Species richness in North Atlantic fish: Process concealed by pattern

Gislason, Henrik; Collie, Jeremy; MacKenzie, Brian; Nielsen, Anders; Borges, Maria de Fátima; Bottari, Teresa; Chaves, Corina; Dolgov, Andrey V.; Dulčić, Jakov; Duplisea, Daniel

Total number of authors:
30

Published in:
Global Ecology and Biogeography

Link to article, DOI:
10.1111/geb.13068

Publication date:
2020

Document Version
Peer reviewed version

Species richness in North Atlantic fish: process concealed by pattern

Henrik Gislason[1], Jeremy Collie[2], Brian R. MacKenzie[3], Anders Nielsen[3], Maria de Fatima Borges[4], Teresa Bottari[5,6], Corina Chaves[4], Andrey V. Dolgov[7,8,9], Jakov Dulčić[10], Daniel Duplisea[11], Heino O. Fock[12], Didier Gascuel[13], Luís Gil de Sola[14], Jan Geert Hiddink[15], Remment ter Hofstede[16], Igor Isajlović[10], Jónas Páll Jonasson[17], Ole Jørgensen[3], Kristján Kristinsson[17], Gudrun Marteinsdottir[18], Hicham Masski[19], Sanja Matić-Skoko[10], Mark R. Payne[3], Melita Peharda[10], Jakup Reinert[20], Jón Sólmundsson[17], Cristina Silva[4], Lilja Stefansdottir[19], Francisco Velasco[21], and Nedo Vrgoč[10]

[1]Corresponding author: DTU Aqua, Technical University of Denmark, Kemitorvet, Building 202, DK2800 Lyngby, Denmark, E-mail:hg@aqua.dtu.dk, [2]Graduate School of Oceanography, University of Rhode Island, Narragansett, USA, [3]DTU Aqua, Technical University of Denmark, Kemitorvet, Building 202, DK2800 Lyngby, Denmark, [4]Instituto Português do Mar e da Atmosfera (IPMA), Lisboa, Portugal, [5]Institute for Coastal Marine Environment (IAMC), National Research Council (CNR), Messina, Italy, [6]Stazione Zoologica Anton Dohrn, Centro Interdipartimentale della Sicilia, Italy, [7]Polar branch of Russian Federal Research Institute of Fisheries and Oceanography (PINRO named after N.M.Knipovich), Murmansk, Russia, [8]Murmansk State Technical University, Murmansk, Russia, [9]Tomsk State University, Tomsk, Russia, [10]Institute of Oceanography and Fisheries, Split, Croatia, [11]Fisheries and Oceans Canada, Institut Maurice-Lamontagne, Mont-Joli, QC, Canada, [12]Thuenen Institute of Sea Fisheries, Bremerhaven, Germany, [13]Agrocampus Ouest, Universite Europeenne de Bretagne, Rennes, cedex, France, [14]Instituto Español de Oceanografía, Málaga, Spain, [15]School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, UK, [16]Van Oord Dredging and Marine Contractors, Rotterdam, The Netherlands, [17]Marine and Freshwater Research Institute, Reykjavík, Iceland, [18]University of

Iceland, Reykjavik, Iceland, [19]Institut National de Recherche Halieutique, Casablanca, Morocco, [20]Faroe Marine Research Institute, Tórshavn, Faroe Islands, [21]Instituto Español de Oceanografía, Santander, Spain.

Abstract

Aim

Previous analyses of marine fish species richness based on presence-absence data have shown changes with latitude and average species size, but little is known about the underlying processes. To elucidate these processes we use metabolic, neutral and descriptive statistical models to analyse how richness responds to maximum species length, fish abundance, temperature, primary production, depth, latitude, and longitude, while accounting for differences in species catchability, sampling effort and mesh size.

Data

Results from 53,382 bottom trawl hauls representing 50 fish assemblages.

Location

The northern Atlantic from Nova Scotia to Guinea.

Time period

1977-2013

Methods

A descriptive Generalised Additive Model was used to identify functional relationships between species richness and potential drivers, after which non-linear estimation techniques were used to

parameterize: 1) a ‘best’ fitting model of species richness built on the functional relationships, 2) an environmental model based on latitude, longitude and depth, and mechanistic models based on 3) metabolic and 4) neutral theory.

Results

In the ‘best’ model the number of species observed is a lognormal function of maximum species length. It increases significantly with temperature, primary production, sampling effort and abundance, and declines with depth and, for small species, with the mesh size in the trawl. The ‘best’ model explains close to 90% of the deviance and the neutral, metabolic, and environmental models 89%. In all four models, maximum species length and either temperature or latitude account for more than half of the deviance explained.

Main conclusion

The two mechanistic models explain the patterns in demersal fish species richness in the northern Atlantic almost equally well. A better understanding of the underlying drivers is likely to require development of dynamic mechanistic models of richness and size evolution, fit not only to extant distributions, but also to historical environmental conditions and to past speciation and extinction rates.

Keywords: marine fish, biodiversity, species size, temperature, density, abundance.

63 Introduction

64

65 Although much has been learned about the richness and distribution of marine species, a mechanistic
66 understanding of the processes responsible for generating and maintaining species richness over
67 evolutionary timescales remains elusive. There is no generally accepted theory to explain the spatial
68 distribution of marine species richness and no general understanding of why some species are more
69 abundant than others (Fine, 2015). This lack of understanding is somewhat surprising. Strong
70 latitudinal gradients in species richness are observed at global and regional scales and these often
71 correlate significantly with environmental variables and life-history traits. Hillebrand (2004)
72 conducted a meta-analysis of gradients in marine biodiversity and found significant relationships
73 between marine species richness, latitude, and species size, while Tittensor et al. (2010) found water
74 temperature to be the main environmental predictor of species richness across a number of marine
75 taxonomic groups. Why latitude, temperature and species size are important is unclear, but size and
76 maximum body size influence the trophic position, mortality, growth and reproduction of many
77 marine species (Andersen et al., 2016), temperature affects their metabolism and food uptake
78 (Gillooly, Brown, West, Savage & Charnov, 2001), and latitude determines the amplitude of the
79 seasonal changes in solar energy input affecting primary production, average temperature and annual
80 temperature range (Cullen, Franks, Karl & Longhurst, 2002).

81

82 Bony fish and elasmobranchs are among the best taxonomically resolved groups of marine animals
83 and are therefore well suited for studies of marine species richness. Estimates suggest that on a

84 global scale around 79% of the species have now been described (Mora, Tittensor & Myers, 2008) and
85 very few species have been declared extinct due to human activities (Davies & Baum, 2012). However,
86 most inventories of fish species richness are based on single recordings of individuals with little
87 consideration of differences in individual density and sampling effort. Including density and sampling
88 effort is important for at least two reasons. The number of species recorded is known to depend
89 statistically on the number of individuals and number of samples examined (Gotelli & Colwell, 2001),
90 and high-density areas may have higher species richness because they harbor more individuals able to
91 maintain a higher number of viable populations (Brown, 2014). Based on species inventories,
92 MacPherson & Duarte (1994) found fish species richness and average maximum fish species size to
93 increase with depth and decline with latitude in the northern Atlantic and Fisher, Franks & Leggett
94 (2010) found the geometric mean fish species size to co-vary with species richness. While Blowes,
95 Belmaker & Chase (2017) found the latitudinal change in reef fish richness to scale with abundance,
96 no one has so far analysed how species richness of marine fish found on soft or sandy bottoms is
97 related to density or abundance on a basin-wide scale.
98
99 To understand how fish species richness in different fish communities is related to density or
100 abundance, species length, and environmental conditions, we analyse an extensive dataset,
101 generated by collating results from 31 standardised bottom trawl surveys from the continental
102 shelves of the northern Atlantic and adjacent areas (Figure 1). Our analysis is based on 123 million
103 individual demersal or benthopelagic fish caught in 53 thousand hauls taken within a total survey area
104 of 3.1 million km^2. Bottom trawl surveys are often stratified to account for spatial or depth related

105 differences in fish assemblage composition and density. We retain the stratification used in the
106 surveys, correct for differences in catchability, and further stratify species into log maximum species
107 length intervals. Using a Generalised Additive Model (GAM) to identify significant variables and
108 relationships we construct a 'best' descriptive model of the number of species caught per log
109 maximum species length interval and survey stratum by transforming the significant relationships
110 identified by the GAM into functional relationships. We also fit an environmental model to the data in
111 which latitude, longitude, depth, total catch and mesh-size are used as independent variables without
112 invoking any biological hypotheses. Using the two descriptive models as reference points we
113 investigate how well mechanistic equilibrium models of species richness based on metabolic (Allen,
114 Brown & Gillooly, 2002; Allen & Gillooly, 2007) and neutral theory (Hubbell, 2001) fit the survey data.
115 Both theories explain the present difference in species richness among fish communities from
116 individual density or abundance, and from fundamental evolutionary processes such as speciation,
117 dispersal and extinction. Recently, they have been combined and used to simulate the latitudinal
118 gradient in species richness in the ocean (Tittensor & Worm, 2016; Worm & Tittensor, 2018).
119
120 In brief, the basic assumption of metabolic theory is that temperature enhances species richness by
121 increasing mutation rates and reducing generation times, while extinction rates are inversely related
122 to the average density per species. In contrast to metabolic theory, neutral theory includes a spatial
123 component and assumes that richness is determined by local abundance and random extinctions
124 among functionally equivalent species counterbalanced by immigration from a surrounding meta-
125 community where speciation takes place. Functionally equivalent species are defined as species that

126 share the same probabilities of death and reproduction (see Appendix S1 in Supporting Information
127 for further information on the two models). Because natural mortality and reproductive output
128 depend on body size in fish, we follow Reuman, Gislason, Barnes, Mélin & Jennings (2014) and
129 assume that functional equivalence, primarily applies for species of similar maximum length. We
130 therefore treat each maximum species length group separately. Comparing the results from the
131 neutral and metabolic models with the two descriptive models, our aim is to elucidate the
132 mechanisms behind the richness differences we observe across fish communities in the northern
133 Atlantic.
134
135 Methods
136
137 Survey data
138 Average catch in number of individuals per species and haul was provided from 31 scientific bottom
139 trawl surveys. The time period from which data was obtained from each survey was selected to
140 provide temporal overlap between the surveys and as long a time period from each survey as feasible
141 to minimise the influence of random fluctuations in recruitment and population abundance. Surveys
142 with less than eight years of data were hence excluded. Although the earliest trawl hauls were taken
143 in 1977 and the most recent in 2013, the period from 2001 to 2006 was covered by all surveys.
144 Slightly more than half of the surveys took place in the period from October to March, a third in the
145 period from April to September, and the remaining surveys included hauls obtained throughout the
146 year (See Appendix S2 Table S2.1 in Supporting Information). Different bottom trawls were used in

147 the surveys. Cod-end mesh sizes ranged from 13 to 40 mm, horizontal trawl openings (wing spread)
148 from 13 to 28 m, vertical openings from 1.9 to 7 m, and towing speeds from 3 to 4.5 knots. Many of
149 the surveys used a stratified random sampling design to account for spatial and depth related
150 differences in species composition. We retained the major strata used in the surveys, providing us
151 with richness and density data from 50 different strata. The average depth in these strata ranged
152 from 28 to 950 m.
153
154 Environmental data
155 Sea surface temperature, average temperature in the upper 200 m of the water column, and near
156 bottom temperatures (Kelvin) were obtained from the World Ocean Atlas 2013 (Locarnini et al., 2013)
157 based on decadal average temperature at 0.25° resolution covering the period 1955-2012 for annual,
158 boreal summer (Jul-Sep) and boreal winter (Jan-Mar). Bottom temperatures were defined as the
159 temperature in the layer closest to the bottom. Spatial averages were calculated for each survey
160 stratum, and the seasonal amplitude calculated as the difference between summer and winter values.
161 Estimates of depth integrated pelagic net primary production (npp, $gCm^{-2}y^{-1}$) based on the satellite-
162 derived Vertically Generalised Production Model (VGPM) (Behrenfeld & Falkowski, 1977) were
163 downloaded from www.science.oregonstate.edu/ocean.productivity at 1/12 degree monthly
164 resolution for the period 2002-2012, from which estimates of mean annual npp were derived for each
165 survey area. Latitude and longitude were calculated as the average of the minimum and maximum
166 coordinates of each survey. Average depth was calculated as the midpoint of the depth range of each
167 stratum (see Appendix S2 Table S2.1).

Fish species data

Among the fish taxa recorded some individuals had not been identified to species. If possible, we allocated these individuals to species, assuming that their relative species composition would be identical to that of the individuals identified within the same survey stratum, and family or genus. Where no species from the family or genus had been identified in a stratum, the family or genus name was retained. Information about the maximum length of each species was downloaded from FishBase (Froese & Pauly, 2016) and used to bin the observations into 11 log maximum length intervals of equal width (from now on denoted log maximum length groups). In 1% of the species records no maximum species length was available. These records were excluded from further calculations.

To estimate absolute fish density and abundance in a given stratum or area we first calculated swept area density for each species. This was done by dividing the average number of individuals caught per haul by the average area swept per haul, estimated by multiplying the wing spread of the trawl by the average distance covered per haul. Swept area abundance was calculated by multiplying swept area density by the size of the survey area. Swept area density and abundance can be converted to absolute density and abundance if catchability is known. Catchability, the fraction of the population in the path of the trawl that is retained and caught by the gear, can be estimated by dividing the swept area estimate of abundance by the absolute abundance provided by a stock assessment. Catchability is likely to differ between areas and species and depends on a number of factors including the

properties of the trawl and species-dependent traits such as the size, behavior and distribution of the individuals (Arreguín-Sánchez, 1996; Walker, Maxwell, Le Quesne & Jennings, 2017). To account for differences in horizontal and vertical distribution we sorted the species into: 1) species whose main distribution is outside the main depth range of the surveys (species mainly occurring in the infra-littoral zone and bathy-demersal or bathy-pelagic species found mainly at more than 200 m of depth), and species whose main distribution is inside the main depth range of the surveys, but either 2) mostly occur on either untrawlable grounds (species that are mainly found associated with reefs or in rocky areas), 3) are likely to have a low catchability (species that bury in the sediment, and pelagic species), or 4) are likely to be regularly retained by the survey gear when available (species resting on the seabed, species found close to but not on the seabed, and midwater species with some bottom contact).

We were able to identify 56 cases where catchability could be derived for the species, time period, and area covered by the survey data (see Appendix S3 and Table S3.1 in the Supporting Information). No catchability estimates could be derived for bathy-pelagic and bathy-demersal stocks, and few estimates could be obtained for infra-littoral species, for species mainly found associated with reefs or in rocky areas, and for burying and pelagic species; species that are likely to be under-sampled by the trawl surveys. The average catchability of these species was only 0.05, while the average catchabilities of the species in group four were 0.34, 1.04 and 0.52 for species that were resting on the seabed, found close to the seabed, or found in midwater, respectively. Note that for some of the species found close to the seabed the estimated catchability exceeded 1.0, probably due to their

response to the herding effect of the bridles, sweeps and doors of the trawl. Due to the few and low catchability estimates available for groups two and three, we decided to use only species from group four in our analysis. To extrapolate the 41 catchability estimates available for the 412 species in this group we fitted a log-linear mixed model to the estimates, using the vertical position of the species (resting on seabed, found close to but above the seabed, or midwater with some bottom contact) as a fixed variable and species identity and survey area as random factors. Drawing samples at random from the resulting stochastic model we generated 1000 estimates of catchability for each combination of species and survey stratum (see Appendix S3). The catchabilities were used to calculate average absolute density and abundance in each survey stratum for each of the species found in the surveys. Average absolute density and abundance were finally cumulated across species within each log maximum length group and survey stratum producing 550 data points as input to the models.

To confirm that the richness of the species in group four had been reasonably well sampled by the surveys we furthermore used the vegan package (Oksanen et al., 2019) to estimate the number of unobserved species in each survey stratum and found that on average a minimum of 7-8% of the species in a particular stratum may not have been recorded. However, considering all of the species found across the surveys few species appear to have been missed (see Appendix S4, Table S4.1 in Supporting Information).

Selection of independent variables

231 The number of species recorded in a survey stratum depends on the species richness in the stratum
232 and the bias introduced by the sampling method. Using a bottom trawl to sample species richness is
233 likely to generate a biased estimate of species richness because the number of species recorded
234 depends on the number of individuals caught and identified (the species accumulation curve); the
235 total area swept by the trawl (a measure of sampling effort); the vertical opening of the trawl
236 (potentially influencing the catch of individuals and species trying to escape over the trawl); and its
237 mesh-size (influencing the proportion of small individuals and species recorded in the catch). To
238 account for the bias we included all four variables in the GAM model. We used the total area swept in
239 each survey stratum rather than the total number of hauls to represent sampling effort because the
240 average duration of the trawl hauls ranged from 15 minutes to one hour across surveys.
241
242 According to the metabolic and neutral models, richness should depend on temperature, species size,
243 and either density or absolute abundance, but the size of the stratum (the species area relationship),
244 net primary production, annual temperature range, latitude, longitude, and depth may also be
245 important co-variates. Temperature may influence richness by affecting fish metabolism, generation
246 time and mutation rate, but vary seasonally depending on latitude and longitude and with depth.
247 Identifying the biologically relevant ambient temperature for a fish species is therefore difficult.
248 Average sea surface temperature may be relevant for the pelagic eggs and larvae, average bottom
249 temperature describes the average ambient temperature encountered by the juveniles and adults at
250 the depth where they are caught by the survey trawls, and average temperature in the upper 200 m
251 of the water column may represent the average temperature encountered during the entire life cycle.

We furthermore found more than a third of the pairwise correlations of the potential independent variables to be significant (See Appendix S2 Figure S2.2). Sea surface temperature, bottom temperature and water column temperatures were highly significantly correlated with each other and with both latitude and longitude, while the seasonal temperature range in the upper 200 m of the water column was significantly correlated to the seasonal temperature ranges near the bottom and at the surface. Net primary production decreased with latitude and increased with temperature, with both correlations highly significant. The vertical opening of the gear was highly significantly correlated to both latitude and to all three temperatures, but not to longitude, reflecting that surveys in high latitudes generally use larger trawls with larger vertical openings than surveys in low latitudes. Total area swept and total stratum area were also highly significantly positively correlated, reflecting that more hauls typically had been taken in large survey strata than in small. Finally, both catch in numbers, average abundance and total swept area were significantly correlated.

Identifying functional relationships

To find the 'best' descriptive model we used a Generalised Additive Model (GAM; Wood, 2006) to identify the functional form and error structure of the relationship between the number of species caught per log maximum length group and the independent variables using the R-package mgcv ver. 1.8.22. In the GAM the log of the expected mean number of species caught, $\mu_{i,j}$, in survey stratum i, maximum length group j, was described using:

$$\log(\mu_{i,j}) = \alpha + s_1(temp\_range_i) + s_2(temp_i) + s_3(abundance_{i,j}) + s_4(depth_i) + s_5(npp_i) + s_6(asurv_i) + s_7(lml_j) + s_8(catch_{i,j}) + s_9(aswept_i) + s_{10}(vertop_i) + s_{11,j}(mesh_i)$$

where α is a proportionality constant; suffix i and j signify survey stratum and maximum length group, respectively, $temp\_range_i$ is the intra-annual temperature range in the stratum (Kelvin); $temp_i$ is temperature (Kelvin); $abundance_{i,j}$ is the average absolute abundance of fish of maximum length j in stratum i; $depth_i$ is depth (m); npp_i is annual net primary production (gC m^{-2} y^{-1}); $asurv_i$ is the total stratum area (km^2); lml_j is midpoint of log maximum length group (cm); $catch_{i,j}$ is the total number of fish caught in stratum i, maximum length group j over the time period of the survey; $aswept_i$ is area swept by the survey trawl (km^2); $mesh_i$ is mesh-size (mm); and $vertop_i$ is the vertical opening of the trawl (m). The $s_1, \ldots, s_{10}$ are general spline smoothers, while $s_{11,j}$ denotes that for each log maximum length group, j, a separate spline smoother was applied to describe the effect of mesh-size on the number of species caught. The $temp_i$ and $temp\_range_i$ variables were either sea surface, average upper 200 m water column or bottom temperature or were replaced by latitude, lat_i, and longitude, lon_i, when the effect of geographic location was examined, and $abundance_{i,j}$ was changed to $density_{i,j}$ to examine which of the two would provide the best fit.

We used thin plate regression splines with a basis dimension of four as smoothers and a log link. To account for the correlation between many of the independent variables, we analysed the effect of including these in separate model versions using residual plots and estimates of concurvity (a non-linear analogue of multi-collinearity) to select the best fitting parameter combinations, and AIC-values

294 to identify the most parsimonious model. Model terms were selected by backwards removal of
295 insignificant variables, after which co-variates generating an estimated concurvity larger than 0.80
296 were sequentially removed to reduce variance inflation and avoid bias. Distributions of residuals were
297 visually inspected for normality and plotted against each co-variate to reveal heteroscedasticity. We
298 compared models with Poisson and negative binomial error distributions, and found the two to
299 provide an almost equally good fit to the data based on AIC-values and comparisons of the observed
300 and theoretically expected variance, where the importance of over-dispersion was assessed by
301 dividing the sum of squared residuals by the sample size minus the number of parameters estimated
302 (Hilbe, 2011). For the negative binomial model this produced a variance ratio of 0.94, confirming the
303 appropriateness of a negative binomial assumption.
304
305 We simplified the GAM model and further reduced its AIC value by inserting the functional
306 relationships indicated by the significant GAM smoothers (see Figure 3). To model the effect of
307 temperature, we assumed that the relationship between species richness and temperature would
308 follow the Arrhenius equation (Gillooly et al., 2001) and consequently used the inverse of
309 temperature in the model. The functional relationships included logarithmic transformations of
310 several of the other independent variables and the addition of a second-order polynomial to capture
311 the change in log species richness with log maximum length. All log transformations used natural
312 logarithms. Using log transformations meant either that zero observations had to be excluded, or that
313 a small positive number had to be added to avoid having to calculate the log of zero. When zero
314 individuals had been caught in a given stratum and log maximum length group, we therefore used the

315 inverse of the total area swept in the stratum to provide a tentative estimate of its maximum density
316 in the stratum. As evidenced by the residuals, this introduced a small bias in the fit (see Appendix S5,
317 Figure S5.3). Because the neutral model cannot easily be linearised, we used non-linear techniques to
318 estimate the parameters of the four models presented below. This also allowed us to retain the zeros
319 and removed the source of the bias in the linearised GAM model.
320
321 Best descriptive model
322 The significant independent variables in the linearised GAM model were used to construct a 'best'
323 non-linear descriptive model of the number of species caught. The 'best' non-linear model followed
324 the simplified GAM equation and contained an Arrhenius expression where β_2, the 'activation energy
325 of metabolism' (Gillooly et al., 2001), was divided by average water column temperature (Kelvin)
326 multiplied by Boltzmanns constant, k (8.62×10^{-5} eV K^{-1}). It also contained total abundance, depth,
327 annual net primary production, and a quadratic log maximum length term, $\exp\left(lml_j + \beta_7\, lml_j{}^2\right)$, to
328 capture the unimodal relationship between species richness and log maximum length, as well as the
329 catch in numbers, the area swept by the trawl, and a mesh-size/log maximum length interaction to
330 account for sampling bias:
331
332 $$\mu_{i,j} = \alpha * \exp\left(\frac{-\beta_2}{k * temp_i}\right) * abundance_{i,j}{}^{\beta_3} * depth_i{}^{\beta_4} * npp_i{}^{\beta_5} * \exp\left(lml_j + \beta_7\, lml_j{}^2\right) *$$
333 $$catch_{i,j}{}^{\beta_8} * aswept_i{}^{\beta_9} * mesh_i{}^{\beta_{11,j}}$$
334

where α, the proportionality constant, subsumes the combined effects of the standardisation of the Arrhenius expression to a reference temperature, and other pre-factors related to abundance, depth, net primary production, the maximum length term, catch in numbers, area swept and mesh-size.

Environmental model

The environmental model assumes that the number of species observed in survey stratum, i, log maximum length group, j, can be calculated from species richness, described by a simple function of latitude, longitude, depth and log maximum length, corrected for differences in catch in numbers, area swept and mesh-size:

$$\mu_{i,j} = \alpha * lat_i^{\beta_0} * lon_i^{\beta_1} * {depth_i}^{\beta_4} * \exp\left(lml_j + \beta_7 {lml_j}^2\right) * {catch_{i,j}}^{\beta_8} * {aswept_i}^{\beta_9} * {mesh_i}^{\beta_{11,j}}$$

Metabolic model

In the Metabolic Theory of Ecology, temperature and body size influence the rate of per capita speciation in the same way as they influence metabolism (Gillooly & Allen, 2007) (see Appendix S1). Combining absolute density with a per capita rate of speciation determined by maximum length and temperature provides the speciation rate. In the equilibrium situation, speciation is counterbalanced by extinction, assumed to decline linearly with the average density per species. We added the effect of differences in number of individuals caught, area swept and trawl mesh-size to the model of Segura et al. (2015) to describe the number of species caught:

$$\mu_{i,j} = \alpha * \exp\left(\frac{-\beta_2}{k * temp_i}\right) * density_{i,j}{}^{\beta_3} * ml_j{}^{\beta_6} * catch_{i,j}{}^{\beta_8} * aswept_i{}^{\beta_9} * mesh_i{}^{\beta_{11,j}}$$

where β_2 is the 'activation energy of metabolism' (Gillooly & Allen, 2007), k is Boltzmann's constant, ml_j is the median maximum length of the species in log maximum length group j, and α, the proportionality constant, accounts for the combined effects of the standardisation of the Arrhenius expression to a reference temperature, as well as other pre-factors related to the density term, and to the maximum length, catch in numbers, area swept and mesh-size terms.

Neutral model

According to the Neutral Theory of Biodiversity and Biogeography, the number of functionally equivalent species in a local community is determined by random extinctions caused by ecological drift, counterbalanced by immigration of species from a larger surrounding meta-community where random speciation takes place (Hubbell, 2001; Rosindell, Hubbell & Etienne, 2011) (see Appendix S1).

Following Reuman et al. (2014), we assume that species of similar log maximum length are functionally equivalent and model each log maximum length group separately, using the approximate formula derived by Etienne & Olff (2004) and Reuman et al. (2014) to describe the relative number of species in each survey stratum and log maximum length group. We also assume that the probability of immigration, λ, is independent of stratum area, but allow it to vary with log maximum length. To account for the effect of differences in the number of individuals examined, effort and sampling gear

on the number of species caught, we add number of individuals caught, total area swept and mesh-size terms to the species richness model of Reuman et al. (2014) providing the following equation:

$$\mu_{i,j} \approx J_{M_j} * \left(\frac{\nu_i}{1-\nu_i}\right) * \log\left[1 - \frac{\lambda_j \, log(\lambda_j)}{1-\lambda_j} * \left(\frac{abundance_{i,j}}{J_{M_j} * (\nu_i/(1-\nu_i))}\right)\right] * {catch_{i,j}}^{\beta_8} * {aswept_j}^{\beta_9} * {mesh_i}^{\beta_{11,j}}$$

Where J_{M_j} is absolute abundance in log maximum length group j in the meta-community, $abundance_{i,j}$ is the absolute abundance of group j in the local community, and ν_i is the per capita speciation rate in area i. Note also that J_{M_j} and ν_i are confounded in the $J_{M_j}(\nu_i/(1-\nu_i))$ term. However, as the speciation rate is likely to be very small, the term can be approximated by the fundamental biodiversity number, $\theta_{i,j} = J_{M_j}\nu_i$ (Rosindell et al., 2011). Because fish evolution is affected by temperature (Wright, Ross, Keeling, McBride & Gillman, 2011), we follow Tittensor & Worm (2016) and make ν_i temperature dependent by adding the Arrhenius equation. Finally, we approximate the change in J_{M_j} with log maximum length by a quadratic term as found in the 'best' descriptive model and thus end up with:

$$J_{M_j}\left(\frac{\nu_{i,j}}{1-\nu_{i,j}}\right) \approx \theta_{i,j} = \alpha * \exp\left(lml_j + \beta_7 \, {lml_j}^2\right) * \exp\left(\frac{-\beta_2}{k * temp_i}\right)$$

where α again is an overall proportionality constant. Hence

$$\mu_{i,j} = \theta_{ij} * \log\left[1 - \frac{\lambda_j \, log(\lambda_j)}{1 - \lambda_j} * \frac{abundance_{i,j}}{\theta_{ij}}\right] * catch_{i,j}{}^{\beta_8} * \; aswept_j{}^{\beta_9} * \; mesh_i^{\beta_{11,j}}$$

where, $j = 1 \ldots 11$, is log maximum length group, i is stratum, and $abundance_{i,j}$ is the total number of individuals in stratum i group j estimated by multiplying the size of stratum i with the absolute density of fish in i belonging to log maximum length group j.

Estimating model parameters

We used the non-linear model fitting R-package TMB (Kristensen, Nielsen, Berg, Skaug & Bell, 2015) to estimate the parameters of the four non-linear models. Fitting each model to the number of species observed we removed any insignificant variables, except if they were important for the theoretical underpinning of a model. We visually inspected the Pearson residuals of each model for normality and plotted them against each co-variate to reveal potential heteroscedasticity. To compare the models we calculated AIC-values (Burnham & Anderson, 2002), R^2 from observed and predicted number of species, and proportion of deviance explained. The latter was estimated by fixing the estimated scale parameter, κ, of the negative binomial distribution used in each of the models, comparing the difference in deviance between a saturated model (with one parameter for each of the 550 observations) and the actual model, to the difference in deviance between a saturated model and a model with only one parameter (Cameron & Windmeijer, 1996). To also illustrate how much of the overall deviance each model term explained, we consecutively replaced each of the independent variables by its overall average and calculated the relative increase in the proportion of deviance explained when the observations were used instead of the average. Having identified the four most

parsimonious models we examined their sensitivity to the uncertainty in the abundance and density data by fitting them to the 1000 separate estimates of density and abundance obtained from the mixed effects catchability model, and calculated the mean and variance of the resulting parameter estimates. We plotted the proportion of the deviance explained by each of the model variables in the 1000 runs, and used these to illustrate the sensitivity of our results to the uncertainty in the catchability estimates. All analyses were undertaken in R version 3.4.4.

Results

Observed number of species and density

The number of observed species, log average swept area density, and log average absolute density follow almost symmetrical distributions when plotted against log maximum length (Figure 2). As expected, the average number of species observed increases with temperature while log average swept area density and log average absolute density change little except in areas with a mean annual sea temperature below 7.5°C where the densities are significantly lower in the intermediate length range.

GAM model

Fitting the GAM to the survey data reveals a strong and highly significant unimodal effect of log maximum length on log number of species observed, a significant effect of absolute fish abundance,

438 significant non-linear positive effects of average temperature in the upper 200 m of the water column
439 and area swept, and a significant positive linear effect of net primary production. Log number of
440 species caught declined significantly with depth and, for the smaller length groups, with increasing
441 mesh-size (Figure 3). Vertical opening, temperature range and catch in numbers were all insignificant,
442 while stratum area was significant (p=0.02), but generated a too high concurvity to be retained due to
443 its high correlation with area swept. The model explained 85% of the deviance and had a lower AIC
444 than model versions in which abundance was replaced by density. Using average temperature
445 produced a lower AIC than bottom temperature and latitude and longitude, and a slightly higher AIC
446 than sea surface temperature, but the best variance ratio. Although there are survey strata that
447 produce significant negative residuals, such as the 50-200m stratum in Guinea which features the
448 lowest number of hauls of all strata, there are no clear patterns in the residuals across survey strata.
449 This suggests that the model provides an equally good description of fish species richness in the
450 Atlantic, Arctic and Mediterranean Seas (Figure 4). Further model diagnostics are shown in Appendix
451 S5, Figures S5.1a&b and S5.2).
452
453 Some of the smooth relationships suggested that the AIC value could be further reduced by using the
454 logarithm or the inverse of the independent variable, and for log maximum length, in particular, that
455 the smoother could be replaced by a second-order term, corresponding to a log-normal like
456 distribution of richness versus maximum length. Replacing the independent variables in the GAM by
457 inverse temperature, log abundance, log depth, net primary production, log area swept, an
458 interaction between mesh-size and log maximum length, and the exponential of a second-order

polynomial in log maximum length, reduced the AIC-value from 2090 to 1860 and increased the percentage of deviance explained to 91%.

Non-linear models

We use non-linear estimation techniques to compare the 'best' descriptive model identified by the GAM to the three other models. Fitting the four models to the average absolute densities and abundances we initially used variance ratio tests to determine whether the bias correcting terms (${catch_{i,j}}^{\beta_8}$, ${aswept_j}^{\beta_9}$ and $mesh_i^{\beta_{11,j}}$) contributed significantly to the fit. We found that ${catch_{i,j}}^{\beta_8}$ did not improve the fit of the 'best' and neutral models significantly, improved the metabolic model marginally, but contributed highly significantly to the fit of the environmental model. The total area swept, ${aswept_j}^{\beta_9}$, contributed significantly to all models, except the environmental, while the term reflecting the interaction between mesh size and maximum length, $mesh_i^{\beta_{11,j}}$, was significant in all four models. In the neutral model the per capita immigration rates, λ_j, were not significantly different from zero; and were therefore replaced by a single overall λ for all log maximum length groups (see Appendix S5 Table S5.1).

Fitting the 'best' model to the average of the absolute abundances explains 90% of the deviance (Table 1). The neutral model provides the second-best fit (ΔAIC=38) followed by the metabolic model (ΔAIC=40) and the environmental model (ΔAIC=46). Note that the difference between the metabolic and neutral models can be explained by the additional parameter included in the former. Many of the parameter estimates are similar across models. The interaction between log maximum length and

mesh-size, $\beta_{11,j}$, is thus negative for the smaller species in all models, implying a general decline in the number of small species caught as mesh-size increases. In all models log maximum length and either temperature or latitude account for most of the deviance explained (Figure 5). The parameter estimates of 'best', metabolic and neutral models are robust to the uncertainty in the modelled catchabilities as shown by the limited distribution of deviance around the mean value of the 1000 estimates. The standard deviations of the parameter estimates are also small (see Appendix S5 Table S5.1). Additional model diagnostics are presented in the Supplementary Information (Appendix S5 Figures S5.4 & S5.5).

Discussion

Our study reveals strong consistent patterns in the number of demersal and benthopelagic fish species across the northern Atlantic. As in previous investigations, we find body size, depth and either temperature or latitude to be important, but our analysis is the first in which differences in the number of individuals caught, area swept and mesh-size are considered, and where net primary production and absolute fish abundance or density are used as covariates. We find fish species richness to increase with temperature, fish abundance, and net primary production, but to decline with depth and latitude. Adjusting for differences in area swept and mesh-size, the 'best' descriptive model explains 90% of the deviance in the number of species caught by log maximum length, temperature, fish abundance, depth and primary production (Table 1). The neutral model in which

501 inverse temperature, a parabolic relationship with log maximum length, area swept and mesh-size are
502 significant, explains 89% of the deviance, and so does the metabolic model. Our analyses furthermore
503 show that both the neutral and metabolic models provide significantly better fits than the
504 environmental model in which local richness is described as a function of log maximum length, catch,
505 latitude, longitude and depth.
506
507 In all four non-linear models more than half of the deviance is explained by a combination of log
508 maximum length and either temperature or latitude (Figure 5). In the data the distribution of the
509 number of species observed across maximum length groups is approximately lognormal (Figure 2).
510 Similar distributions have been obtained for marine bivalves (Roy, Jablonsky & Martien, 2000),
511 terrestrial snakes (Boback & Guyer, 2003), and insects (Siemann, Tilman & Haarstad, 1996), while
512 more right-skewed distributions have been found for birds and mammals (Purvis, Orme & Dolphin,
513 2003; Smith & Lyons, 2013). A lognormal distribution also provided a highly significant fit in the best,
514 neutral and environmental models (Table 1). Contrary to this, metabolic theory predicts that species
515 richness should scale with body mass raised to a power of 0.75, hence maximum length to a power of
516 2.25. This prediction was not confirmed by our analysis in which the power was estimated to be -1.00
517 (±0.48 conf. lim.) and thus highly significantly different from the expected.
518
519 The average water column temperature from 0-200 m is only a marginally better predictor of the
520 observed number of fish species than surface temperature, but much better than bottom
521 temperature, and latitude and longitude. Latitude and average temperature are negatively correlated,

but the correlation breaks down at intermediate latitudes, where average temperature generally is higher in the eastern part of the northern Atlantic due to the influence of the Gulf Stream. The increase in the number of fish species caught with temperature seems to be well described by the Arrhenius equation. Metabolic theory emphasizes the role of temperature and body size on mutation rate and generation time, and it is interesting that the Arrhenius constant, β_2, is 0.47 (± 0.06 conf. lim.) and 0.52 eV (±0.06 conf. lim.), respectively, in the metabolic and neutral models. This range is not far from the average activation energy of metabolism of 0.65 eV predicted by metabolic theory (Gillooly & Allen, 2007; Bailly et al., 2014), and close to empirical estimates of the activation energy of fish metabolism. Clarke & Johnston (1999) and Gillooly et al. (2001) both used the Arrhenius equation to describe the relationship between the resting metabolism of fish and temperature, and independently estimated the activation energy as 0.43 eV. Barneche et al. (2014) used a model with a temperature optimum to account for metabolic inactivation at high temperatures and found an activation energy of 0.59 eV. How temperature influences the rates of speciation and extinction is not completely known, and other co-varying factors may be involved (see e.g. Rabosky et al., 2018).

The 'best' and neutral models contain positive relationships between abundance and the number of species observed. The 'best' model also includes a significant positive relationship with net primary production. Areas of high productivity have been hypothesised to have higher species richness because they harbor more individuals able to maintain a higher number of viable populations (Brown, 2014), although a recent review by Storch, Bodhalkvá & Okie (2018) found the empirical evidence in favor of this hypothesis to be mixed. However, in areas where abundance has been significantly

543 reduced by fishing, primary production may better reflect fish abundance and density in the
544 unexploited state and hence be a better predictor of richness. Without primary production included in
545 the model, the three largest positive differences between the observed and predicted number of
546 species were generated by the data from the shelf off Mauretania, which features the highest primary
547 production, but has been subject to marked overexploitation (Meissa & Gascuel, 2014). Note
548 however, that abundance or density never accounted for more than 10% of the total deviance in the
549 'best', neutral and metabolic models, explaining the robustness of these models to the uncertainty in
550 the catchabilities (Figure 5).
551
552 Tittensor & Worm (2016) and Worm & Tittensor (2018) used a neutral model to simulate species
553 richness in the ocean and allowed speciation rate and generation time to depend on temperature.
554 Thermal effects on speciation rate generated a stable but weak latitudinal richness gradient in their
555 model, while thermal effects on generation time produced a transient latitudinal richness gradient
556 that eventually disappeared. Combining the effect of an increase in abundance caused by the increase
557 in ocean area towards the equator and a temperature-dependent speciation rate produced the most
558 realistic gradient in richness. Fitting a neutral model to the survey data we found a strong effect of
559 temperature on species richness and a weaker influence of fish abundance. Furthermore, the shelf
560 areas in the eastern Atlantic down to 200 m, the depth range where our fish species have their
561 maximum abundance, increases with latitude from the Equator to the Arctic (Pilson & Seitzinger,
562 1996). A consistent decline in habitat area with latitude is therefore unlikely to explain our results.
563

564 The parameter describing the probability of immigration in the neutral model could not be estimated
565 with sufficient precision. The known functional dependency between per capita immigration
566 probability and the speciation rate in the surrounding meta-community makes it difficult to estimate
567 both parameters simultaneously (Jabot & Chave, 2011). The immigration probability may depend on
568 temperature and size, as assumed by Reuman et al. (2014), but the evidence for temperature related
569 differences in larval dispersal is lacking (Leis et al., 2013), and when immigration probability was
570 assumed to be size dependent, none of the estimates of λ_j were significant. Additional analysis of
571 species distributions and information on the genetic divergence of subpopulations is necessary to
572 fully understand the relationship. The neutral model has been criticised for predicting unrealistically
573 long species ages for common species and too short species ages for new species with few individuals
574 (Chisholm & O'Dwyer, 2014). Recent work has shown that more realistic species ages are generated
575 when protracted speciation and weak selection caused by small differences in hereditary fitness are
576 incorporated in the model (Rosindell et al., 2015), but no approximate solution for the number of
577 species in each community is yet available for this model.
578
579 Despite the large sample sizes and good geographical coverage of the survey data, several problems
580 may be associated with using bottom trawl survey data to study fish species richness and density
581 patterns. The main aim of a scientific bottom trawl survey is often to provide reliable estimates of the
582 relative abundance and year-class strength of commercially important fish species, and less attention
583 may therefore be given to identifying species that are rare or of little or no commercial value. Trawl-
584 survey catches may furthermore provide biased estimates of the species composition and density due

585 to species and size-specific differences in the probability of the individuals being retained by the trawl
586 (Arreguín-Sánchez, 1996). Some species and sizes are herded into the path of the trawl by the action
587 of the otter doors and trawl sweeps, others escape under the fishing line or over the headline, while
588 yet others are able to outswim the trawl. Among those entering the trawl the smaller individuals and
589 species may escape through the meshes. Factors that have been reported to influence the catch
590 efficiency of survey trawls include time of day, light intensity, turbidity, current strength and
591 direction, depth, sweep length, net spread, vertical opening, trawl speed, haul duration, and the size
592 and type of the ground gear (Arreguín-Sánchez, 1996; Fraser, Greenstreet & Piet, 2007). Although we
593 corrected our analysis for differences in species catchability, we were unable to fully account for all of
594 the factors that may lead to species and size specific differences in catchability. This was due to the
595 sparsity of spatially and temporally overlapping stock assessments, the absence of individual length
596 measurements for many of the non-commercial species, and our use of average catch rates rather
597 than individual hauls**.** However, as seen in Figure 5, density or abundance only explains less than 10%
598 of the deviance. The sensitivity of our overall conclusions to the uncertainty in the catchabilities is
599 therefore modest, and the parameter estimates and the relative importance of the variables change
600 little in the different models. Finally, our use of a single estimate of maximum length for each species
601 hides the fact that maximum body length in fish is likely to vary from area to area (Rypel, 2013).
602 However, the maximum length of a species in a given area is difficult to estimate as it depends on
603 local fishing mortality and sampling effort.
604

605 We base our analysis on the number of fish species and individuals observed over a recent period of
606 time in different regions of the northern Atlantic, Arctic and Mediterranean Seas. It is now well
607 documented that changes in fish distributions have occurred over the last decade or two in many
608 regions of the North Atlantic and that these are significantly associated with changes in temperature,
609 (Perry, Low, Ellis & Reynolds, 2005; Hiddink & Ter Hofstede, 2008; Fossheim et al., 2015; Batt,
610 Morley, Selden, Tingley & Pinsky, 2017). We have fitted our models to data from a period when
611 temperatures have been increasing, but where regulatory processes generally seem to maintain
612 existing patterns in species richness (Gotelli et al., 2017). Future analyses should investigate whether
613 these patterns will persist over longer time periods and how our model parameters will be modified
614 by temperature change, for example by conducting the analyses on different time periods
615 characterised by different mean temperatures. Such analyses could provide insight into the relative
616 importance of temperature having a direct effect on metabolic processes vs. its effects on other
617 ecosystem features that affect species richness. For example, Marbá, Jordà, Augustí, Girard & Duarte
618 (2015) showed that the activation energy for many biological responses in the Mediterranean Sea is
619 far higher than the reported activation energy for metabolism, suggesting that temperature increases
620 are having additional ecosystem effects on biotic responses beyond their effect on metabolic
621 processes and speciation rates. The effects of global warming on fish communities have been
622 predicted from stacked species distribution models (SSDMs; e.g. Jones & Cheung, 2015), but these
623 models have so far largely ignored the regularity in the distribution of fish species richness and
624 abundance with log maximum length. This regularity accounts for a third or more of the deviance
625 explained by our models (Figure 5) and may thus be used to improve the predictive capability of the

626 SSDMs significantly. But while the right-hand side of the richness versus log maximum length
627 distribution, consisting of species with a maximum length larger than app. 50 cm, has been explained
628 by size spectrum theory (Reuman et al., 2014), little is known about the processes shaping the left-
629 hand side.
630
631 Numerous hypotheses have been put forward to explain the latitudinal pattern in species richness
632 (Brown, 2014; Fine, 2015). Finding log maximum length, temperature, absolute fish abundance, depth
633 and net primary production to explain 90% of the deviance in the distribution of demersal fish species
634 richness across the northern Atlantic, and both neutral and metabolic equilibrium models to explain
635 close to 89%, conveys an important message. When 89% of the deviance in the extant species
636 richness can be explained by two competing mechanistic hypotheses, and by a model based on
637 latitude, longitude and depth, and when many of the independent variables are significantly
638 correlated, it seems relevant to question how much the present patterns in species richness and
639 abundance can tell us about the underlying environmental, ecological and evolutionary processes
640 (Gotelli et al., 2009). We probably need dynamic mechanistic models with more realistic descriptions
641 of speciation, dispersal and extinction plus additional data to reveal how past changes in
642 environmental (e.g. temperature, currents, ice cover, shelf area) and biotic (e.g. primary production)
643 variables may have contributed to shaping the present distribution of species richness and the strong
644 lognormal relationship between richness and maximum length (Fine, 2015; Descombes et al., 2018).
645 Such data should include information from paleo-geographical and climatological reconstructions of
646 past environmental conditions as well as information about body size evolution, diversification rates

and species lifetimes from molecular phylogenetics and the fossil record (Romano et al., 2016; Alfaro et al., 2018). In addition to providing a baseline from which we can evaluate future change, our data and results point to new possibilities for understanding demersal fish species biogeography in the northern Atlantic.

Acknowledgements

Thanks to all the scientists and crew members engaged in the Scientific Trawl Surveys that provided the data for this paper. Thanks also to E. Collie and four anonymous referees for suggesting improvements to the manuscript. Initial data compilations from EU waters were conducted as part of the EU Network of Excellence MarBEF (Marine Biodiversity and Ecosystem Functioning; contract number GOCE-CT-2003-505446), and supported by the Center for Macroecology, Evolution and Climate (Danish National Research Foundation). The first author received support from the EU FP7-KBBE project VECTORS (project ID: 266445).

661 References

662 Alfaro, M.E., Faircloth, B.C., Harrington, R.C., Sorenson, L., Friedman, M., Thacker, … Near, T.J., 2018.
663 Explosive diversification of marine fishes at the Cretaceous-Palaeogene boundary. *Nature*
664 *Ecology and Evolution*, 2, 688-696.

665 Allen, A.P., Brown, J.H. & Gillooly, J.F., 2002. Global biodiversity, biochemical kinetics, and the
666 energetic-equivalence rule. *Science*, 297, 1545-1548.

667 Allen, A.P., & Gillooly, J.F., 2007. The mechanistic basis of the metabolic theory of ecology. *Oikos,*
668 116, 1073-1077.

669 Andersen, K.H., Berge, T., Gonçalves, R.J., Hartvig, M., Heuschele, J., Hylander, S., ... Olsson, K., 2016.
670 Characteristic sizes of life in the oceans, from bacteria to whales. *Annual Review of Marine*
671 *Science*, 8, 217-241.

672 Arreguín-Sánchez, F., 1996. Catchability: a key parameter for fish stock assessment. *Reviews in Fish*
673 *Biology and Fisheries*, 6, 221-242.

674 Bailly, D., Cassemiro, F.A., Agostinho, C.S., Marques, E.E. & Agostinho, A.A., 2014. The metabolic
675 theory of ecology convincingly explains the latitudinal diversity gradient of Neotropical
676 freshwater fish. *Ecology*, 95, 553-562.

677 Barneche, D.R, Kulbicki, M., Floeter, S.R., Friedlander, A.M., Maina, J., & Allen, A.P., 2014. Scaling
678 metabolism from individuals to reef-fish communities at broad spatial scales. *Ecology Letters*,
679 17, 1067-1076.

680 Batt, R.D., Morley, J.W., Selden, R.L., Tingley, M.W. & Pinsky, M.L., 2017. Gradual changes in range
681 size accompany long-term trends in species richness. *Ecology Letters*, 20, pp.1148-1157.

682 Behrenfeld, M.J. & Falkowski, P.G., 1977. Photosynthetic rates derived from satellite-based
683 chlorophyll concentration. *Limnology and Oceanography*, 42, 1-20.
684 Blowes, S. A., Belmaker, J. & Chase, J. M., 2017. Global reef fish richness gradients emerge from
685 divergent and scale-dependent component changes. *Proceedings of the Royal Society B:*
686 *Biological Sciences*, 284, 20170947.
687 Boback, S.M., & Guyer, C., 2003. Empirical evidence for an optimal body size in snakes. *Evolution*,
688 57, 345-351.
689 Brown, J. H., 2014. Why are there so many species in the tropics? *Journal of Biogeography*, 41, 8-22.
690 Burnham, K.P., & Anderson, D. R., 2002. *Model selection and multimodel inference: a practical*
691 *information theoretic approach*. 2nd ed. Springer, New York, 488pp.
692 Cameron, A.C. & Windmeijer, F.A., 1996. R-squared measures for count data regression models with
693 applications to health-care utilization. *Journal of Business and Economic Statistics*, 14, 209-220.
694 Chisholm, R.A. & O'Dwyer, J.P., 2014. Species ages in neutral biodiversity models. *Theoretical*
695 *Population Biology*, 93, 85-94.
696 Clarke, A., & Johnston, N.M., 1999. Scaling of metabolic rate with body mass and temperature in
697 teleost fish. *Journal of Animal Ecology*, 68, 893-905.
698 Cullen, J. J., Franks, P. J., Karl, D. M., & Longhurst, A., 2002. Physical influences on marine ecosystem
699 dynamics. In Robinson A.R., McCarthy, J.J. & Rothschild, B.J. (eds.). *The Sea*, 12, 297-336.
700 Davies, T.D. & Baum, J.K., 2012. Extinction risk and overfishing: reconciling conservation and
701 fisheries perspectives on the status of marine fishes. *Scientific reports*, 2, p.561.

Descombes, P., Gaboriau, T., Albouy, C., Heine, C., Leprieur, F., & Pellissier, L., 2018. Linking species diversification to palaeo-environmental changes: A process-based modelling approach. *Global Ecology and Biogeography*, 27, 233-244.

Etienne, R.S., & Olff, H., 2004. How dispersal limitation shapes species body size distributions in local communities. *The American Naturalist,* 163, 69-83.

Fine, P.V., 2015. Ecological and evolutionary drivers of geographic variation in species diversity. *Annual Review of Ecology, Evolution, and Systematics*, 46, 369-392.

Fisher, J.A., Frank, K.T., & Leggett, W.C., 2010. Global variation in marine fish body size and its role in biodiversity–ecosystem functioning. *Marine Ecology Progress Series*, 405, 1-13.

Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R.B., Aschan, M.M., & Dolgov, A.V., 2015. Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature Climate Change*, 5, 673–677.

Fraser, H.M., Greenstreet, S.P. and Piet, G.J., 2007. Taking account of catchability in groundfish survey trawls: implications for estimating demersal fish biomass. *ICES Journal of Marine Science*, 64, 1800-1819.

Froese, R., & Pauly, D., (eds.), 2016. FishBase. World Wide Web electronic publication. www.fishbase.org, version (01/2016).

Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M., & Charnov, E.L., 2001. Effects of size and temperature on metabolic rate. *Science*, 293, 2248-2251.

Gillooly, J.F., & Allen, A.P., 2007. Linking global patterns in biodiversity to evolutionary dynamics using metabolic theory. *Ecology*, 88, 1890-1894.

723 Gotelli, N.J., Anderson, M.J., Arita, H.T., Chao, A., Colwell, R.K., Connolly, S.R., … Willig, M.R., 2009.
724 Patterns and causes of species richness: a general simulation model for macroecology. *Ecology*
725 *Letters,* 12, 873-886.
726 Gotelli, N. J., & Colwell, R. K., 2001. Quantifying biodiversity: procedures and pitfalls in the
727 measurement and comparison of species richness. *Ecology Letters*, 4, 379-391.
728 Gotelli, N.J., Shimadzu, H., Dornelas, M., McGill, B., Moyes, F., & Magurran, A.E., 2017. Community-
729 level regulation of temporal trends in biodiversity. *Science advances*, 3, p.e1700315.
730 Hiddink, J.G., & Ter Hofstede, R., 2008. Climate induced increase in species richness of marine fishes.
731 *Global Change Biology*, 13, 453-460.
732 Hilbe, J.M., 2011. *Negative Binomial Regression*. 2nd ed. Cambridge University Press, 553pp.
733 Hillebrand, H., 2004. Strength, slope and variability of marine latitudinal gradients. *Marine Ecology*
734 *Progress Series*, 273, 251-267.
735 Hubbell, S.P., 2001. *The unified neutral theory of biodiversity and biogeography.* Monographs in
736 Population Biology, Vol. 32. Princeton University Press. 375pp.
737 Jabot, F., & Chave, J., 2011. Analyzing tropical forest tree species abundance distributions using a
738 non-neutral model and through approximate Bayesian inference. *The American Naturalist*, 178,
739 E37-E47.
740 Jones, M.C., & Cheung, W.W.L., 2015. Multi-model ensemble projections of climate change effects
741 on global marine biodiversity, *ICES Journal of Marine Science*, 72,741–752.
742 Kristensen, K., Nielsen, A., Berg, C.W., Skaug, H., & Bell, B., 2015. TMB: automatic differentiation and
743 Laplace approximation. *arXiv preprint arXiv:1509.00660*.

744 Leis, J.M., Caselle, J.E., Bradbury, I.R., Kristiansen, T., Llopiz, J.K., Miller, M.J., ... Swearer, S.E., 2013.
745 Does fish larval dispersal differ between high and low latitudes? *Proceedings of the Royal*
746 *Society of London B: Biological Sciences*, 280, p.20130327.
747 Locarnini, R. A., Mishonov, A. V., Antonov, J. I., Boyer, T. P., Garcia, H. E., Baranova, … Seidov, D.,
748 2013. World Ocean Atlas 2013, Volume 1: Temperature. S. Levitus, Ed., A. Mishonov Technical
749 Ed.; NOAA Atlas NESDIS 73, 40pp.
750 Macpherson, E., & Duarte, C. M., 1994. Patterns in species richness, size, and latitudinal range of
751 East Atlantic fishes. *Ecography*, 17, 242-248.
752 Marbà, N., Jordà, G., Agustí, S., Girard, C., & Duarte, C.M., 2015. Footprints of climate change on
753 Mediterranean Sea biota. *Frontiers in Marine Science*, 2:56 doi: 10.3389/fmars.2015.00056.
754 Meissa, B., & Gascuel, D., 2014. Overfishing of marine resources: some lessons from the assessment
755 of demersal stocks off Mauritania. *ICES Journal of Marine Science*, 72, 414-427.
756 Mora, C., Tittensor, D.P., & Myers, R.A., 2008. The completeness of taxonomic inventories for
757 describing the global diversity and distribution of marine fishes. *Proceedings of the Royal*
758 *Society of London B: Biological Sciences*, 275, 149-155.
759 Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., ... Wagner, H., 2019. Vegan:
760 Community Ecology Package. R package version 2.2-1.
761 Perry, A.L., Low, P.J., Ellis, J.R., & Reynolds, J.D., 2005. Climate change and distribution shifts in
762 marine fishes. *Science*, 308, 1912–1915.
763 Pilson, M.E., & Seitzinger, S.P., 1996. Areas of shallow water in the North Atlantic. Biogeochemistry,
764 35, 227-233.

765 Purvis, A., Orme, C.D.L., & Dolphin, K., 2003. *Why are Most Species Small-Bodied?* Macroecology:
766 Concepts and Consequences, pp.155–173. Oxford University Press, Oxford.
767 Rabosky, D.L., Chang, J., Title, P.O., Cowman, P.F., Sallan, L., Friedman, … Alfaro, M.E., 2018. An
768 inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, 55, 392–395
769 Reuman, D.C., Gislason, H., Barnes, C., Mélin, F., & Jennings, S., 2014. The marine diversity
770 spectrum. *Journal of Animal Ecology*, 83, 963-979.
771 Romano, C., Koot, M.B., Kogan, I., Brayard, A., Minikh, A.V., Brinkmann, W., … Kriwet, J., 2016.
772 Permian–Triassic Osteichthyes (bony fishes): diversity dynamics and body size evolution.
773 *Biological Reviews*, 91, 106-147.
774 Rosindell, J., Harmon, L.J., & Etienne, R.S., 2015. Unifying ecology and macroevolution with
775 individual-based theory. *Ecology Letters*, 18, 472-482.
776 Rosindell, J., Hubbell, S.P., & Etienne, R.S., 2011. The unified neutral theory of biodiversity and
777 biogeography at age ten. *Trends in Ecology and Evolution*, 26, 340-348.
778 Roy, K., Jablonski,D., & Martien, K.K., 2000. Invariant size-frequency distributions along a latitudinal
779 gradient in marine bivalves. *Proc. Nat. Acad. Sci.*, 97, 13150–13155.
780 Rypel, A.L., 2013. The cold-water connection: Bergmann's rule in North American freshwater fishes.
781 *The American Naturalist*, 183, 147-156.
782 Segura, A.M., Calliari, D., Kruk, C., Fort, H., Izaguirre, I., Saad, J.F., & Arim, M., 2015. Metabolic
783 dependence of phytoplankton species richness. *Global Ecology and Biogeography*, 24, 472-482.
784 Siemann, E., Tilman, D., & Haarstad, J., 1996. Insect species diversity, abundance and body size
785 relationships. *Nature*, 380, 704-706.

786 Smith, F.A., & Lyons S.K., 2013. *Animal Body Size: Linking Pattern and Process across Space, Time,*
787 *and Taxonomic Group*. University of Chicago Press. 272pp.
788 Storch, D., Bodhalkvá, E., & Okie, J., 2018. The more-individuals hypothesis revisited: the role of
789 community abundance in species richness regulation and the productivity-diversity
790 relationship. *Ecology Letters*, 21, 920-937.
791 Tittensor, D.P., Mora, C., Jetz, W., Lotze, H. K., Ricard, D., Berghe, E. V., & Worm, B., 2010. Global
792 patterns and predictors of marine biodiversity across taxa. *Nature*, 466, 1098-1101.
793 Tittensor, D.P. & Worm, B., 2016. A neutral-metabolic theory of latitudinal biodiversity. *Global*
794 *Ecology and Biogeography*, 25, 630-641.
795 Walker, N. D., Maxwell, D. L., Le Quesne, W. J., & Jennings, S., 2017. Estimating efficiency of survey
796 and commercial trawl gears from comparisons of catch-ratios. *ICES Journal of Marine Science*,
797 74, 1448-1457.
798 Wood, S.N., 2006. *Generalized additive models: an introduction with R*. Boca Raton, Florida:
799 Chapman and Hall/CRC. 391pp.
800 Worm, B., & Tittensor, D.P., 2018. *A Theory of Global Biodiversity*. Monographs in Population
801 Biology 60. Princeton University Press, 214 pp.
802 Wright, S.D., Ross, H.A., Keeling, D.J., McBride, P., & Gillman, L.N., 2011. Thermal energy and the
803 rate of genetic evolution in marine fishes. *Evolutionary Ecology*, 25, 525-530.
804
805
806

807

808 Data accessibility

809 The richness and abundance data and the R-code that support the findings of this study are deposited

810 on GitHub (https://github.com) in the repository 'DTUAqua/biodiversity'.

811

812

813 Appendix 1 – Data Sources

814

815 Anon., 2006. Methodic manual on instrumental surveys of commercial hydrobiont stocks in PINRO
816 investigations areas. Murmansk, PINRO Press, 163 pp. (in Russian).

817 Benchoucha, S., Berraho, A., Bazairi, H., Katara, I., Benchrifi, S., & Valavanis, V.D., 2008. Salinity and
818 temperature as factors controlling the spawning and catch of Parapenaeus longirostris along
819 the Moroccan Atlantic Ocean. *Hydrobiologia*, 612: 109-123.

820 Bertrand, J.A., Gil de Sola, L., Papaconstantinou, C., Relini, G., & Souplet, A., 2002. The general
821 specification of the MEDITS surveys. *Scientia Marina* 66 (Suppl. 2), 9 -17.

822 Bourdages H., & Oullet, S., 2011. Geographic distribution and abundance indices of marine fish in
823 the northern Gulf of St. Lawrence (1990-2009). *Can. Tech. Rep. Fish. & Aquat. Sci*. 2964.

824 Domain, F., Chavance, P., & Diallo, A., (éds.), 1999. La pêche côtière en Guinée : ressources et
825 exploitation. IRD édition, Paris, *Collection colloques et séminaires*, 394 p.

826 Fowler, G.M., & and Showell, M.A., 2009. Calibration of bottom trawl survey vessels: comparative
827 fishing between the Alfred Needler and Teleost on the Scotian Shelf during the summer of
828 2005. *Can. Tech. Rep. Fish. Aquat. Sci.* 2824: iv + 25 p.

829 Gascuel, D., Labrosse, P., Meissa, B., Taleb Sidi, M.O., & Guénette, S., 2007. Decline of the demersal
830 resources in the North-West Africa: an analysis of Mauritanian trawl-survey data over the past
831 25 years. *African Journal of Marine Science*, 29: 331-345.

832 ICES 2017. Manual of the IBTS North Eastern Atlantic Surveys. Series of ICES Survey Protocols SISP
833 15. 92 pp. http://doi.org/10.17895/ices.pub.3519

834 Jørgensen O.A., 1998. Survey for Greenland Halibut in NAFO Division 1C-1D. *NAFO Sci. Council*
835 *Reports.* Doc. 98/25. Serial No. N3010, 26 pp.
836 Magnussen, E., 2002. Demersal fish assemblages of Faroe Bank: species composition, distribution,
837 biomass spectrum and diversity. *Marine Ecology Progress Series*, 238, 211-225.
838 Marine Research Institute, 2010. Manuals for the Icelandic bottom trawl surveys in spring and
839 autumn. Marine Research in Iceland: 125 pp.
840 https://www.hafogvatn.is/static/research/files/fjolrit-156.pdf
841 Rätz, H-J., 1999, Structures and Changes of the Demersal Fish Assemblage off Greenland, 1982-96.
842 *NAFO Sci. Council Studies*, 32: 1-15.
843

Table 1. Parameter estimates from TMB-model fits using average absolute density and abundance. Standard error in parentheses and significance levels indicated by stars (***=<0.001, **=< 0.01, *=< 0.05) (one-sided t-test, n=550). NS= Non Significant term retained in the model fit. NSR= Non Significant term removed from the model.

Parameter		Best descriptive model	Neutral	Metabolic	Environmental
Constant	$(log\alpha)$	16.90 (1.63)***	22.95 (1.35)***	24.89 (1.65)***	3.093 (0.687)***
Latitude	(β_0)				-0.518 (0.055)***
Longitude	(β_1)				0.426 (0.073)***
Temperature	(β_2)	0.322 (0.035)***	0.521 (0.029)***	0.466 (0.029)***	
Abundance	(β_3)	0.034 (0.009)***			
Density	(β_3)			0.056 (0.011)***	
Depth	(β_4)	-0.115 (0.029)***			-0.167 (0.034)***
Net prim. prod.	(β_5)	0.217 (0.045)***			
Max. length	(β_6)			-1.000 (0.246)***	
Log. max. length^2	(β_7)	-0.131 (0.028)***	-0.131 (0.031)***		-0.235 (0.029)***
Immigration	(λ)		NS		
Catch	(β_8)	NSR	NSR	NSR	0.067 (0.010)***
Area swept	(β_9)	0.079 (0.023)***	0.129 (0.022)***	0.176 (0.022)***	NSR
Mesh:mlgr$_{1.5}$	$(\beta_{11,1})$	-1.537 (0.181)***	-1.351 (0.184)***	-1.675 (0.242)***	-1.070 (0.187)***
Mesh:mlgr$_{2.0}$	$(\beta_{11,2})$	-1.378 (0.162)***	-1.205 (0.164)***	-1.421 (0.202)***	-1.021 (0.168)***
Mesh:mlgr$_{2.5}$	$(\beta_{11,3})$	-0.977 (0.120)***	-0.875 (0.124)***	-0.972 (0.143)***	-0.755 (0.125)***
Mesh:mlgr$_{3.0}$	$(\beta_{11,4})$	-0.598 (0.099)***	-0.509 (0.103)***	-0.552 (0.108)***	-0.458 (0.103)***
Mesh:mlgr$_{3.5}$	$(\beta_{11,5})$	-0.401 (0.078)***	-0.335 (0.081)***	-0.347 (0.082)***	-0.340 (0.082)***
Mesh:mlgr$_{4.0}$	$(\beta_{11,6})$	-0.222 (0.066)***	-0.165 (0.070)**	-0.167 (0.070)*	-0.192 (0.070)***
Mesh:mlgr$_{4.5}$	$(\beta_{11,7})$	NS	NS	NS	NS
Mesh:mlgr$_{5.0}$	$(\beta_{11,8})$	NS	NS	NS	NS
Mesh:mlgr$_{5.5}$	$(\beta_{11,9})$	NS	NS	NS	NS
Mesh:mlgr$_{6.0}$	$(\beta_{11,10})$	NS	NS	NS	NS
Mesh:mlgr$_{6.5}$	$(\beta_{11,11})$	NS	NS	NS	NS
Scale parameter	$(log\kappa)$	3.752 (0.402)***	3.058 (0.239)***	3.085 (0.247)***	3.049 (0.239)***
Proportion of deviance explained		0.900	0.892	0.891	0.890
Pearson's R^2 (observed vs. predicted)		0.838	0.787	0.792	0.789
AIC		1891	1929	1931	1937
ΔAIC			38	40	46

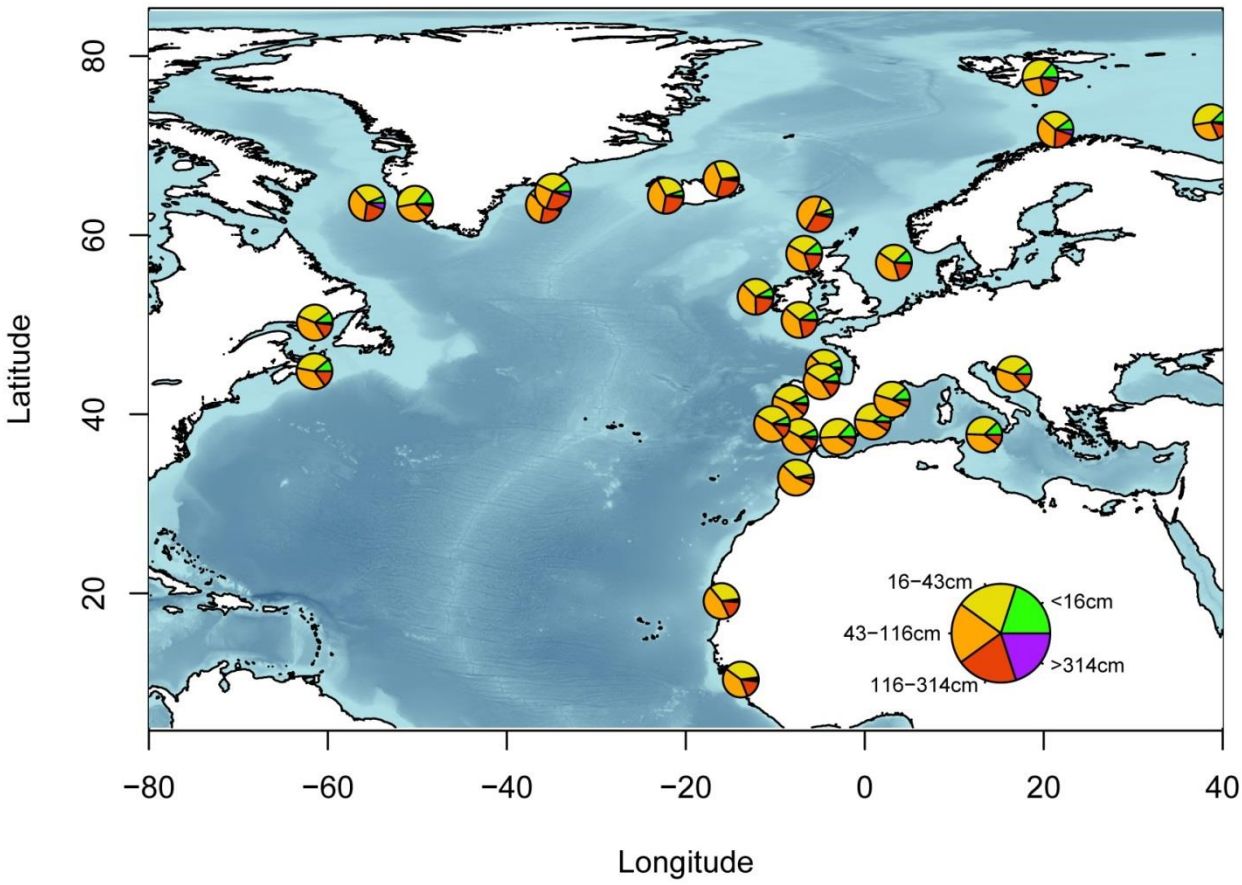
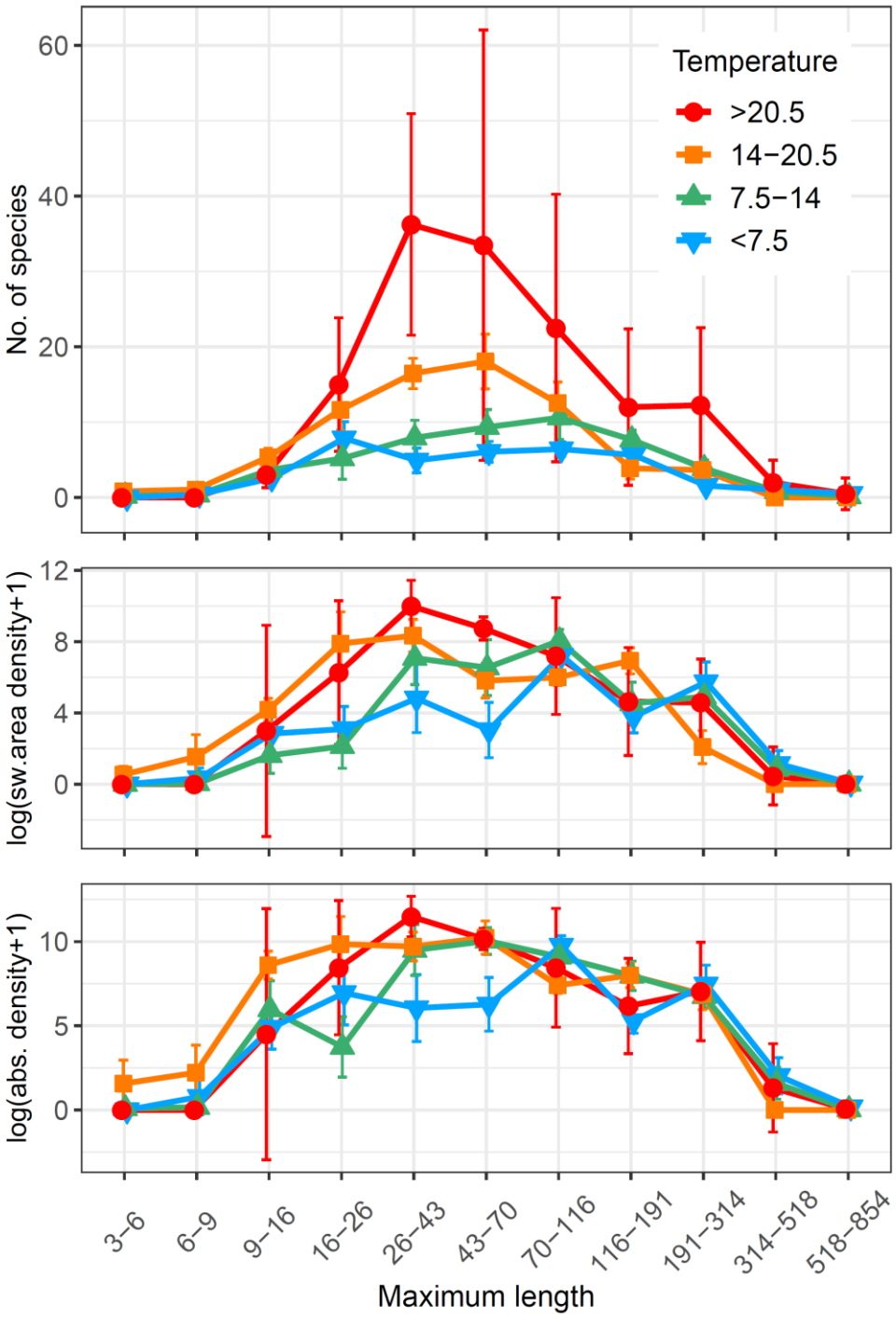


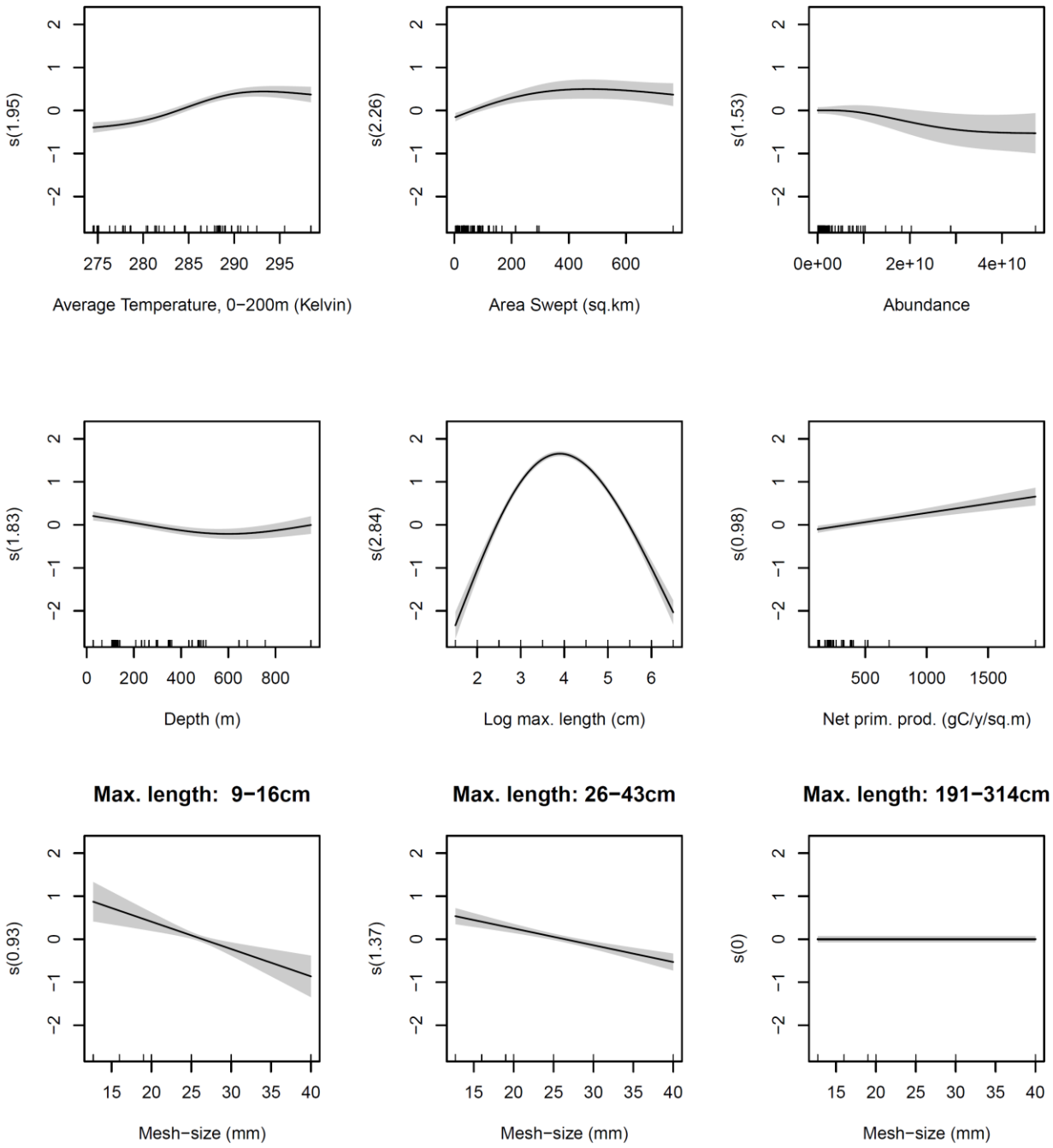
Figure 1. Pies showing the locations of the surveys and the relative number of species recorded in each of the maximum length groups indicated in the lower right-hand corner of the map (plotted with the R-package 'marmap').



855

856 Figure 2. Average number of species, log swept area density (No*km^{-2}) and log absolute density
857 (No*km^{-2}) (±95% conf. limits) versus maximum length (cm) in four different sea surface temperature
858 intervals (°C).

Figure 3. Estimated smoothing curves from the GAM using average sea temperature and other covariates to model the number of species observed by log maximum length group. Estimated degrees of freedom in brackets on the y-axis labels. Shaded area: 2*SE. Mesh-size smooths in bottom row only shown for three numerically abundant maximum length groups.



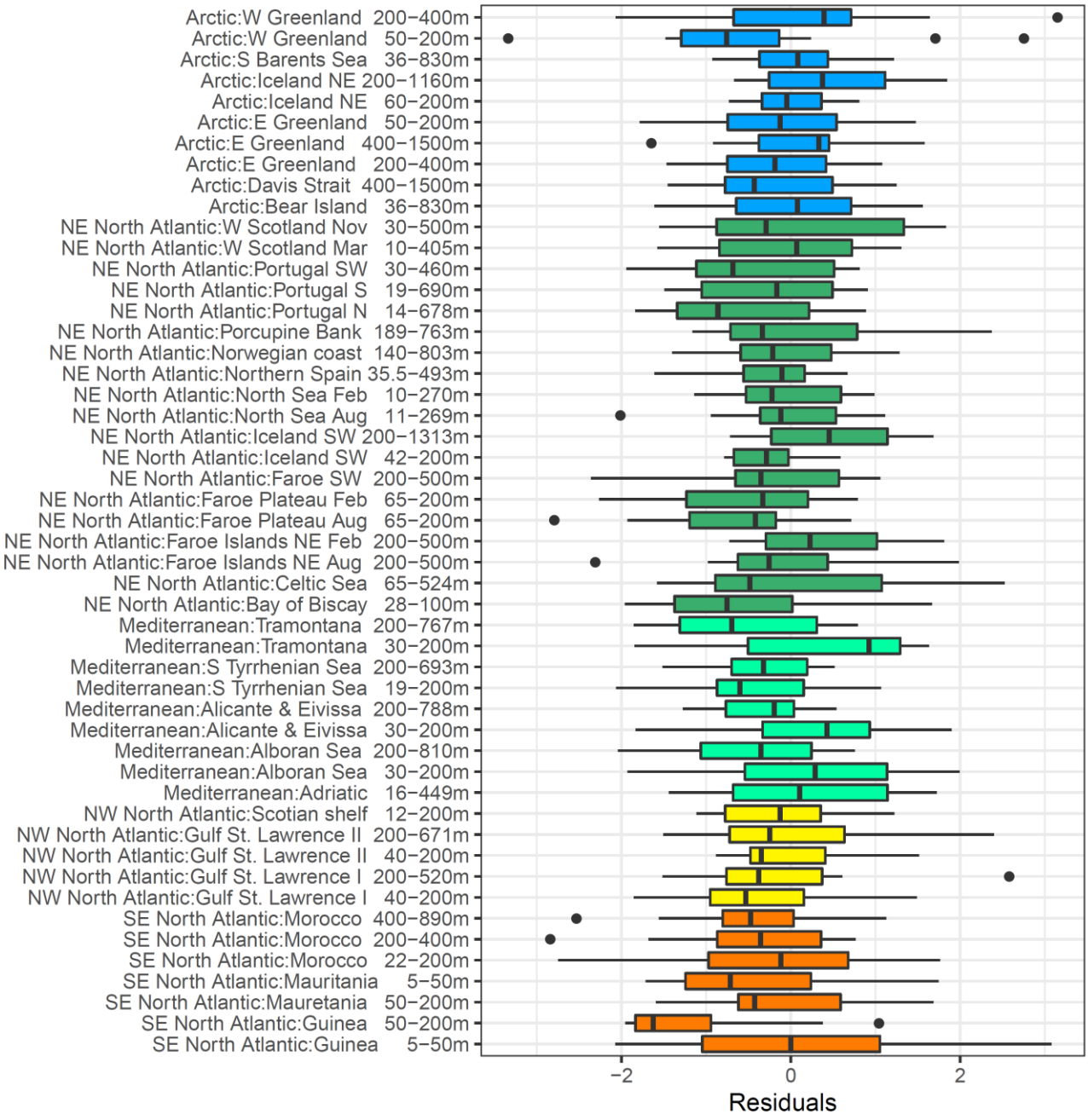
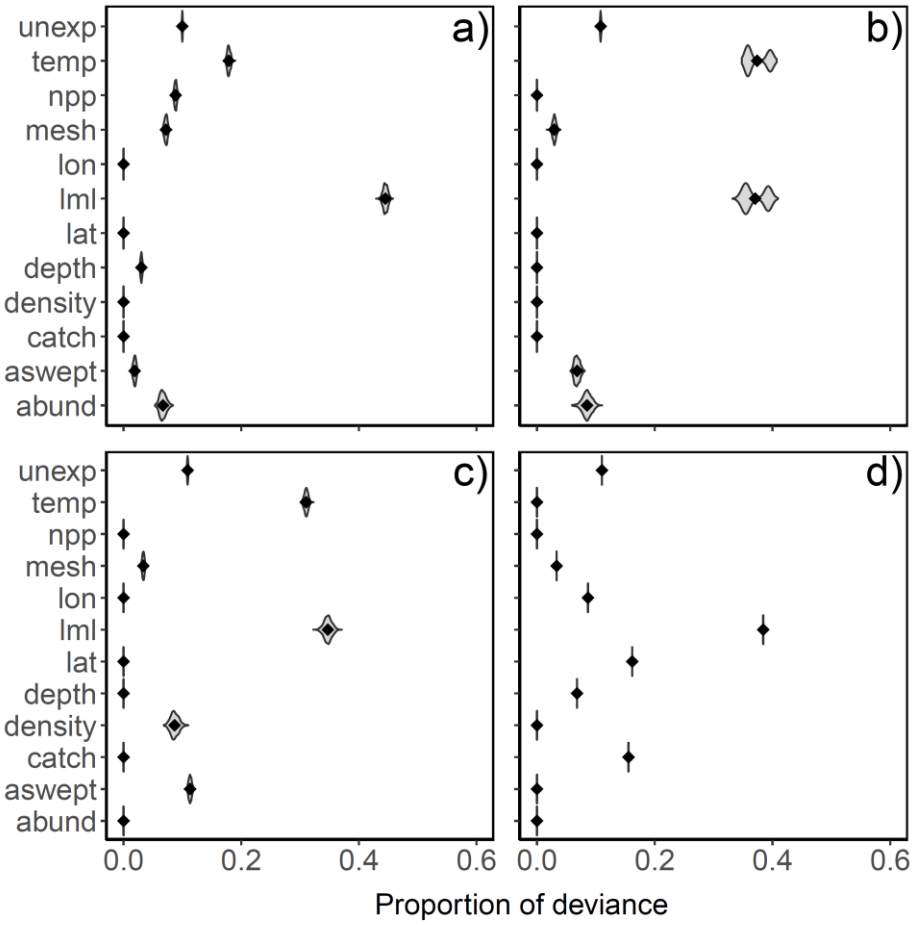


Figure 4. Box and whisker plot of log survey strata residuals from GAM model (box limits show 25% and 75% quartiles; the vertical bar in the middle of the box is the median of the residuals; whiskers show max. and min. values; and black dots are outliers; colour indicate geographic regions).



870

871

872 Figure 5.Violin plots of the relative contribution of the variables in each of the four models to the total
873 deviance explained by each model. Results from 1000 non-linear model runs with stochastic
874 catchabilities. Unexplained deviance: unexp. Models: a) 'best' descriptive, b) neutral, c) metabolic, d)
875 environmental.