temperatures, surface salinity, SML and bottom temperature and salinity (v test = 2.4 to 3.4; p value = 1.5.10<sup>-2</sup> to 7.0.10<sup>-4</sup>). The second cluster includes species with larger ranges of bottom and surface



**FIGURE 3** Scatterplot of the predicted percentile of the observation by the models in the training and testing set. The dotted rectangle indicates models that slightly under or overestimate the maximum biomass. Outside of that rectangle are the models that strongly under or overestimate the maximum biomass.

temperature and SML ( $v$  test = 2.0 to 2.45;  $p$  value = 4.2 to 1.4.  $10^{-2}$ ), and lower mode values of SML, slope, depth, and bottom salinity ( $v$  test = -2.1 to -5.2,  $p$  value = 3.2.  $10^{-2}$  to 2.0.  $10^{-7}$ ). The third cluster is characterized by low mode values of bottom temperature, surface salinity and temperature and chlorophyll concentrations ( $v$  test from -2.5 to -3.9;  $p$  value from 1.4.  $10^{-2}$  to 9.3.  $10^{-5}$ ), high mode values of bottom salinity, depth, slope, and days of ice ( $v$  test from 2.0 to 4.2;  $p$  values from 4.2.  $10^{-2}$  to 2.8.  $10^{-5}$ ), and large range of surface temperature, slope, days of ice, SML, depth, surface salinity, and chlorophyll a concentrations ( $v$  test from 2.0 to 3.3,  $p$  value from 4.5.  $10^{-2}$  to 1.1.  $10^3$ ).

### 3.2.2 | Habitat suitability mapping

Species can be categorized in five groups according to their most frequent most limiting factor over the years: bottom temperature (13 species, such as *Trisopterus esmarkii*, Figure 5), depth (10 species, such as *Arctozenus risso*), surface temperature (4 species, like *Triglops nybelini*), sediment (5 species, like *Triglops murrayi*), and

bottom salinity (only one species: *Amblyraja hyperborea*). Slope (most limiting factor in 2% of the samples over the whole time period), surface mixed layer depth (2%), surface salinity (4%), chlorophyll a (5%), and ice cover (8%) never were the most frequent most limiting factor. However, environmental conditions only weakly limited the biomass in about 50% or more of the sampled locations for 18 species (Figure 5, right panel, in red). Species most frequently limited by sediment were all weakly limited by the environment in more than 50% of the stations they were sampled in.

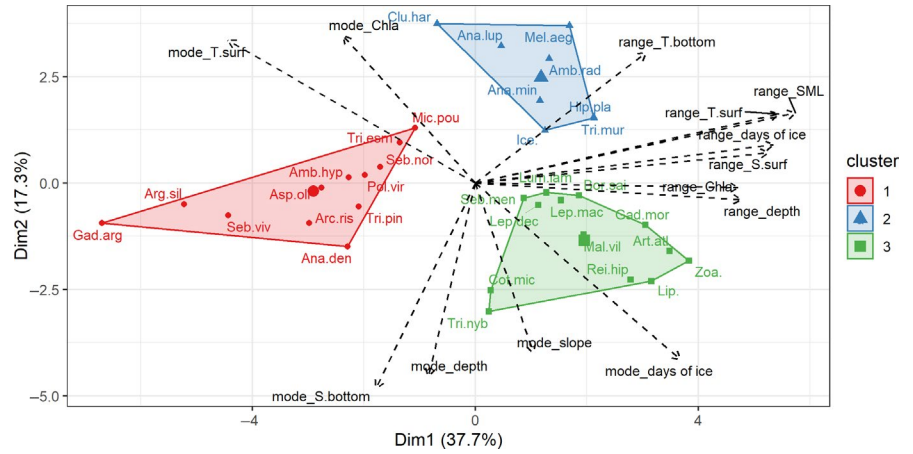
### 3.2.3 | Predictability of suitable habitats

For 21 of the 33 species, the maximum contrast to dynamic predictors was higher than that of the fixed ones (Figure 6). This maximum predictor was bottom salinity for 1 species, ice for 3, bottom temperature for 8, and surface temperature for 9. The 12 other species had higher contrast in fixed predictors. The maximum predictor was depth for all them. It should be noted that for 14 species, the factor causing the most contrasted response (Figure 6) was different from the species most frequent most limiting factor (Figure 5).

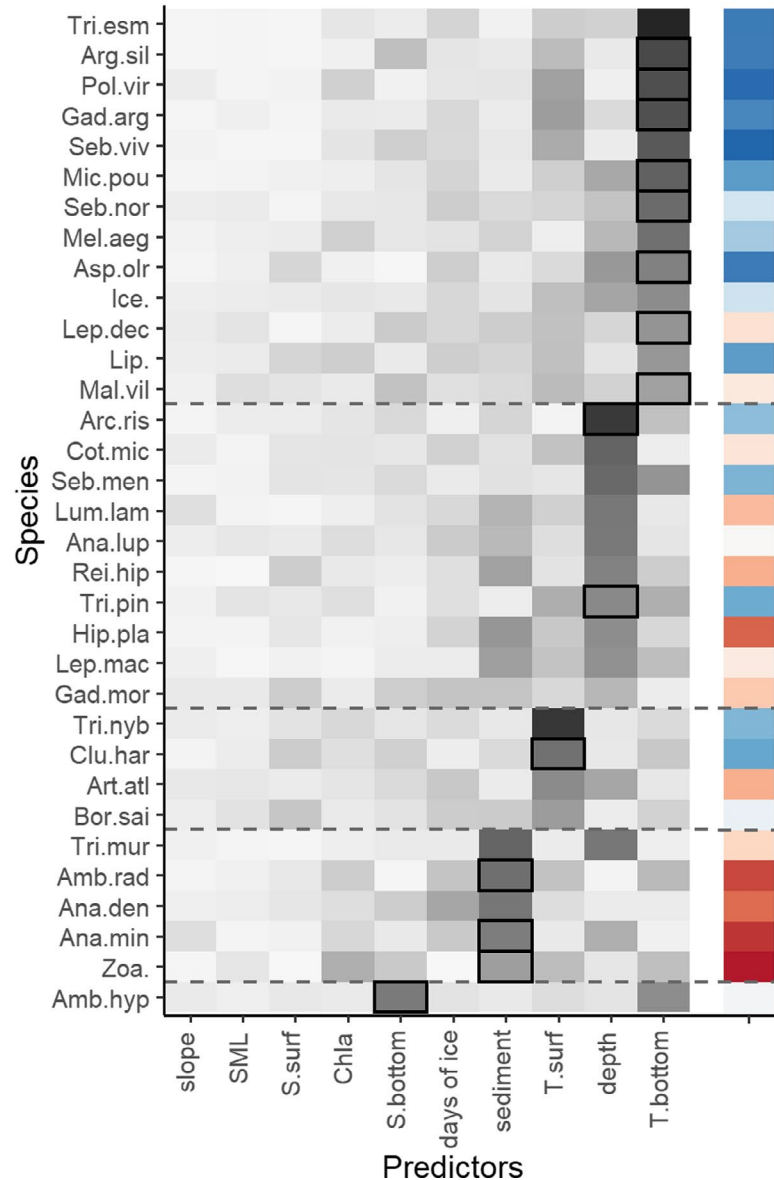
Synthesis: The PCA was performed on (a) the average proportion of stations limited by the most frequent most limiting factor (Figure 5, left panel), (b) the average proportion of stations where the biomass is weakly limited by the environment (Figure 5, right panel), (c) the value of the highest contrast among dynamic, and (d) fixed predictors (Figure 6). The PCA explained 84% of the variability among the data. The first axis was driven by the opposition between species that are weakly limited by the selected predictors and those that show a contrasted response and/or are often limited by a single factor (Figure 7). The second axis was mainly driven by the proportion of stations where the species are limited by a single, most frequent, most limiting factor. This axis was also driven in a lesser extent by the maximum contrast among fixed predictors.

The cluster analysis highlights three clusters (Figure 7). The first cluster is characterized by species with a high proportion of stations where their biomass is weakly limited ( $v = 4.1$ ,  $p$  value = 3.8.  $10^{-5}$ ) and low maximum contrasts ( $v = -3.8$  and  $-5.0$ ,  $p = 4.6. 10^{-4}$  and 4.4.  $10^{-7}$  for fixed and dynamic predictors, respectively). These are typically species which niche could not be modeled properly. *Anarhichas minor* is a paragon (i.e., it is the closest to the center of the cluster) while Zoarcidae and *Amblyraja radiata* are typical species of this cluster (i.e., they are the more distant from the other two clusters). The second cluster is characterized by species limited by several most limiting factors (low values of “% most frequent most limiting factor”:  $v = -3.1$ ,  $p = .002$ ). *Anarhichas lupus* is a paragon, and *Boreogadus saida*, *Leptagonus decagonus*, or *Mallotus villosus* are typical species of this cluster. The third cluster is associated with high frequency of limitation by a single most limiting factor ( $v = 4.3$ ,  $p = 1.3. 10^{-5}$ ), high maximum contrast in both dynamic and fixed predictors ( $v = 2.5$  and 2.0,  $p = 1.3. 10^{-2}$  and 4.1.  $10^{-2}$ , respectively), and low proportion of weak limiting conditions ( $v = -3.9$ ,  $p = 1.0. 10^{-4}$ ). *Gadiculus argenteus* is a paragon, and *Trisopterus esmarkii* and *Triglops nybelini* are typical species of this cluster.

**FIGURE 4** Principal component analysis and hierarchical clustering of species niche descriptors. Only variables with a high contribution to the construction of both axes are shown [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

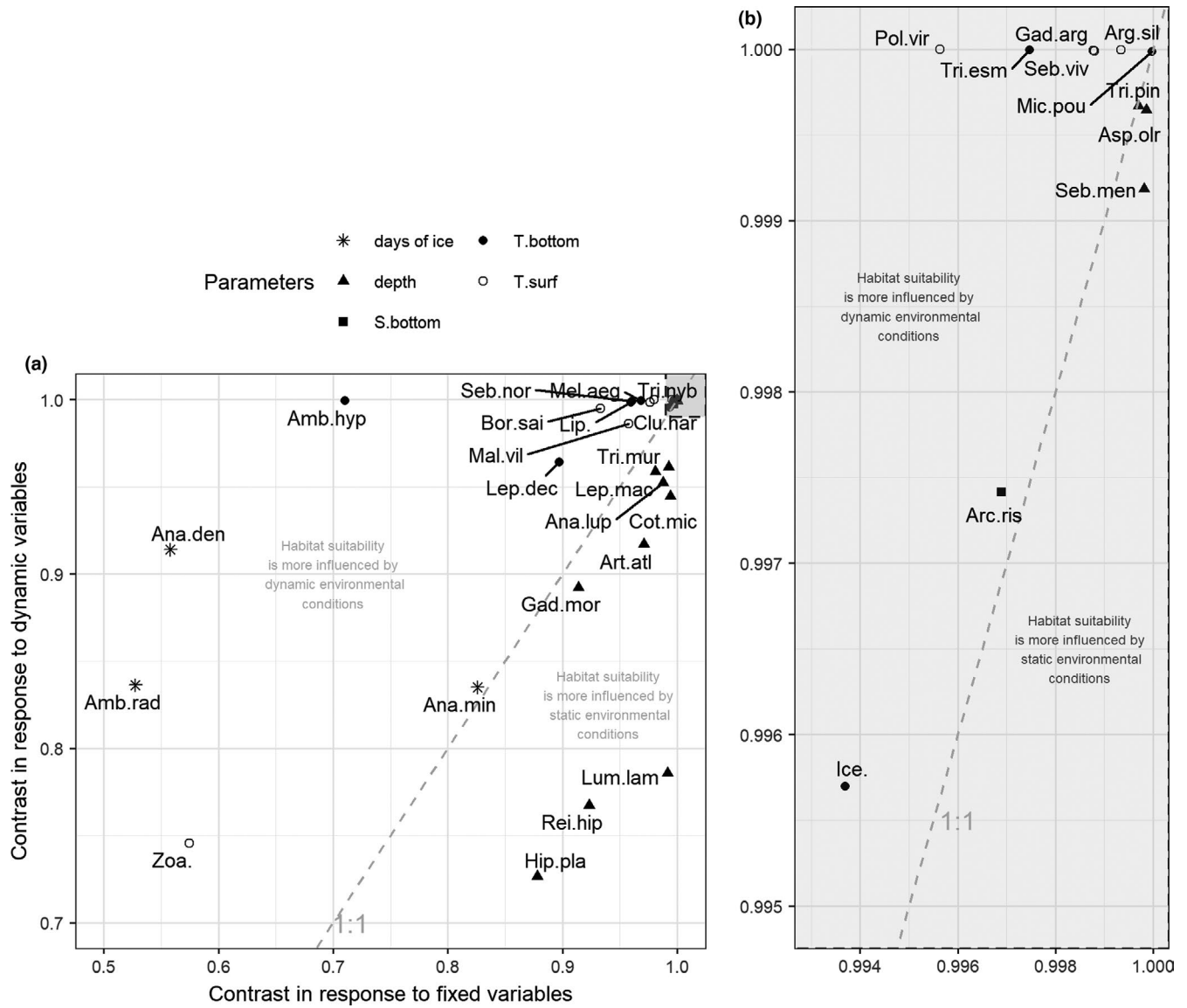


Mean proportion of locations where the biomass is limited by the predictor (%)      is weakly limited (%)

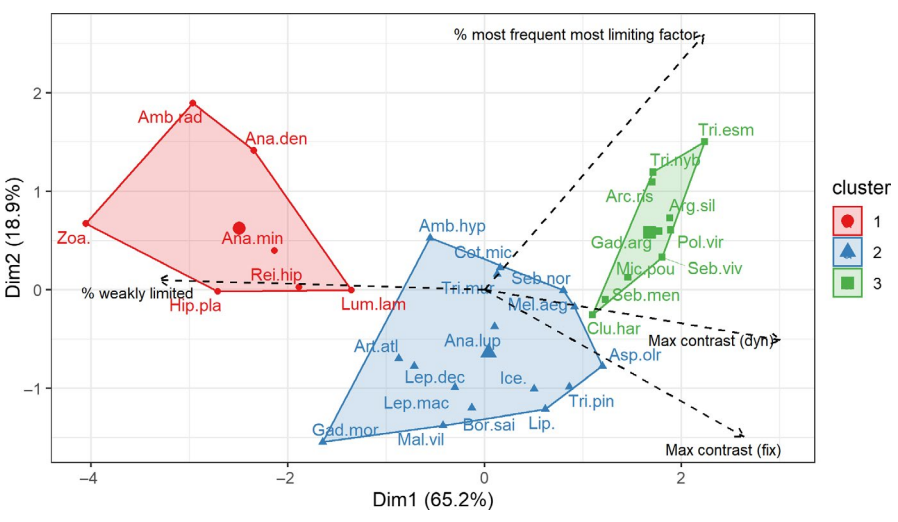


**FIGURE 5** Frequency of the limiting effect across space and years. Right panel: for each species, mean proportion of samples weakly limited (the predicted biomass is >25% of the model maximum). Left panel: for each species, mean proportion of samples limited by each factor. Black rectangles identify for each species the most frequent most limiting predictor, but only if its predictive power is acceptable (predicted quantile of the testing dataset ranging from 98.5 to 99.5) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]





**FIGURE 6** Scatterplot of species maximum contrasts in response to fixed versus dynamic variables. The shape of the point indicates which parameter is the one with the maximum contrast. The 1:1 line is grey and dashed. (b) is a zoom in the grey area of (a)



**FIGURE 7** Species hierarchical clustering projected on a principal component analysis of the descriptors of habitat suitability predictability [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

## 4 | DISCUSSION

### 4.1 | Environmental conditions limiting fish distribution in the Barents Sea

Among the six predictors causing in average the most contrasted responses in the biomass of the species, five were also most limiting of species habitat in the Barents Sea: bottom temperature, depth, surface temperature, sediment, and bottom salinity.

Depth has frequently been reported to be one of the most important predictor of demersal fish distribution (e.g., Chatfield, Niel, Kendrick, & Harvey, 2010; Moore, Harvey, & Van Niel, 2010; Moore, Van Niel, & Harvey, 2011). In this study, depth was often limiting either on the shelf for species living in deep areas (e.g., polar sculpin, *Cottinculus microps*, or spotted barracudina *Arctozenus risso*), or on the deepest and shallowest areas for species preferring shallow waters (e.g., snakeblenny, *Lumpenus lampraeformis*, or wolfish *Anarhichas lupus*).

Bottom temperatures were slightly more often limiting for the Barents Sea species, especially for species that are distributed in the southwestern part of the Barents Sea (e.g., Norway pout *Trisopterus esmarkii*, greater argentine *Argentinus silus*, saithe *Pollachius virens*, and silvery pout *Gadiculus argenteus*). Their spatial distribution appears to be limited by the low bottom temperatures currently occurring in the rest of the Barents Sea. Byrkjedal and Høines (2007) obtained similar results in a study focusing on the southwestern part of the Barents Sea and explained the strong influence of the temperature by the conjunction of the cold, sub-zero, Arctic and warm Atlantic water at the polar front, creating strong latitudinal gradients of temperature. The other species most limited by bottom temperatures are arctic ones (e.g., capelin *Mallotus villosus*, liparids, or the Atlantic poacher *Leptagonus decagonus*). For those species, bottom temperature is less frequently limiting, and surface temperatures are often second in limiting their habitat.

Surface temperatures cause high contrast in the species responses and are frequently the most limiting either (a) northeast of the polar front, for the Atlantic herring *Clupea harengus*, or (b) in the south for species considered as arctic (e.g., polar cod *Boreagadus saida* and bigeye sculpin *Triglops nybellini*). Those species have been shown to follow yearly variations in sea ice extent in other subarctic areas (Wyllie-Echeverria & Wooster, 1998). In our samples, surface temperature and ice cover are often limiting in the same area, in the north, so the limitation of the species responses by low surface temperature might also be a proxy of the limitation by cold, ice-covered water masses north of the polar front.

The emergence of bottom salinity as a major limiting factor of *Amblyraja hyperborea* is surprising. This species is a typical polar species that prefers cold temperatures and deeper waters than those of the Barents Sea (Dolgov, Grekov, Shestopal, & Sokolov, 2005; Peklova, Hussey, Hedges, Treble, & Fisk, 2014). Its response to bottom salinity is indeed very contrasted with a very narrow range and a preference for high salinities, but it should be

noted that its highest contrast and second most limiting predictor are bottom temperature. There might thus be a confusion between these two factors, and possibly with other factors such as depth. For example, in 2013, the stations where bottom salinity was the most limiting factor were the shallow banks around Murmansk and Svalbard as well as the north and eastern slopes of the Bear Island Trough. In the first case, the ice and river outflows cause low salinities on the banks, but this effect might be confounded with that of depth as these areas are too shallow for the skate. Bear Island Trough, however, is the deepest point of the Barents Sea. An alternative explanation might be the large variations of current velocities of the area (Ingvaldsen, Asplin, & Loeng, 2004) and the potentially associated turbidity that might constraint this species movement or predation.

Lastly, five species are limited by the type of sediment in the Barents Sea and have low contrast in response to most of the predictors. All of them are frequently only weakly limited and are quite widespread in the region. Because of the differences in the sampling of the various types of sediment, and although there are few differences in biomasses among samples, sediment causes a high contrast for all of them. It is thus more often picked as the most limiting factor when comparing with the other factors. Therefore, sediment is probably not a strong limiting factor of fish habitat in the Barents Sea. Identifying their suitable habitats might necessitate other unavailable environmental predictors.

Another variable that could be considered in future studies is light availability. Light constrains numerous processes like primary production, visual predation (Langbehn & Varpe, 2017), or zooplankton depth in the Barents Sea (Aarflot, Aksnes, Opdal, Skjoldal, & Fiksen, 2019). It might change the limiting factors for boreal species entering the Barents Sea, as light conditions might be a particularly strong tradeoff at those latitudes (Poloczanska et al., 2016). However, a proxy of primary production was already included in the selected variables with the chlorophyll a, and it is probable that the effect would have been confounding with variables with strong latitudinal gradient-like sea ice cover. Also, most of the stations sampled are below 150 m (the average depth of the Barents Sea is 230 m), where most of the light spectrum does not reach and visual predation is reduced.

### 4.2 | Assessing our capacity to identify and predict species suitable habitats

Not all the species used in this study fulfill the three requirements for the predictability of their suitable habitat mentioned in the introduction. A recent study (Smith, Godsoe, Rodríguez-Sánchez, Wang, & Warren, 2019) showed that grouping related taxa that are likely to share environmental tolerances, or splitting species in smaller population units that have adapted independently can improve niche estimates. In the present study, widespread spatial distributions and environmental tolerance can partially reflect the variety of habitats used by different age groups (e.g., cod *Gadus morhua*) or species (eel pouts Zoarcidae). In our case, length or age information

was not available in the aggregated dataset that we had. Modeling habitat suitability at a finer biological scale (e.g., by age or population units) might be required to improve habitat suitability models for these groups (McPherson & Jetz, 2007; Morán-Ordóñez et al., 2017; Porfirio et al., 2014; Thuiller, Lavorel, & Araújo, 2005).

A high contrast to at least one predictor is needed to be able to identify limiting factors of the species habitat, and the limiting conditions should occur within the Barents Sea. Group 1 of the second clustering analysis (Figure 7) gathers species that do not meet those two criteria. Those are the species similar to *Amblyraja radiata*, with low maximum contrast and high proportion of weakly limited samples, which tend to thrive in all ranges of depth and temperatures over the Barents Sea (Dolgov et al., 2005). The dataset used in the current study included sufficient information on environmental conditions in which these species are found, but little on what conditions limit their abundance. To increase our chances of properly capture the niche of these species, the spatial scale of the study needs to be expanded to the limits of distribution of those species, for example by aggregating data from all subarctic seas.

For the two other groups, it is possible to identify and predict their suitable habitats. Modeling and predicting suitable habitats for species from group 3 are quite straightforward and these are the species for which we can anticipate niche change with most confidence. In the case of group 2, the niche model must be complex, multivariate, and may require the examination of interactions between limiting factors. Indeed, group 3 is characterized by species which habitat is mostly limited by a single factor. This is the case of all the southwestern species entering the Barents Sea whose niche is only partially known as their distribution lies mainly in the North Atlantic, like the mesopelagic *Gadiculus argenteus*. For example, blue whiting (*Micromesistius poutassou*) and adult saithe (*Pollachius virens*) expand into the Barents Sea when their stock is large in the Norwegian sea (for blue whiting: Heino, Engelhard, & Godø, 2008) or as a seasonal migration during the second quarter and third quarter (for saithe: Olsen et al., 2010). Inside this group, species with habitats mainly limited by dynamic variables like bottom or surface temperatures are the most susceptible to shift poleward in response to climate change, in the limits of their depth, sediment, and slope preferences (like *Gadiculus argenteus*, Figure 8). It has already been observed for some: Perry, Low, Ellis, and Reynolds (2005) noticed that *Micromesistius poutassou* and *Trisopterus esmarkii* distribution boundaries have shifted northward in relation to the warming between 1977 and 2001 in the North Sea, and in the Barents Sea, both species and *Argentina silus* are part of the boreal or intermediate communities that also have shifted between 2004 and 2012 (Fossheim et al., 2015). The habitat shift of the species in this group is also supported by ecological niche models predictions, which have shown a gain in suitable habitat in the Barents Sea for saithe and haddock (*Melanogrammus aeglefinus*) in the middle of the Barents Sea between 1960 and 2090 (Lenoir, Beaugrand, & Lecuyer, 2011). Hollowed et al. (2013) also hypothesized a northward shift of *Clupea harengus*. Also belonging to group 3, species that are less susceptible to follow their thermal

niche are those most limited by static predictors like depth (e.g., beaked redfish (*Sebastes mentella*) in deep waters, Figure 8, or snakeblenny (*Lampanyx lamprotaeformis*) in shallow waters). This supports a recent study projecting that depth will strongly limit the availability of new suitable habitats for fish impacted by climate change (Rutterford et al., 2015). This effect might be compensated if deep or shallow corridors exist to connect past and current suitable areas.

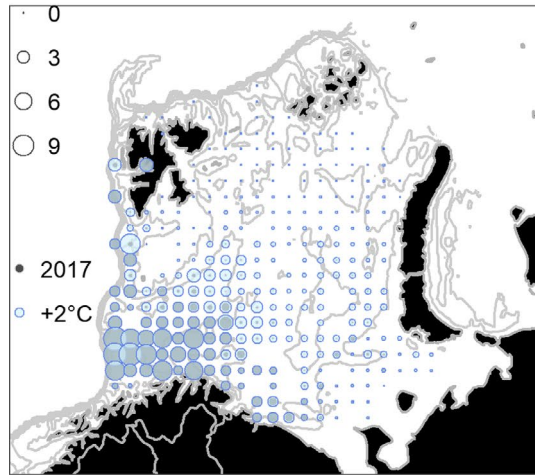
Group 2 is the largest, with half of the studied species. It includes mainly arctic species like the Atlantic poacher (*Leptagonus decagonus*, Figure 8), but also widespread, like cod (*Gadus morhua*) or species from the central Barents Sea, like the mustache sculpin (*Triglops murrayi*). Those species are limited equally by several predictors and being able to predict their future habitat necessitates to apply the QGAM models to maps of projected environmental conditions. As an illustration, Figure 8 shows predicted maximum biomasses for year 2017 and a coarse scenario of increased surface and bottom temperature of + 2°C. Such procedure can also be applied on more exhaustive and realistic scenarios from oceanographic projections.

Models used for predictions should be robust when applied to new conditions. Although it is not possible to quantitatively assess model's performance in future climate, the recent rapid warming in the Barents Sea provides suitable conditions to test the performance of the habitat models in two periods with contrasting ocean climate, corresponding to the two periods used for our training and testing datasets. Half of the models performed well when applied to the testing dataset and can make reliable predictions on species future habitats. The poorer model performances of the other models may reflect that the training dataset did not include enough of the variability in the species response to the predictor, that is, that the conditions that occurred between 2015 and 2017 were outside of the range of the previous years. For those models, prediction can still be done, but the resulting habitat suitability might be over/underestimated and distribution maps should be interpreted in a more qualitative sense.

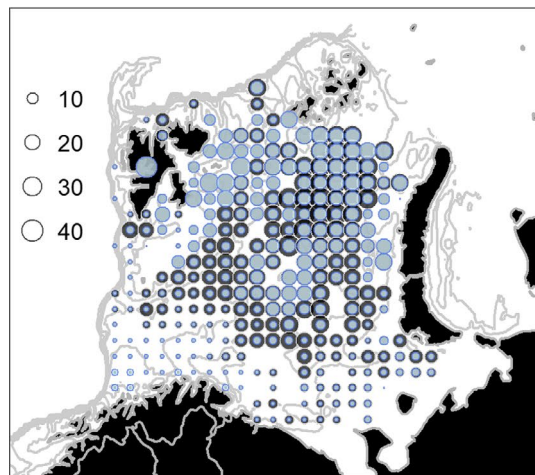
#### 4.3 | Possible uses of individual species QGAM models

The shapes of QGAM models could provide an approximation of the potential niche (Cade et al., 2005; Jiménez-Valverde et al., 2008). In this study, QGAMs were fitted with a maximum degree of freedom of 3, so that the resulting models display simple shapes that can be interpreted in the context of the niche theory. Most frequently, models display bell shapes that can sometimes be asymmetrical, skewed, and/or incomplete (i.e., only one side of the bell is visible). V shapes occur occasionally (in response to salinity or ice cover) and are more difficult to interpret. Causes for these v shapes could include the existence of two population within the Barents Sea with different habitat preferences, or strong non-linear links to other variables with strong spatial structure (proximity to coast, river outflow, depth, etc.).

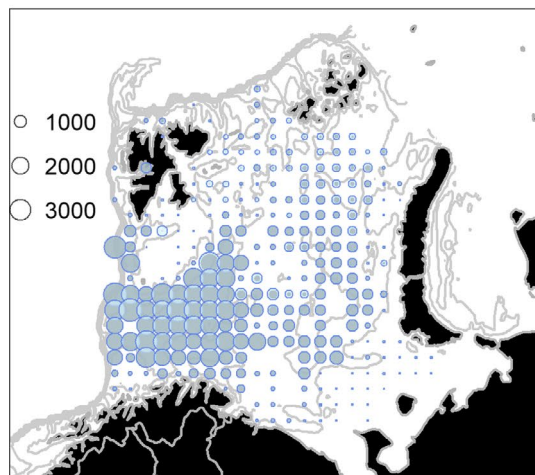
*Gadiculus argenteus*



*Leptagonus decagonus*



*Sebastes mentella*



**FIGURE 8** Suitable habitat predictions for 2017 (blue circles) and for a climatic scenario of + 2°C in surface and bottom waters (red circles). Size of the dot indicates the estimated maximum (99<sup>th</sup> quantile) of the biomass (kg/km<sup>2</sup>) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

When clustering descriptors of those shapes (range, mode), we reached three typologies of niche that coincide more or less with three communities previously defined (Fosheim et al., 2015): (a) Atlantic warm and salty water-associated species that appear to have a partial niche with narrow breadth because the Barents Sea is a northern border of their distribution, (b) mainly arctic and intermediate water masses species preferring colder and fresher waters, and (c) widespread or intermediate water species that can cope with a large range of bottom temperatures and thrive in most of the Barents Sea.

By using species-specific models, the broad patterns observed at the scale of the community can be precised at the species level, not only on the main commercial species but also on the less studied but frequently sampled fish. Maps of habitat suitability and description of the niche can be used in fisheries management and conservation to infer potential distributions. For some of the species, however, the niche is only partially described, and larger scale studies with precise metadata are needed.

Beyond environmental responses, species spatial distribution can be explained by a numerous collection of other processes, such as density-dependent habitat selection, spatial dependency (linked to schooling behavior, for example, or predator avoidance), interspecific and intraspecific interactions, memory processes like homing and demographic structure (Planque, Loots, Petitgas, Lindstrøm, & Vaz, 2011). Thus, the habitat suitability is only the background process of several other controls on species distribution. Approaches like quantile regression, that give space for other controls to operate, can be an input to a number of other processes such as density-dependence, homing, biotic interactions, and others. QGAM models allow to group species that share the same niche and are thus more likely to interact ecologically. Combined with local co-occurrence studies, they could be used to highlight intense predation or competition hotspots. In end-to-end models, these QGAMs outputs can be used to constrain specie's habitats. Taking into account, the biotic interactions and human activities may then further constrain the species' abundances, possibly leading to better approximations of species actual distributions.

**5 | CONCLUSIONS**

The use of QGAM allowed to quantify the potential environmental niche of 33 fish species in the Barents Sea. The models showed a wide variety of responses to environmental stressors. The application of the Liebig's law on the mapped conditions of the region highlighted the importance of depth, temperatures, and salinity as limiting factors for many species, some of which responding to a single predictor, others being locally limited by a great variety of factors, and finally some for which no niche could be drawn. While species responding more strongly to dynamic variables should be the most responsive to changes in their habitats, static limiting factors might act as a barrier to range shift. An advantage of the QGAM methods is that the models can easily be used as input for

habitat preferences within end-to-end models. This would allow to predict suitable habitats maps on top of which other processes would refine the species distribution. This empirical knowledge should greatly benefit to any complex modeling attempt in the Barents Sea.

## ACKNOWLEDGEMENTS

This work is part of the BSECO project funded by Arktis 2030 (BSECO Barentshavet i endring Contract nr. QZA-15/0137). We are grateful to Dr. Randi Ingvaldsen for her help with collecting the ice cover data, and to Dr. Edda Johannesen and all the people who have worked to make a rich and reliable dataset from the demersal trawl surveys. We are also grateful to all the people involved in the joint ecosystem surveys at the Institute of Marine Research (IMR), Norway, and Polar Branch of the Federal State Budget Scientific Institution (PINRO), Russia.

## CONFLICT OF INTEREST

None.

## AUTHOR CONTRIBUTIONS

BH wrote the manuscript along with GC, BP, and AF. BP and GC conceived the presented idea. BH analyzed the modeling results. All authors discussed the results and contributed to the final manuscript.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Husson B, Certain G, Filin A, Planque B. Suitable habitats of fish species in the Barents Sea. *Fish Oceanogr*. 2020;29:526–540. <https://doi.org/10.1111/fog.12493>