

1 Suitable habitats of fish species in 2 the Barents Sea

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17

18 Abstract

19 Many marine species are shifting their distribution poleward in response to climate change.
20 The Barents Sea, as a doorstep to the fast-warming Arctic, is experiencing large scale
21 changes in its environment and its communities. This paper aims at understanding what
22 environmental predictors limit fish species habitats in the Barents Sea and discuss their
23 possible evolution in response to the warming of the Arctic.

24 Species distribution models usually aim at predicting the probability of presence or the average
25 abundance of a species, conditional on environmental drivers. A complementary approach is
26 to determine suitable habitats by modelling the upper limit of a species' response to
27 environmental factors. Using quantile regressions, we model the upper limit of biomass for 33
28 fish species in the Barents Sea in response to 10 environmental predictors. Boreal species
29 are mainly limited by temperatures and most of them are expected to be able to expand their
30 distribution in the Barents Sea when new thermally suitable habitats become available, in the
31 limit of bathymetric constraints. Arctic species are often limited by several predictors, mainly
32 depth, bottom and surface temperature and ice cover, and future habitats are hard to predict
33 qualitatively. Widespread species like the Atlantic cod are not strongly limited by the selected
34 variables at the scale of the study, and current and future suitable habitats are harder to
35 predict. These models can be used as input to integrative tools like end-to-end models on the
36 habitat preference and tolerance at the species scale to inform resource management and
37 conservation.

38

39 Key words: quantile regression, habitat suitability models, climate change, species
40 distribution, species shifts, environmental drivers

41 **1 INTRODUCTION:**

42 There is growing evidence of spatial shifts of species distribution correlated with climate
43 change (Chen et al., 2011; Hickling et al., 2006; Parmesan and Yohe, 2003; Thomas, 2010).
44 The Arctic is warming faster than any other ocean in the world (IPCC, 2014). Cheung et al.
45 (2009) investigated the potential geographical changes in marine biodiversity worldwide in
46 response to warming and suggested a general increase of species richness in Arctic waters
47 due to northward migrations of species. The region would experience higher species turnover
48 rates due to invasion and local extinction than anywhere on the globe. As such, describing
49 distribution patterns, understanding drivers and projecting potential changes at the species

50 scale is of crucial importance for conservation and management purposes (Marzloff et al.,
51 2016; Pecl et al., 2017; Porfirio et al., 2014).

52 The Barents Sea is situated on the border of the Arctic. It is under the influence of two water
53 masses outflowed from the warm, saline Atlantic in the south west and the cold, less saline
54 Arctic in the north east (Loeng, 1991). Those two masses separate two main communities ,
55 arctic and boreal, that differ, among other thing, in fish species composition (e.g. Fossheim et
56 al., 2015; Johannesen et al., 2012), traits (Frainer et al., 2017) and trophic structure (Kortsch
57 et al., 2015). Important commercial fish (e.g. Atlantic cod, *Gadus morhua*, Atlanto-scandic
58 herring, *Clupea harengus*, and capelin, *Mallotus villosus*) are present in both types of
59 communities and respond to climatic signals (Chambault et al., 2018; Hamre, 1994; Matishov
60 et al., 2012). During past decades, the Barents Sea has been experiencing an increase in
61 Atlantic water inflow and coinciding heat content in the water column, as well as loss of sea
62 ice in the northeast (Årthun et al., 2012; Dalpadado et al., 2012; Lind et al., 2018). In the
63 meantime, the distribution of demersal fish has been altered with a general displacement of
64 boreal communities towards the northeast (Fossheim et al., 2015). Unfortunately, studies in
65 Arctic and subarctic waters have sometimes suffered from a lack of appropriate data to provide
66 robust conclusions about changes in individual species biogeography (Ingvaldsen et al.,
67 2015). Hollowed et al. (2013) estimated, based on expert knowledge, the potential of 17
68 species of the sub-arctic regions to shift their distribution northward, following the increased
69 production in newly ice-free areas. This set of species was quite evenly divided into species
70 with high, medium and low potential to change their distribution. However, changes in spatial
71 distribution at the scale of individual species remain uncertain. There is a need for empirical
72 studies that would help better identify the main drivers of changes in species distributions,
73 which species are likely to respond most, and to which degree it is possible to make prediction
74 about future geographical distributions based on currently available information.

75 Because environment is generally assumed to be the main driver of species distribution
76 (Pearson & Dawson, 2003), most spatial distribution models (SDM) rely solely on
77 environmental covariates. As such, they predict the suitability of a habitat to host a species

78 based on its mean response (in presence/absence or in abundances) to environmental
79 conditions. An alternative approach is to explicitly focus on how those factors may limit species
80 habitats by predicting the upper limit of the species response, i.e. a high quantile (e.g. >0.9)
81 instead of the mean. The statistical method of quantile regression (QR) (Cade et al., 1999;
82 Cade & Noon, 2003) provides a useful framework for assessing limiting factors from
83 observational data. It predicts the expected response for a given quantile q . With $q = 0.5$, QR
84 predicts the median response. With high q 's (>0.9), QR predicts the upper limit of the
85 response. For a set of environment conditions, it is possible to determine the most limiting
86 factor by considering several single-covariate models and identifying the one that predicts the
87 lowest response (Austin, 2007). This approach inherits from the Sprengel-Liebig law of the
88 minimum (van der Ploeg et al., 1999), which considers that a response variable can only be
89 as high as allowed by the most limiting factor.

90 Quantile regression originated in economics (Koenker and Bassett, 1978) and has been used
91 in ecology to investigate prey-size-predator size relationship (Bethea et al., 2004), DNA
92 variation across environmental gradients (Knight and Ackerly, 2002), response to metal
93 concentrations (Schmidt et al., 2012), and fish recruitment-environment relationship (Planque
94 and Buffaz, 2008). Review papers have highlighted its utility for the prediction of suitable
95 habitats (Austin, 2007; Elith and Leathwick, 2009; Hegel et al., 2010), with some applications
96 for terrestrial (Cade et al., 1999; Carrascal et al., 2016; Jarema et al., 2009; Schröder et al.,
97 2005) and aquatic species (Ateweberhan et al., 2018; Cozzoli et al., 2013; Dunham et al.,
98 2002; Lancaster and Belyea, 2006; Lauria et al., 2011; Vaz et al., 2008). Most of the ecological
99 applications of quantile regression have assumed linear relationships between the biological
100 response and the predictors. Based on theoretical considerations, the species response to an
101 environmental factor is expected to be bell-shaped (Hutchinson, 1957; Whittaker, 1967) and
102 recent studies have applied non-linear quantile regression models to allow for this (Anderson,
103 2008; Cozzoli et al., 2013; Dunham et al., 2002; Halkos, 2011; Schröder et al., 2005).

104 The aim of the present work is to (i) quantify the limiting effect of the environmental factors
105 that impact on the spatial distribution of fish in the Barents Sea, (ii) assess the predictability of

106 future geographical distributions based on currently available information and (iii) identify
107 which species are most likely to respond to future environmental changes. For this purpose,
108 we analyze data from the autumn ecosystem survey in the Barents Sea on the 33 most
109 frequently sampled fish species and 10 environmental variables that can potentially limit their
110 habitat. We develop QR nonlinear models for all combinations of species and environmental
111 factors.

112 **2 MATERIAL AND METHODS**

113 **2.1 DATA:**

114 **2.1.1 Fish biomass by species**

115 Fishes were caught by a Campelen 1800 bottom trawl during the autumn IMR-PINRO joint
116 ecosystem survey between 2004 and 2017 (Eriksen et al., 2018). The spatial extent is quite
117 large (around 1.6 million km²), with 278 stations per year in average, depending on the sea
118 ice extent in the North-eastern part of the sea. The sampling effort is regular in space with 35
119 nautical miles (35*1.852 km) between each trawling. The same stations are visited every year,
120 in the limit of technical, time or climatic feasibility. A grid of 35 x 35 nm was fitted in an albers
121 equal area projection, so that each grid cell contains only one station. The bulk of the fish
122 species in the catch of the Campelen bottom trawl contained demersal species. However,
123 benthopelagic and pelagic fish were also regularly caught in high abundances by the trawl
124 and they are kept in the analyses. Estimated species biomasses were standardized by unit
125 area, considering an opening of 25 m of the trawl. Only the trawls towed between 50 m and
126 500 m depth, in 15 to 60 minutes were kept. Towing speed was about 3 knots. In total, data
127 comprised 3827 stations and 78 species over the 14 years. Taxa that were absent in more
128 than 95% of the stations were removed, reducing the number of species to 33.

129 **2.1.2 Environmental predictors**

130 Eleven variables reflecting the environmental conditions of fish habitat were gathered.
131 Considerations on the nature and number of predictors to include according to sample size
132 are described in appendix 1.

133 During the ecosystem survey, CTD were used to measure surface (10 m, T.surf) and bottom
134 temperature ($^{\circ}\text{C}$, T.bottom) and salinity (S.surf and S.bottom) at each station. Two
135 stratification variables were calculated from temperature and salinity profiles following Planque
136 et al. (2006). The surface mixed layer depth (SML, m) was calculated from a double layer
137 model, and the potential energy anomaly (PotEnAno, $\text{kg}\cdot\text{m}^{-1}\cdot\text{s}^{-1}$, Simpson & Bowers, 1981)
138 was estimated as the energy required to mix vertically the entire water column.

139 Bathymetry (m) and slope (degrees) were extracted from NOAA raster for the Barents Sea
140 (Jakobsson et al., 2012). Sediment type was defined by extraction of seafloor description by
141 NGU (Contains data under the Norwegian license for public data (NLOD) made available by
142 Norway's geological survey (NGU)). The 16 sediment classes described on the map were
143 aggregated in 7 coarser classes following the EUNIS sediment hierarchical classification
144 (Davies et al., 2004). Chlorophyll a (chl_a, mg/m^3) average concentration between March and
145 July of each year, as estimated by the NASA from ocean color (NASA OBPG, 2018). Number
146 of days with ice cover (daysofice) were counted from daily sea ice extent maps from the NOAA
147 (Cavalieri et al., 1996). For all those variables, values were extracted at the bottom trawl
148 station position, i.e. there is only one of each per grid cell and per year.

149 Correlation analysis (described in appendix 2) showed a high correlation of potential energy
150 anomaly with depth, so the former was removed from the analysis. To assess the potential of
151 a species habitat suitability to be predicted in a changing environment, the ten remaining
152 predictors were categorized into *fixed* (bathymetry, slope, sediment) and *dynamic* (all the
153 others).

154 **2.2 ANALYSIS**

155 **2.2.1 Species response to environmental predictors**

156 Prior to the regression analysis, species biomass data were log+d-transformed, where d is
157 half the lowest biomass of the species. All quantitative environmental parameters were
158 discretized in 20 categories of equal frequency to facilitate the model fitting process. In the

159 case of days of ice cover, as there was a lot of 0, the first category comprised all the 0s, and
160 the 19 others were spread equiprobably over the rest of the distribution.

161 One quantile generalized additive model (QGAM) was fitted for each pair of species-predictor
162 (330 models) using the `qgam` function in the `qgam` package in R (Fasiolo et al., 2017) and
163 setting the quantile level at 99%. The use of QGAMs allows for greater flexibility in the shape
164 of the relationship between the predictor and the species response than linear quantile
165 regression. It can capture bell-shaped responses, or responses that reach a plateau for high
166 or low levels of the predictor. Other considerations about the theoretical roots, strengths and
167 weaknesses of the methods are quickly described in appendix 3. To avoid regressions with
168 shapes too complex to be ecologically meaningful, the number of degrees of freedom in the
169 GAMs was limited to 3. For the qualitative variable (sediment), linear QR was applied to fit the
170 99th quantile within each sediment category. The `rq` function from `quantreg` package in R
171 (Koenker, 2018) was used.

172 Models were fitted using observations for years 2004 to 2013. They were then evaluated on
173 observations for years 2014-2017. The evaluation was based on two metrics. The first metric
174 is the proportion of observations in the evaluation dataset that were below the predicted 99th
175 quantile. It is expected that 99% of the observations should fall below model predictions. If the
176 observed proportion is higher, this means that the model is overestimating the maximum
177 biomass (i.e. underestimating the limiting effect of the predictor). If the observed proportion is
178 lower, too many observations in the evaluation dataset are higher than the expected maximum
179 value, so the model is underestimating the maximum biomass (i.e. overestimating the limiting
180 effect of the predictor). We categorized the variation from the 99th quantile into a “slight” (98.5
181 to 99.5% of data below the predictions) and a “strong” (less than 98.5% or more 99.5%)
182 over/underestimation of the maximum biomass. We considered that a model has a good
183 predictive power if the predictions show a slight deviation from the 99th quantile.

184 The second metric, termed ‘contrast’, is measured for each model on the predicted values, by
185 the difference between minimum and maximum relative to the maximum. High (close to one)
186 contrast occurs when the expected response of the species varies greatly across the

187 environmental gradient. The predictor influences the species biomass, and has a limiting effect
188 when biomasses are low. Low (close to zero) contrast occurs when there are little variations
189 in the predicted species biomass along the environmental gradient. The predictor has a low
190 effect on the species and is not limiting in the range of the Barents Sea. In the case of the
191 sediment type, three of the seven classes (“Compacted sediments or sedimentary bedrock”,
192 “Sand, gravel and pebbles”, and “Thin or discontinuous sediment on bedrock”) were
193 associated to less than 1% of all the samples (appendix 4). Those sediment types are ignored
194 for the calculation of the contrast to ensure that the metric is built on sediment categories that
195 carry enough information.

196 **2.2.2 Spatial prediction of suitable habitats**

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

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

215 dynamic or fixed predictor). From those maps, we looked at the proportion of locations where
216 a given species biomass is limited by a given predictor. It is computed by i) counting for each
217 predictor the number of stations where it is the most limiting for a given species a given year,
218 ii) dividing that count by the number of stations sampled that year and iii) calculating the mean
219 of that proportion over the years. It provides a measure of the limiting power of each predictor
220 at the scale of the whole Barents Sea and across species.

221 **2.2.3 Predictability of future suitable habitats**

222 To be able to predict a species suitable habitats in the Barents Sea using QGAMs, it is
223 necessary that i) at least one selected predictor, dynamic or fixed, has an impact on the taxon
224 response (i.e. the species-predictor model has a high contrast), ii) the value of the predictor(s)
225 for which the species biomass is limited occurs in the study area and at the temporal scale of
226 the study, iii) the modelled response is robust to new conditions (i.e. predicted maximum
227 quantile on the evaluation dataset should be close to the 99th), iv) possible differences in
228 specific respond of different groups of individuals (by age, size, physiological state and other)
229 within a taxa to the environmental predictor(s) are avoided.

230 To evaluate the potential of a species suitable habitat to shift in a changing environment, we
231 also look at the maximum contrast in fixed and dynamic predictor models. Species with a
232 highest contrast in response to dynamic predictors are more susceptible to shift their habitat
233 to follow changing environmental conditions.

234 **3 RESULTS**

235 **3.1 RESULTS STRUCTURE**

236 Norway pout (*Trisopterus esmarkii*) is used to illustrate the detailed results of the quantile
237 regression on a single species in response to three predictors: two that are associated with a
238 high and a low contrast in the species response and one qualitative predictor. This species
239 was chosen because it showed high contrast in its responses to the selected variables and
240 high consistency of the predicted quantiles between the training and the testing datasets.

241 The results for all other species analyzed in this study are provided in appendix 5. Tables
242 summarizing the species responses to the different predictors are in appendix 6. Some
243 figures use abbreviated species names. The correspondence between abbreviated and full
244 names is provided in appendix 6.
245 A synthesis of the models of habitat suitability across all species is presented. In both parts,
246 habitat suitability maps are shown only for 2013, which was the year with the widest spatial
247 coverage. Maps for all the species are presented in appendix 7.

248 **3.2 LIMITS TO THE DISTRIBUTION OF THE NORWAY POUT (*TRISOPTERUS*** 249 ***ESMARKII*)**

250 **3.2.1 Species responses to environmental predictors**

251 **Convergence and predicted quantiles:** *T. esmarkii* modelled response to depth, slope and
252 sediment converged successfully. When fitted to the training dataset, 99.1% of the
253 observations were below the modelled response to depth, and 99.0% were below the model
254 for both slope and sediment (Figure 1). When the same models were applied to the testing
255 dataset, 99.3% of the observations were below the depth model, and 99.4% below the slope
256 model. Both models thus slightly overestimate the maximum biomass allowed by those
257 predictors when applied to new environmental conditions. For sediment, the model strongly
258 overestimates the maximum biomass of the predictor, with 99.9% of the data below the model.

259 **Model contrast:** The contrast in the response to depth was very high, 0.997. Such high value
260 indicates that the minimum of the predicted maximum biomass was close to zero, i.e. that the
261 sampling includes environmental conditions that are very limiting for the species. The
262 response to slope shows the lowest contrast (0.81), indicating a relatively lower impact of
263 slope on the species response. The contrast of the modelled response to sediment was
264 intermediate with 0.90.

265 **Model shape:** The responses of *T. esmarkii* to depth and slope are bell-shaped (Figure 1A
266 and 1B respectively), although the response to slope is flatter. The “stair” pattern in the model
267 predictions comes from the discretization of the predictors prior to fitting. The shape of the

268 qualitative predictor, the sediment, is not relevant. The range of observations along the depth
269 gradient is wide, covering 76% of the bathymetric range of the Barents Sea (from 73 m to 410
270 m depth, while conditions across the locations sampled scope from 52 to 494m). The
271 maximum predicted biomasses occur at ~240 m, while the minimal (i.e. the limiting values)
272 occur at ~70 m. For slope, most of the non-null biomasses were observed in areas with low
273 degree of slope. For the sediment, the minimum prediction was close to 0 on compacted
274 sediment or sedimentary bedrock, and maximum for coarse sediment.

275 **Other predictors:** All the modelled responses of *T. esmarkii* to the other predictors converged.
276 Between 99.0% and 99.2% of the training dataset observations were below the model. The
277 surface and bottom salinity and surface mixed layer depth models slightly overestimate the
278 maximum biomass when applied to the testing dataset, with 99.2 to 99.4% of the data below
279 the predictions. The other models more strongly overestimate the maximum biomass with 99.8
280 to 99.9% of the testing data below the models. Contrast is high for all the variables: from 0.73,
281 0.88, and 0.97 for surface mixed layer depth, *surface* and *bottom salinity* respectively to >0.99
282 for all other predictors.

283 The response of the species to surface temperature and salinity, bottom temperature, surface
284 mixed layer depth, days of ice cover and chlorophyll *a* concentrations show complete or partial
285 bell shapes (see appendix 5). The range of response to the different predictors is large,
286 scoping from 55 to 96% of the conditions over the Barents Sea. Modelled response to bottom
287 salinity shows a V shape. High biomasses of *T. esmarkii* are associated with warm surface
288 (~10°C) and bottom (>2.5°C) temperatures, high salinities (>34.5), rather shallow and weak
289 stratification (SML ~40-50m).

290 **3.2.2 Habitat suitability mapping**

291 When applying the models for *T. esmarkii* for a given year, predictions are rather low (i.e.
292 some factors are very limiting) in most of the Barents Sea, except in the south-west (e.g. in
293 2013, Figure 2A). Bottom temperature limited biomass in the majority (60.9%) of the stations
294 in 2013 (58.3% in average across all years) and was most limiting in all the central area of the
295 Barents Sea. Other environmental parameters are much less limiting. Depth (12.8% in 2013,

296 12.7% in average) is most limiting on the shallow areas of Murmansk bank and north of Bear
297 Island, or in the depth of the Bear Island trough. Surface temperature was the third most
298 frequent limiting factor in 2013 (9.0%); but second in average (14.0%). The ice coverage is
299 the last predictor limiting more than 10% of the samples on average (11.6% on average, 5.4%
300 in 2013). Both surface temperature and ice cover are most limiting in the north, between
301 Svalbard and Franz Joseph Land. All other parameters are most limiting for less than 5% of
302 all the samples in 2013 and on average over the years.

303 **3.2.3 Predictability of the suitable habitats:**

304 The maximum contrast in the modeled response of *T. esmarkii* distribution was to depth
305 (contrast: 0.991) among the static predictors and to bottom temperature (contrast > 0.999)
306 among the dynamic predictors. However, depth is not that often a limiting factor in the Barents
307 Sea. It is thus probable that this species suitable habitat will shift in response to changes in
308 temperature, in the limit of the bathymetric constrains. The predictive power of the *T. esmarkii*
309 – T. bottom model is poor as it tends to overestimate the maximum biomass, while that of the
310 *T. esmarkii* – depth model is good. This means that the predicted habitat suitability might be
311 overestimated if based only on bottom temperature.

312 **3.3 LIMITS TO THE DISTRIBUTION OF 33 FISH SPECIES**

313 **3.3.1 Species responses to environmental predictors**

314 **Convergence and predicted quantiles:** All models successfully converged. The training and
315 testing sets performed quite differently on predicting the 99th quantile (Figure 3). When fitted
316 on the training set, most of the models (94%) were between 98.5% and 99.5% of the data.
317 Only 6% strongly overestimated the maximum biomass (i.e. were above more than 99.5% of
318 the data). None of them strongly underestimated the maximum biomass.

319 The models performed less well at predicting the 99th quantile when applied to the testing data
320 set, as only 50% of the models were between 98.5 to 99.5% of the data; 38% strongly
321 overestimated the maximum biomass and 11% strongly underestimated it. One model is an
322 outlier, performing very poorly in the testing set: *Arctozenus risso* response to sediment. This

323 may be because this species reached higher biomasses in 2016, during the testing set, than
324 any other year before.

325 **Model contrast:** Most of the model showed relatively high level of contrast: 45% had high
326 contrast (>0.90), and 37% had an intermediate contrast (0.50 to 0.90). Slope has the lowest
327 mean contrast (0.44) across the 33 species, followed by surface mixed layer depth (0.58).
328 Surface salinity and chlorophyll a are associated to similar contrast in the species response
329 (~ 0.75). Following predictors display high contrasts: sediment (0.83), ice cover (0.85), bottom
330 salinity (0.86) and bottom temperature (0.87). Depth and surface temperature models are the
331 most contrasted with an average of 0.90.

332 Among temporally fixed predictors, the most contrasted modeled responses were to depth (24
333 of the 33 species), sediment (8 species) and slope (1 species). Bottom and surface
334 temperature caused the highest contrast among dynamic predictors for 12 and 13 species
335 respectively, ice cover for 5 and bottom salinity for 3.

336 **Model shapes:** Most model shapes can be interpreted as a complete or a partial bell, with
337 large differences in amplitude, from very contrasted to very flat models. Occasionally, species
338 response models to surface or bottom salinity or ice coverage would take a v shape.
339 Distribution of the species responses along the different predictor gradients can be found in
340 appendix 5.

341 **3.3.2 Habitat suitability mapping**

342 The mean proportion of samples limited by a single predictor over the years ranged from 0.3
343 to 58.8% (Figure 4, left panel). Some predictors limit on average 50% or more of a single
344 species samples: bottom temperature (50.4% of *Argentina silus* samples, 58.3% of
345 *Trisopterus esmarkii* samples), depth (53.9% of *Arctozenus risso* samples) and surface
346 temperature (54.3% of *Triglops nybelini* samples).

347 Bottom temperature is the most frequent most limiting predictor (22% of all samples). Depth
348 is most limiting in 20% of the samples, and surface temperature and sediment in 14%. Slope
349 (2%), surface mixed layer depth (2%), surface salinity (4%), chlorophyll a (5%), bottom salinity
350 (7%) and ice cover (8%) are the least limiting among the species. However, these predictors

351 are not always strongly limiting the species biomasses. For 15 of the 33 species,
352 environmental conditions weakly limit the biomass in most of the sampled locations (Figure 4,
353 right panel). Dynamic predictors are most often limiting for 17 species and fixed ones only for
354 1 (*Arctozenus risso*).

355 **3.3.3 Predictability of suitable habitats**

356 Profiles of species responses to the selected predictors vary a lot in the Barents Sea (Figure
357 4). Some species are strongly limited by a low number of predictors, mainly dynamic ones
358 (Figure 4, top species), while others are rather evenly limited by several predictors (Figure 4,
359 bottom species). Most frequent most limiting predictors that have good predictive power
360 (predicted quantile of the testing dataset between 98.5 and 99.5) are sediment, depth and
361 bottom and surface temperature and bottom salinity. Nearly half (15 out of 33) of the
362 considered species are most frequently most limited by a predictor for which the model has
363 good predictive power.

364 It is the case of species situated toward the top of figure 4 for which we can thus evaluate
365 current suitable habitats. They are limited by a low number of parameters. Those are e.g.
366 *Arctozenus risso*, *Argentina silus*, *Pollachius virens*, *Gadiculus argenteus* and *Micromesistius*
367 *poutassou*.

368 *Trisopterus esmarkii*, *Triglops nybelini* and *Sebastes viviparus* are also strongly limited by few
369 predictors, but their predictive power is less good so the model might over or underestimate
370 the habitat suitability.

371 Species for which it is hard to decipher suitable from unsuitable habitats are situated toward
372 the bottom of figure 4 and most of their sample are only weakly limited: e.g. *Amblyraja radiata*,
373 *Gadus morhua*, *Zoarcidea*, *Hippoglossoides platessoides*, *Anarhichas minor* or *Anarichas*
374 *denticulatus*. Although some are limited by few predictors, and despite the good predictive
375 power of the corresponding models, those species tend to be mostly weakly limited by the
376 environmental variables, i.e. display high predicted biomasses on most of the Barents Sea.

377 For 21 of the 33 species, the maximum contrast to dynamic predictors is higher than that of
378 the fixed ones (Figure 5). This maximum predictor is bottom salinity for 1 species, ice for 3,

379 bottom temperature for 8 and surface temperature for 9. All those species are thus more
380 susceptible to shift their habitat to follow a change in the environment, particularly those with
381 the highest maximum contrast. The 12 other species have higher contrast in fixed predictors.
382 The maximum predictor is depth for all those 12 species. Those are more constrained by depth
383 and their habitat might not be influenced by a change in dynamic environmental conditions.

384 **4 DISCUSSION:**

385 In the present work we explored the limiting effect of 10 environmental predictors on the
386 individual responses of 33 fish species of the Barents Sea and assessed our capacity to
387 predict their suitable habitats. From the results, we can estimate the species ability to track
388 potential changes in their suitable habitats in response to climate change.

389 **4.1 LIMITING EFFECT OF ENVIRONMENTAL PREDICTORS ON INDIVIDUAL** 390 **SPECIES SUITABLE HABITATS**

391 The shapes of QGAM models provide the information about the limiting effect of predictors on
392 species. In this study, QGAMs were fitted with a maximum degree of freedom of 3, so that the
393 resulting models display simple shapes that can be interpreted in the context of the niche
394 theory. Most frequently, models display bell shapes that can sometimes be skewed and/or
395 incomplete (i.e. only one side of the bell is visible). V-shapes occur occasionally (in response
396 to salinity or ice cover) and are more difficult to interpret. Causes of those v shapes could
397 include the existence of two population within the Barents Sea with different habitat
398 preferences, or strong non-linear links to other variables with strong spatial structure (proximity
399 to coast, river outflow, depth, etc.).

400 The flatness of the model shape is an indicator of the limiting power of the predictor and is
401 reflected in the contrast metric. Some predictors are more contrasted (i.e. limiting) than others.
402 Depth and surface and bottom temperature have the highest average contrast over the
403 considered species. This is consistent with the literature, as many authors have highlighted
404 the importance of depth and temperature in the habitat requirements of demersal fish over the

405 world (see Johnson et al., 2013 for a review). In the habitat suitability maps, they are also the
406 most frequent most limiting predictors across the study area. The reason for these three
407 parameters to limit the distribution of shallow-water species (< 200m depth) in depth and
408 latitude is well studied (Brown & Thatje, 2015; Pörtner, 2010) and is linked to the thermal, oxic
409 and hydrostatic conditions necessary for those species to maintain aerobic metabolism.

410 Depth has been reported to be one of the most, if not the most, important predictor of demersal
411 fish distribution, regardless of the method used or the geographical location of the study
412 (Chatfield et al., 2010; Leathwick et al., 2006; Moore et al., 2010, 2011; Ross et al., 2015;
413 Rutterford et al., 2015; Smoliński & Radtke, 2017). In this study, depth was often limiting either
414 on the shelf for species living in deep areas (e.g. spotted barracudina *Arctozenus risso* or
415 deepwater redfish *Sebastes mentella*, mainly found in the Bear Island Trough), or on the
416 deepest and shallowest areas (for e.g. snakeblenny, *Lumpenus lampretiformis*, or wolfish
417 *Anarhichas lupus*).

418 Limiting values of bottom temperature for the distribution of the demersal fish occur often in
419 the Barents Sea. For species that are distributed in the south west part of the Barents Sea
420 (e.g. Norway pout *Trisopterus esmarkii*, greater argentine *Argentinus silus*, saithe *Pollachius*
421 *virens*, silvery pout *Gadiculus argenteus*) this predictor was the most limiting in more than half
422 of their samples. Their spatial distribution appear to be limited by the low bottom temperatures
423 currently occurring in the rest of the Barents Sea. Byrkjedal & Høines (2007) obtained similar
424 results in a study focusing on the south-western part of the Barents Sea, and explained the
425 strong influence of the temperature by the conjunction of the cold, subzero, Artic and warm
426 Atlantic water at the polar front, creating strong latitudinal gradients of temperature.

427 Surface temperatures cause high contrast in the species response are frequently the most
428 limiting either i) in the north, approximately northeast of the polar front, for some species
429 distributed mostly in the south of the Barents Sea (e.g. Atlantic herring *Clupea harengus* and
430 Saithe *P. virens*), or ii) in the south for species considered as arctic (e.g. polar cod *Boreagadus*
431 *saida* and bigeye sculpin *Triglops nybellini*). Some of those species have been shown to follow
432 yearly variations in sea ice extent in other sub-arctic areas (Wyllie-Echeverria and Wooster,

433 1998). In our samples, surface temperature and ice cover are often limiting in the same area,
434 in the North, so the limitation of the species responses by low surface temperature might also
435 be a proxy of the limitation by cold, ice covered water masses north of the polar front.
436 The most limiting factors of species suitable habitats revealed by the QGAMs are consistent
437 with the literature and reflect the strong environmental gradients existing across the Barents
438 Sea.

439 **4.2 ASSESSING OUR CAPACITY TO IDENTIFY SPECIES SUITABLE HABITATS**

440 All the species are not impacted in the same way by the different predictors, and suitable
441 habitats are thus not equally identifiable across species.

442 Some of the species have a taxonomic resolution too coarse to ensure a uniform response to
443 the predictors across all individuals. A recent study (Smith et al., 2019) showed that grouping
444 related taxa that are likely to share environmental tolerances, or splitting species in smaller
445 population units that have adapted independently can improve niche estimates. In the case of
446 cod (*Gadus morhua*), or eel pouts (zoarcids) the widespread spatial distributions and
447 environmental tolerance partially reflect the variety of habitats used by different age groups
448 (cod) or species (eel pouts). Modelling habitat suitability at a finer biological scale (e.g. by age
449 or species) might be required to improve habitat suitability models for these groups (M.
450 McPherson & Jetz, 2007; Morán-Ordóñez et al., 2017; Porfirio et al., 2014; Thuiller et al.,
451 2005). In addition, suitable habitats are also hard to identify for species that are abundant and
452 widespread like Long rough dab (*Hippogloissoides platessoides*), Greenland halibut
453 (*Reinhardtius hippoglossoides*), Thorny skate (*Amblyraja radiata*) and two species of wolfish
454 (*Anarhichas minor* and *denticulatus*). Long rough dab inhabits most of the Barents Sea and
455 operates an east to west spawning migration against the larval drift, which allows it to maintain
456 its position in the region (Walsh, 1996). This shows its wide tolerance for the conditions in the
457 Barents Sea. The habitat mapping in the current study show that Long rough dab and
458 Greenland halibut are never strongly limited by environmental conditions, except by extreme
459 depths in shallow (for Greenland halibut) or deep areas (for Long rough dab). Thorny skate,

460 on the other hand, thrives in all ranges of depth and temperatures of the Barents Sea (Dolgov
461 et al., 2005). All those species are very abundant across the whole Barents Sea and thus
462 mostly weakly limited by selected environmental factors. There is therefore substantial
463 information on where these species are, but little on where there aren't. It is thus difficult to
464 identify their unsuitable habitats and how environmental conditions may limit their distributions.
465 Species for which it is possible to identify suitable habitats are e.g. the spotted barracudina
466 (*Arctozenus risso*), the greater argentine (*Argentina silus*), saithe (*Pollachius virens*), silvery
467 pout (*Gadiculus argenteus*), Norway pout (*Trisopterus esmarkii*), Norway redfish (*Sebastes*
468 *viviparus*), or Blue whiting (*Micromesistius poutassou*). Those are exclusively south-western
469 species inhabiting rather deep areas with warmer Atlantic bottom waters at the entrance of
470 the Barents Sea. For example, blue whiting and adult saithe resides in the Norwegian Sea
471 and expands into the Barents Sea when the Norwegian stock is large (for blue whiting: Heino
472 et al., 2008) or as a seasonal migration during the second and third quarter (for saithe: Olsen
473 et al., 2010). For all those boreal species, suitable habitats are mainly limited by only one
474 predictor (most of the time the bottom temperature). *Triglops nybelini* is the only arctic species
475 for which there is a clear limitation by a single factor, the surface temperature, which highly
476 linked to ice cover in the north-east.

477 Some species habitats can be determined even though each predictor limits only a small
478 portion of samples; i.e. there is no clear limitation by a single factor. For those species, the
479 proportion of samples that are weakly limited by the environment is not as important as for
480 widespread species, so we have some information on where the species is absent, or in low
481 abundances. It is the case for the habitats of polar cod (*Boreogadus saida*), capelin (*Mallotus*
482 *villosus*), eel pouts (liparids), Atlantic poacher (*Leptagonus decagonus*), daubed shanny
483 (*Leptoclinus maculatus*) or scaled sculpin (*Icelus* spp.). Those are mainly arctic species,
484 abundant but not widespread in the Barents Sea, spatially limited to colder waters north of the
485 polar front (Fossheim et al., 2006; Hop & Gjørseter, 2013). We can determine suitable
486 habitats, but we need for that to consider several predictors.

487

488 The biogeography and the environmental affinity and tolerance of a species in the Barents
489 Sea seems to be major indicators of our capacity to identify its habitat. Together with the
490 results of the current study, this help us build hypotheses on the potential shifts in suitable
491 habitats for individual species of the Barents Sea.

492 **4.3 PREDICTING FUTURE HABITAT SUITABILITY IN RESPONSE TO CLIMATE** 493 **CHANGE**

494 Quantitative predictions of suitable habitats for fish in the Barents Sea can be obtained by
495 applying the QGAM models on projected maps of predictors showing the possible future
496 environmental conditions. The predictive power of a model determines how well it will perform
497 when transferred to a new area or another time, which is particularly important in the context
498 of climate change (Dormann, 2007; Porfirio et al., 2014). Although it is not possible to
499 quantitatively assess model's performance in future climate, the recent rapid warming in the
500 Barents Sea provides suitable conditions to test the performance of the habitat models in two
501 periods with contrasting ocean climate. Half of the models performed well when applied to the
502 testing dataset. The poorer performances of the other models may reflect that the training
503 dataset did not include enough of the variability in the species response to the predictor. For
504 those models, prediction can still be done, but the resulting habitat suitability might be
505 over/underestimated.

506
507 Without projected environmental maps, it is still possible to use the results from the QGAM fit
508 to hypothesize qualitatively the evolution of Barents Sea fish suitable habitats in response to
509 environmental changes. Recent climate predictions show increasing water temperatures in
510 the Barents Sea (Stenevik & Sundby, 2007) and decrease in sea ice possibly leading to ice
511 free winters by 2061-2088 (Onarheim & Årthun, 2017). Species that would be more sensitive
512 to these projected changes, i.e. that would be forced to move to track suitable habitats, are
513 those that display a highest contrast in response to dynamic - rather than fixed - variables.
514 This is the case for two thirds of the species. The limiting factors are bottom and surface

515 temperature (that is projected to increase with climate change), bottom salinity (correlated to
516 depth) and ice cover (which is projected to decrease). However, species tracking their
517 environment might be limited in their progress by unsuitable fixed environmental conditions. A
518 good example is *Anarhichas lupus*, which responds with the highest contrast to ice but is more
519 often limited by depth across the Barents Sea. Predicting its future suitable habitat necessitate
520 to consider both fixed and dynamic parameters. This supports a recent study projecting that
521 depth will strongly limit the availability of suitable habitats (Rutterford et al., 2015).

522

523 Predicting potential shifts in suitable habitat for a species thus requires integrating all the
524 information gathered in the current study on niche preferences and ranges, most contrasted
525 models, spatially most limiting factors, response to dynamic and fixed factors and predictability
526 of suitable habitats. Here we make tentative qualitative predictions on the future of demersal
527 fish in the Barents Sea based on the two most limiting predictors of the region: bottom
528 temperature and depth (Figure 6).

529 The warming of the Barents Sea is likely to increase the extent of suitable habitat for species
530 with preferences for warmer waters (right side of the figure 6). They are susceptible to migrate
531 or expand northward as new habitats become available, if the depth is suitable. The species
532 concerned respond strongly to and are spatially more limited by either bottom or surface
533 temperature. They are species for which it is easy to estimate qualitatively their future habitat
534 because few predictors control their niche at the scale of the Barents Sea. Species that prefer
535 intermediate depths (*Micromesistius poutassou*, *Argentina silus*, *Gadiculus argenteus*,
536 *Sebastes norvegicus* and *viviparus*, *Trisopterus esmarkii* and *Pollachius virens*) and two
537 shallower species (*Clupea harengus* and *Melanogrammus aeglefinus*) are likely to migrate
538 north as most of the Barents Sea is in the range of their suitable depths. This is supported in
539 the literature. Ecological niche models have predicted a gain in suitable habitat in the Barents
540 Sea for saithe (*P. virens*) and haddock (*M. aeglefinus*) in the middle of the Barents Sea
541 between 1960 and 2090 (Lenoir et al., 2011). (Hollowed et al., 2013) also hypothesized a
542 northward shift of *C. harengus*. Some of those species have already been noticed to displace

543 northward: (Perry et al., 2005) noticed that *M. poutassou* and *T. esmarkii* distribution
544 boundaries have shifted northward in relation to the warming between 1977 and 2001 in the
545 North Sea, and in the Barents Sea, both species and *A. silus* are part of the boreal or
546 intermediate communities that also have shifted between 2004-2012 (Fossheim et al., 2015).
547 Unlike this group of species, *A. lupus* is already widespread on the shallow banks of the
548 Barents Sea and is spatially limited by depth and sediment in its northern boundary. It is thus
549 unlikely that the warming will open new suitable habitats for that species. However, this
550 species is also limited by other parameters so future suitable habitats are hard to predict.

551

552 Temperature increase in the Barents Sea will cause the loss of the coldest habitats of the
553 region. Species that prefer cold habitats (left side of figure 6) are the most threatened as they
554 will then experience temperatures warmer than their current optima. To come back to
555 temperatures closer to their optimum, they would need to migrate further north into the deep
556 Arctic ocean, or retract around Svalbard where they would ultimately be trapped if they don't
557 tolerate high depths. The concerned species are mainly arctic ones with large depth tolerance,
558 so both scenarios are possible. Ribbed sculpin (*Triglops pingelii*) and Arctic alligatorfish
559 (*Aspidophoroides olrikii*) are exceptions as they respond more strongly to depth and might not
560 be able to retract to deeper and colder areas. However, all those species are part of the group
561 for which suitable habitats are harder to predict qualitatively because of the many predictors
562 involved in the biomass limitation. To understand potential shifts in their future habitat, the
563 knowledge gained on their habitat requirements needs to be integrated and applied to
564 projected environmental conditions.

565

566 Species currently preferring intermediate temperatures (0 to 2°C) can be divided into shallow
567 and intermediate depth loving species and deep associated ones. Shallower species
568 (optimum >300m) are generally widespread. Some are common over the whole Barents Sea
569 (like *Gadus morhua*, *Hippoglossoides platessoides* or *Ambyraja radiata*) and little can be said
570 about their future habitat. Others are widespread in the north and south-east of the Barents

571 Sea (*Leptoclinus maculatus*, *Lumpenus lamprætaeformis*, *Leptagonus decagonus*, *Arctediellus*
572 *atlanticus*, *Triglops nybellini* and *Amblyraja hyperborea*). They all tolerate a wide range of
573 depth conditions so they would be able to track their preferred environmental conditions by
574 moving northward or diving deeper. However most of them are also limited by other predictors,
575 so their future suitable habitats is hard to estimate qualitatively.

576 Deeper species (*Cottunculus microps*, *Reinhardtius hippoglossoides*, *Anarhichas*
577 *denticulatus*, *Arctozenus risso* and *Sebastes mentella*) are mainly found around the Bear
578 island Trough. Their response to climate change depends more on their tolerance to shallower
579 depths. *R. hippoglossoides* and *A. denticulatus* are widespread, with wide tolerance to depth
580 and might be able to expand northward. In Hollowed et al. (2013), *R. hippoglossoides* is indeed
581 suspected to move in or expand in the high Arctic. *S. mentella* is more constrained by
582 shallower depths but has expanded into the Barents Sea during the period of the study (as
583 hypothesized by Hollowed et al., 2013). *A. risso* however, is not very tolerant to shallower
584 depth and respond strongly to salinity (which is itself very correlated to depth). If its habitat
585 conditions were to change, the species could not move northward on the shallower Barents
586 Sea shelf.

587 Similar tradeoffs will constantly occur for all species as changes in dynamic variables will
588 interact with limitations caused by fixed ones. Light conditions might be a particularly strong
589 tradeoff at those latitudes (Poloczanska et al., 2016).

590 **5 CONCLUSIONS**

591 The use of QGAM allowed to explore the potential environmental niche of 33 fish species in
592 the Barents Sea. The models show a wide variety of responses to environmental stressors.
593 The application of the Liebig's law on the mapped conditions of the region highlighted the
594 importance of depth and temperatures as limiting factors for most of the species. But the set
595 of selected predictors influence each taxon differently, which leads to some species suitable
596 habitats being more difficult to predict than others. While species responding more strongly to
597 dynamic variables should be the most responsive to changes in their habitats, this study

598 highlighted the importance of considering their interaction with fixed predictors when predicting
599 future suitable habitats.

600 In the face of the complexity of the response at the individual species scale, it seems clear
601 that explaining and predicting the responses of whole communities to changes in their habitat
602 is challenging. Yet, ecosystem studies need for those individual responses to be integrated at
603 larger scales. An advantage of the QGAM methods is that the models can easily be used as
604 habitat preferences prior that input end-to-endo models. This would allow to predict suitable
605 habitats maps on top of which other processes would refine the species distribution. Such
606 empirical knowledge at the basis of the modelling process would greatly benefit our models
607 and can inform resource management and conservation.

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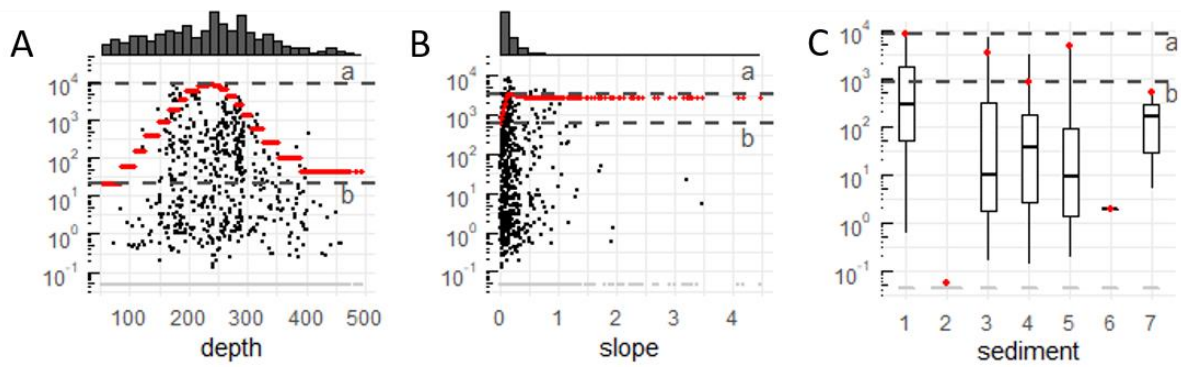
866

867 7 TABLES

868 No tables in this paper

869 8 FIGURES

870



871

872 Figure 1: examples of *Trisopterus esmarkii* modelled log₁₀ responses to three environmental

873 predictors: depth, slope, and sediment type. A and B: black dotted scatterplot of the log of non-null

874 biomasses of the species in response to the predictor. Red dots indicate modelled log of maximum

875 biomass predictions. On top of the scatterplot, the marginal density shows the distribution of samples

876 conditional to the predictor values. C: Boxplot of response to the sediment. The model prediction is

877 the 99th quantile for each sediment class: 1= Coarse sediment, 2= Compacted sediment or sedimentary

878 bedrock, 3= Mixed sediment, 4= Mud, clay and sandy mud, 5= Sand and muddy sand, 6= Sand, gravel

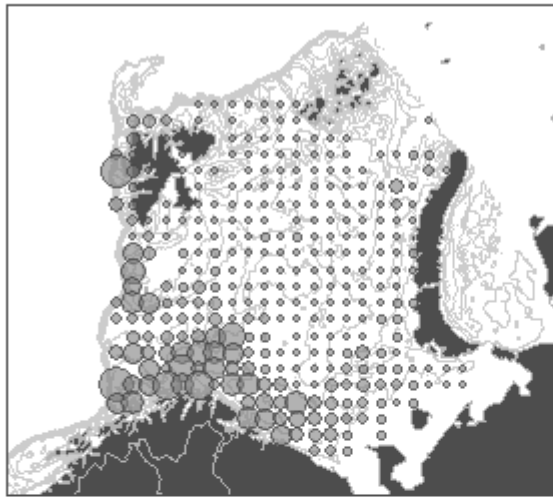
879 and pebbles, 7= Thin or discontinuous sediment on bedrock. All panels: horizontal dashed lines indicate

880 references for the calculation of the contrast: a: max predicted maximum biomass, b: min predicted

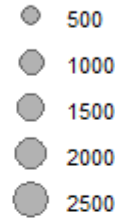
881 maximum biomass. Contrast = (a-b)/a.

Trisopterus esmarkii

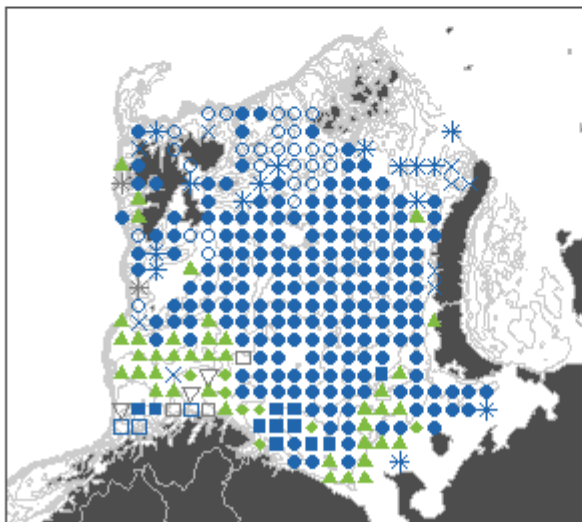
A



Predicted maximum (99%) biomass (kg/km²)



B



Most limiting factor



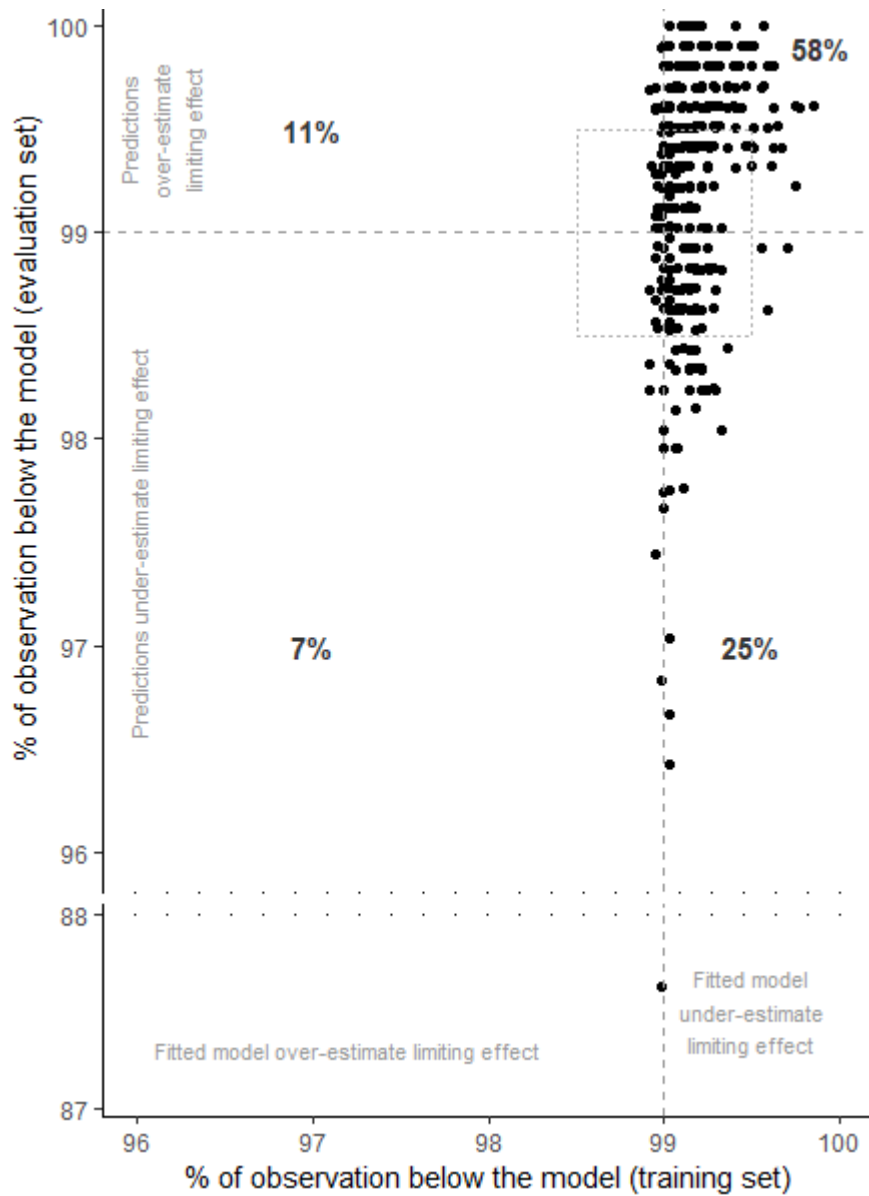
882

883 *Figure 2: Spatial predictions in 2013 of Trisopterus esmarkii A) suitable habitat (maximum biomass)*

884 *and B) most limiting predictor. Color indicates the predictor's category: fixed (sediment, depth,*

885 *slope), dynamic (all the others) or not weakly limiting. (predicted biomass > 25% of the model*

886 *maximum)*



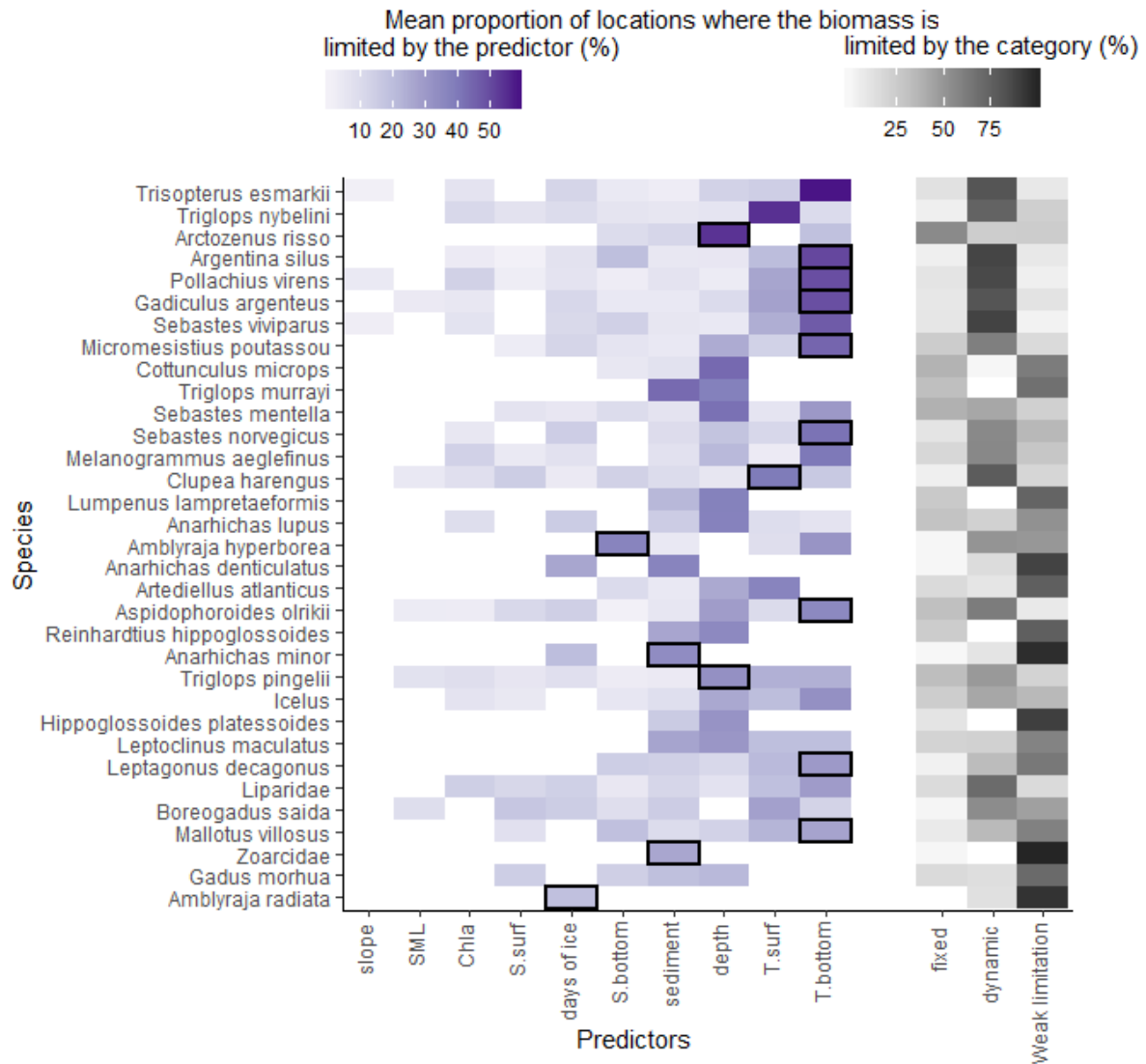
887

888 *Figure 3: scatterplot of the predicted percentile of the observation by the models in the training and*

889 *testing set. The dotted rectangle indicates models that slightly under or overestimate the maximum*

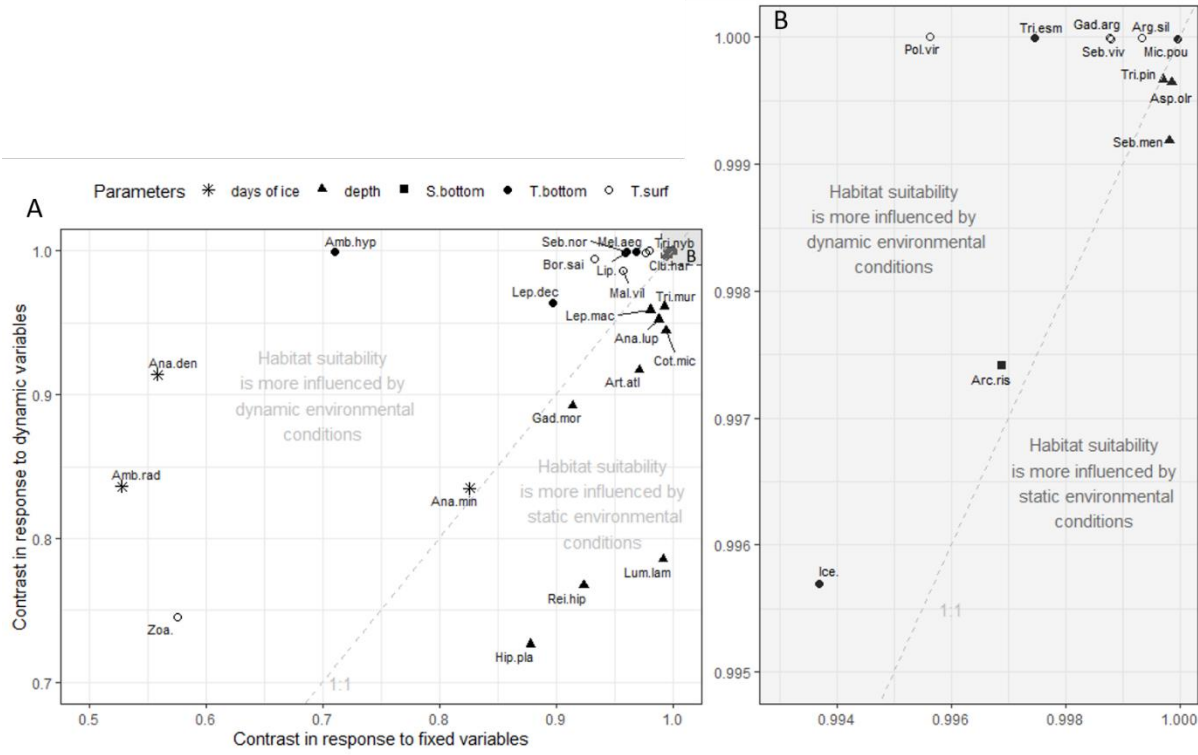
890 *biomass. Outside of that rectangle are the models that strongly under or overestimate the maximum*

891 *biomass.*



892

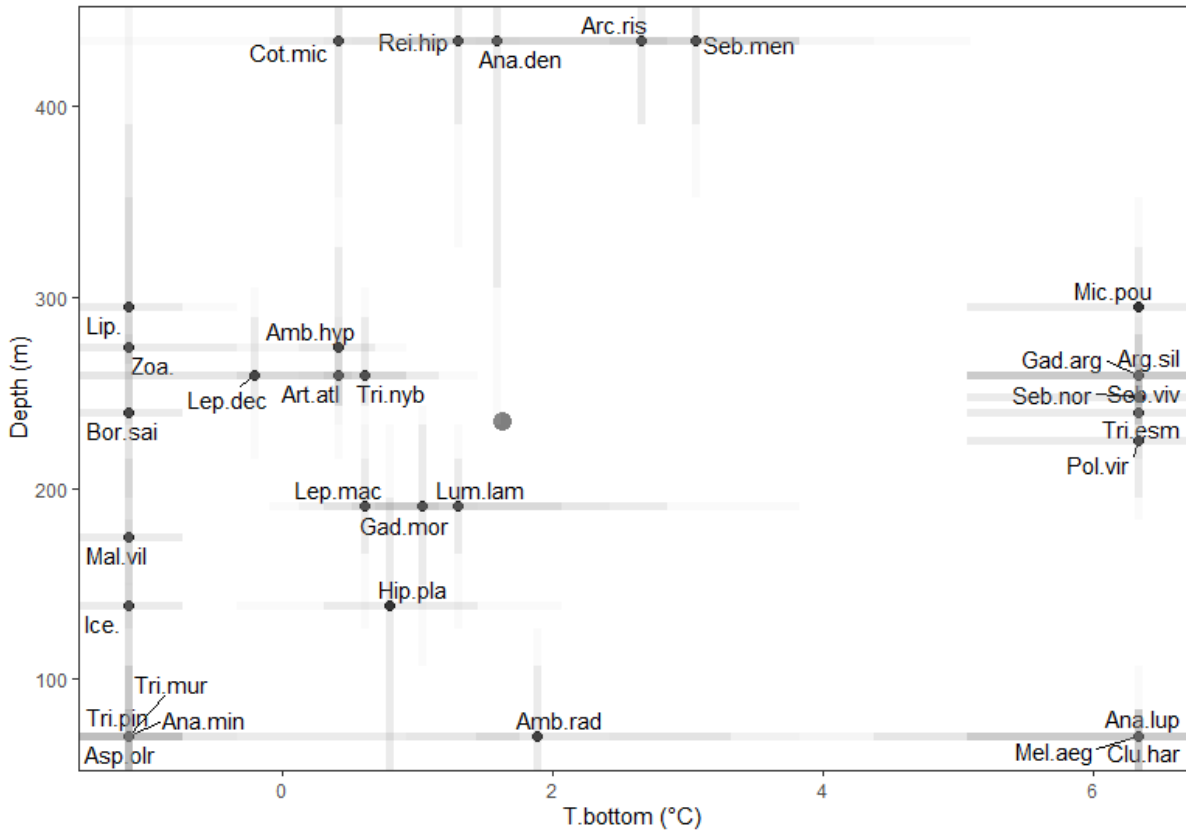
893 *Figure 4: Frequency of the limiting effect across space and years. Right panel: for each species, mean*
 894 *proportion of samples limited by each predictor category: fixed, dynamic, or weakly limiting. Fixed*
 895 *parameters are slope, depth and sediment. Dynamic predictors are all the others. Predictors are*
 896 *weakly limiting a sample if the corresponding predicted biomass is >25% of the model maximum. Left*
 897 *panel: for each species, mean proportion of samples limited by each factor. Only the samples strongly*
 898 *limited are shown (predicted biomass <25% of the model maximum). Black rectangles identify for*
 899 *each species the most frequent most limiting predictor, but only if its predictive power is acceptable*
 900 *(predicted quantile of the testing dataset ranging from 98.5 to 99.5).*



901

902 *Figure 5: Scatterplot of species maximum contrasts in response to fixed versus dynamic variables. The shape of the point indicates which parameter is the*

903 *one with the maximum contrast. The 1:1 line is grey and dashed. B is a zoom in the grey area of A.*



904

905 Figure 6: Bottom temperature - depth habitat preferences of the Barents Sea demersal fish. Dots
906 indicate the predictor value at which the species predicted biomass is maximum. Grey lines indicate
907 the width of the species optimum i.e.for which predictors values the predicted biomasses reach 90
908 (dark grey) and 80% (light grey) of their maximum. Big grey dot indicates the average values of depth
909 and bottom temperature in the Barents Sea.

910

911 9 APPENDICES

912 Supplementary material can be found as PDF on the server

913