Species richness in North Atlantic fish: Process concealed by pattern

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1 Title

The explanatory power of metabolic, neutral and descriptive models of fish species richness in the
northern Atlantic

4

- 5 Running Title
- 6 Fish species richness
- 7
- 8 Abstract
- 9 Aim Previous analyses of marine fish species richness based on presence-absence data have shown

10 changes with latitude and average species size, but little is known about the underlying processes. To

11 elucidate these processes we use metabolic, neutral and descriptive statistical models to analyse how

- 12 richness responds to maximum species length, fish abundance, temperature, primary production,
- 13 depth, latitude, and longitude, while accounting for differences in species catchability, sampling effort
- 14 and mesh size.
- 15 Data Results from 53,382 bottom trawl hauls representing 50 fish assemblages.

16 **Location** The northern Atlantic from Nova Scotia to Guinea.

17 **Time period** 1977-2013

- 18 Methods A descriptive Generalised Additive Model was used to identify functional relationships
- 19 between species richness and potential drivers, after which non-linear estimation techniques were
- 20 used to parameterise 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. 34 Introduction

35

Although much has been learned about the richness and distribution of marine species, a mechanistic 36 37 understanding of the processes responsible for generating and maintaining species richness over 38 evolutionary timescales remains elusive. There is no generally accepted theory to explain the spatial distribution of marine species richness and no general understanding of why some species are more 39 40 abundant than others (Fine, 2015). This lack of understanding is somewhat surprising. Strong 41 latitudinal gradients in species richness are observed at global and regional scales and these often 42 correlate significantly with environmental variables and life-history traits. Hillebrand (2004) 43 conducted a meta-analysis of gradients in marine biodiversity and found significant relationships 44 between marine species richness, latitude, and species size, while Tittensor et al. (2010) found water 45 temperature to be the main environmental predictor of species richness across a number of marine 46 taxonomic groups. Why latitude, temperature and species size are important is unclear, but size and maximum body size influence the trophic position, mortality, growth and reproduction of many 47 marine species (Andersen et al., 2016), temperature affects their metabolism and food uptake 48 49 (Gillooly, Brown, West, Savage & Charnov, 2001), and latitude determines the amplitude of the 50 seasonal changes in solar energy input affecting primary production, average temperature and annual temperature range (Cullen, Franks, Karl & Longhurst, 2002). 51

52

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

55 global scale around 79% of the species have now been described (Mora, Tittensor & Myers, 2008) and 56 very few species have been declared extinct due to human activities (Davies & Baum, 2012). However, most inventories of fish species richness are based on single recordings of individuals with little 57 consideration of differences in individual density and sampling effort. Including density and sampling 58 59 effort is important for at least two reasons. The number of species recorded is known to depend statistically on the number of individuals and number of samples examined (Gotelli & Colwell, 2001), 60 61 and high-density areas may have higher species richness because they harbor more individuals able to 62 maintain a higher number of viable populations (Brown, 2014). Based on species inventories, MacPherson & Duarte (1994) found fish species richness and average maximum fish species size to 63 64 increase with depth and decline with latitude in the northern Atlantic and Fisher, Franks & Leggett 65 (2010) found the geometric mean fish species size to co-vary with species richness. While Blowes, Belmaker & Chase (2017) found the latitudinal change in reef fish richness to scale with abundance, 66 67 no one has so far analysed how species richness of marine fish found on soft or sandy bottoms is related to density or abundance on a basin-wide scale. 68

69

To understand how fish species richness in different fish communities is related to density or
abundance, species length, and environmental conditions, we analyse an extensive dataset,
generated by collating results from 31 standardised bottom trawl surveys from the continental
shelves of the northern Atlantic and adjacent areas (Figure 1). Our analysis is based on 123 million
individual demersal or benthopelagic fish caught in 53 thousand hauls taken within a total survey area
of 3.1 million km². Bottom trawl surveys are often stratified to account for spatial or depth related

76 differences in fish assemblage composition and density. We retain the stratification used in the 77 surveys, correct for differences in catchability, and further stratify species into log maximum species length intervals. Using a Generalised Additive Model (GAM) to identify significant variables and 78 79 relationships we construct a 'best' descriptive model of the number of species caught per log 80 maximum species length interval and survey stratum by transforming the significant relationships identified by the GAM into functional relationships. We also fit an environmental model to the data in 81 82 which latitude, longitude, depth, total catch and mesh-size are used as independent variables without invoking any biological hypotheses. Using the two descriptive models as reference points we 83 investigate how well mechanistic equilibrium models of species richness based on metabolic (Allen, 84 85 Brown & Gillooly, 2002; Allen & Gillooly, 2007) and neutral theory (Hubbell, 2001) fit the survey data. 86 Both theories explain the present difference in species richness among fish communities from 87 individual density or abundance, and from fundamental evolutionary processes such as speciation, 88 dispersal and extinction. Recently, they have been combined and used to simulate the latitudinal gradient in species richness in the ocean (Tittensor & Worm, 2016; Worm & Tittensor, 2018). 89

90

In brief, the basic assumption of metabolic theory is that temperature enhances species richness by increasing mutation rates and reducing generation times, while extinction rates are inversely related to the average density per species. In contrast to metabolic theory, neutral theory includes a spatial component and assumes that richness is determined by local abundance and random extinctions among functionally equivalent species counterbalanced by immigration from a surrounding metacommunity where speciation takes place. Functionally equivalent species are defined as species that

97	share the same probabilities of death and reproduction (see Appendix S0 in Supporting Information
98	for further information on the two models). Because natural mortality and reproductive output
99	depend on body size in fish, we follow Reuman, Gislason, Barnes, Mélin & Jennings (2014) and
100	assume that functional equivalence, primarily applies for species of similar maximum length. We
101	therefore treat each maximum species length group separately. Comparing the results from the
102	neutral and metabolic models with the two descriptive models, our aim is to elucidate the
103	mechanisms behind the richness differences we observe across fish communities in the northern
104	Atlantic.
105	
106	Methods
107	
108	Survey data
109	Average catch in number of individuals per species and haul was provided from 31 scientific bottom
110	trawl surveys. The time period from which data was obtained from each survey was selected to
111	provide temporal overlap between the surveys and as long a time period from each survey as feasible
112	to minimise the influence of random fluctuations in recruitment and population abundance. Surveys
113	with less than eight years of data were hence excluded. Although the earliest trawl hauls were taken
114	in 1977 and the most recent in 2013, the period from 2001 to 2006 was covered by all surveys.
115	Slightly more than half of the surveys took place in the period from October to March, a third in the
116	period from April to September, and the remaining surveys included hauls obtained throughout the
117	year (See Appendix S1 Table S1.1 in Supporting Information). Different bottom trawls were used in

the surveys. Cod-end mesh sizes ranged from 13 to 40 mm, horizontal trawl openings (wing spread)
from 13 to 28 m, vertical openings from 1.9 to 7 m, and towing speeds from 3 to 4.5 knots. Many of
the surveys used a stratified random sampling design to account for spatial and depth related
differences in species composition. We retained the major strata used in the surveys providing us with
richness and density data from 50 different strata. The average depth in these strata ranged from 28
to 950 m.

124

125 Environmental data

Sea surface temperature, average temperature in the upper 200 m of the water column, and near 126 127 bottom temperatures (Kelvin) were obtained from the World Ocean Atlas 2013 (Locarnini et al., 2013) 128 based on decadal average temperature at 0.25° resolution covering the period 1955-2012 for annual, boreal summer (Jul-Sep) and boreal winter (Jan-Mar). Bottom temperatures were defined as the 129 130 temperature in the layer closest to the bottom. Spatial averages were calculated for each survey stratum, and the seasonal amplitude calculated as the difference between summer and winter values. 131 Estimates of depth integrated pelagic net primary production (npp, gCm⁻²y⁻¹) based on the satellite-132 133 derived Vertically Generalised Production Model (VGPM) (Behrenfeld & Falkowski, 1977) were downloaded from www.science.oregonstate.edu/ocean.productivity at 1/12 degree monthly 134 resolution for the period 2002-2012, from which estimates of mean annual npp were derived for each 135 136 survey area. Latitude and longitude were calculated as the average of the minimum and maximum coordinates of each survey. Average depth was calculated as the midpoint of the depth range of each 137 138 stratum (see Appendix S1 Table S1.1).

140 Fish species data

Among the fish taxa recorded some individuals had not been identified to species. If possible, we 141 142 allocated these individuals to species, assuming that their relative species composition would be 143 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 144 145 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 146 intervals of equal width (from now on denoted log maximum length groups). In 1% of the species 147 148 records no maximum species length was available. These records were excluded from further 149 calculations.

150

151 To estimate absolute fish density and abundance in a given stratum or area we first calculated swept 152 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 153 154 average distance covered per haul. Swept area abundance was calculated by multiplying swept area 155 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 156 157 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 158 159 is likely to differ between areas and species and depends on a number of factors including the

160 properties of the trawl and species-dependent traits such as the size, behavior and distribution of the 161 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 162 distribution is outside the main depth range of the surveys (species mainly occurring in the infra-163 164 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) 165 166 mostly occur on either untrawlable grounds (species that are mainly found associated with reefs or in 167 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 168 169 the seabed, species found close to but not on the seabed, and midwater species with some bottom 170 contact).

171

172 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 S2 and Table S2.1 in the Supporting Information). 173 No catchability estimates could be derived for bathy-pelagic and bathy-demersal stocks, and few 174 175 estimates could be obtained for infra-littoral species, for species mainly found associated with reefs 176 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 177 178 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 179 180 species found close to the seabed the estimated catchability exceeded 1.0, probably due to their

181 response to the herding effect of the bridles, sweeps and doors of the trawl. Due to the few and low 182 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 183 group we fitted a log-linear mixed model to the estimates, using the vertical position of the species 184 185 (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 186 187 from the resulting stochastic model we generated 1000 estimates of catchability for each 188 combination of species and survey stratum (see Appendix S2). The catchabilities were used to calculate average absolute density and abundance in each survey stratum for each of the species 189 190 found in the surveys. Average absolute density and abundance were finally cumulated across species 191 within each log maximum length group and survey stratum and used as input to the models. 192

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 S3, Table S3.1 in Supporting Information).

199

200 Selection of independent variables

201 The number of species recorded in a survey stratum is likely to provide a biased estimate of species 202 richness because it depends on the number of individuals caught and identified (the species accumulation curve); the total area swept by the trawl (a measure of sampling effort); the size of the 203 204 survey stratum (because large strata may contain a larger diversity of environmental conditions and 205 habitats than small); and the mesh-size of the trawl (influencing the proportion of small individuals and species in the catch). To account for the bias we included all four variables in the GAM model. We 206 207 used the total area swept in each survey stratum rather than the total number of hauls to represent sampling effort because the average duration of the trawl hauls ranged from 15 minutes to one hour 208 209 across surveys.

210

211 According to the metabolic and neutral models, richness should depend on temperature, species size, 212 and either density or absolute abundance. Temperature may influence richness by affecting fish 213 metabolism, generation time and mutation rate, but vary seasonally depending on latitude and 214 longitude and with depth. Identifying the biologically relevant ambient temperature for a fish species 215 is therefore difficult. Average sea surface temperature may be relevant for the pelagic eggs and 216 larvae, average bottom temperature describes the average ambient temperature encountered by the 217 juveniles and adults at the depth where they are caught by the survey trawls, and average 218 temperature in the upper 200 m of the water column may represent the average temperature 219 encountered during the entire life cycle. We furthermore found more than a third of pairwise comparisons of the potential independent variables to be significantly correlated (See Appendix S1 220 221 Figure S1.2). Sea surface temperature, bottom temperature and water column temperatures were

222 highly significantly correlated with each other and with both latitude and longitude, while the 223 seasonal temperature range in the upper 200 m of the water column was significantly correlated to 224 the seasonal temperature ranges near the bottom and at the surface. Net primary production 225 decreased with latitude and increased with temperature, with both correlations highly significant. The 226 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 227 228 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 229 in large survey strata than in small. Finally, both catch in numbers, average abundance and total 230 231 swept area were significantly correlated.

232

233 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:

239

240
$$\log(\mu_{i,j}) = \alpha + s_1(temp_range_i) + s_2(temp_i) + s_3(abundance_{i,j}) + s_4(depth_i) + s_5(npp_i) + s_6(asurv_i) + s_7(lml_j) + s_8(catch_{i,j}) + s_9(aswept_i) + s_{10}(vertop_i) + s_{11,j}(mesh_i)$$

243 where α is a proportionality constant; suffix *i* and *j* signify survey stratum and maximum length group, respectively, *temp_range*; is the intra-annual temperature range in the stratum (Kelvin); 244 *temp*_i is temperature (Kelvin); *abundance*_{i,i} is the average absolute abundance of fish of maximum 245 length j in stratum i; depth_i is depth (m); npp_i is annual net primary production (gC m⁻² y⁻¹); $asurv_i$ 246 is the total stratum area (km²); lml_i is midpoint of log maximum length group (cm); $catch_{i,i}$ is the 247 248 total number of fish caught in stratum *i*, maximum length group *j* over the time period of the survey; 249 *aswept*_i is area swept by the survey trawl (km²); $mesh_i$ is mesh-size (mm); and $vertop_i$ is the vertical opening of the trawl (m). The $s_1, ..., s_{10}$ are general spline smoothers, while $s_{11,i}$ denotes that 250 for each log maximum length group, *j*, a separate spline smoother was applied to describe the effect 251 252 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, 253 254 lat_i , and longitude, lon_i , when the effect of geographic location was examined, and $abundance_{i,i}$ was changed to $density_{i,i}$ to examine which of the two would provide the best fit. 255 256 We used thin plate regression splines with a basis dimension of four as smoothers and a log link. 257 258 Latitude, longitude, sea surface temperature, bottom temperature, and temperature in the water

column were highly significantly correlated, and so were absolute abundance and density. To account
for these correlations, we analysed the effect of including these parameters 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 to identify the most parsimonious
model. Model terms were selected by backwards removal of insignificant variables, after which co-

264 variates generating an estimated concurvity larger than 0.80 were sequentially removed to reduce 265 variance inflation and avoid bias. Distributions of residuals were visually inspected for normality and plotted against each co-variate to reveal heteroscedasticity. We compared models with Poisson and 266 negative binomial error distributions, and found the two to provide an almost equally good fit to the 267 268 data based on AIC-values and comparisons of the observed and theoretically expected variance, where the importance of over-dispersion was assessed by dividing the sum of squared residuals by 269 270 the sample size minus the number of parameters estimated (Hilbe, 2011). For the negative binomial model this produced a variance ratio of 0.94, confirming the appropriateness of a negative binomial 271 272 assumption.

273

We simplified the GAM model and further reduced its AIC value by inserting the functional 274 275 relationships indicated by the significant GAM smoothers (see Figure 3). To model the effect of 276 temperature, we assumed that the relationship between species richness and temperature would follow the Arrhenius equation (Gillooly et al., 2001) and consequently used the inverse of 277 278 temperature in the model. The functional relationships included logarithmic transformations of 279 several of the other independent variables and the addition of a second-order polynomial to capture 280 the change in log species richness with log maximum length. All log transformations used natural logarithms. Using log transformations meant either that zero observations had to be excluded, or that 281 282 a small positive number had to be added to avoid having to calculate the log of zero. When zero individuals had been caught in a given stratum and log maximum length group, we therefore used the 283 284 inverse of the total area swept in the stratum to provide a tentative estimate of its maximum density

in the stratum. As evidenced by the residuals, this introduced a small bias in the fit (see Appendix S4,
Figure S4.3). Because the neutral model cannot easily be linearised, we used non-linear techniques to
estimate the parameters of the four models presented below. This also allowed us to retain the zeros
and removed the source of the bias in the GAM model.

289

290 Best descriptive model

The significant independent variables in the linearised GAM model were used to construct a 'best' 291 non-linear descriptive model of the number of species caught. The 'best' non-linear model followed 292 the simplified GAM equation and contained an Arrhenius expression where β_2 , the 'activation energy 293 294 of metabolism' (Gillooly et al., 2001), was divided by average water column temperature (Kelvin) multiplied by Boltzmanns constant, k ($8.62 \times 10^{-5} \text{ eV K}^{-1}$). It also contained the catch in numbers, the 295 296 area swept by the trawl, and a mesh-size/log maximum length interaction, total abundance, depth, annual net primary production, and a quadratic log maximum length term, $\exp(lml_i + \beta_7 lm{l_i}^2)$, to 297 298 capture the unimodal relationship between species richness and log maximum length:

299

300
$$\mu_{i,j} = \alpha * \exp\left(\frac{-\beta_2}{k * temp_i}\right) * abundance_{i,j}^{\beta_3} * depth_i^{\beta_4} * npp_i^{\beta_5} * \exp\left(lml_j + \beta_7 lml_j^2\right) * depth_i^{\beta_4} + npp_i^{\beta_5} * \exp\left(lml_j + \beta_7 lml_j^2\right) * depth_i^{\beta_4} + npp_i^{\beta_5} * \exp\left(lml_j + \beta_7 lml_j^2\right) * depth_i^{\beta_4} + npp_i^{\beta_5} * \exp\left(lml_j + \beta_7 lml_j^2\right) * depth_i^{\beta_4} + npp_i^{\beta_5} * \exp\left(lml_j + \beta_7 lml_j^2\right) * depth_i^{\beta_4} + npp_i^{\beta_5} * \exp\left(lml_j + \beta_7 lml_j^2\right) * depth_i^{\beta_5} + npp_i^{\beta_5} * \exp\left(lml_j + \beta_7 lml_j^2\right) * depth_i^{\beta_5} + npp_i^{\beta_5} * \exp\left(lml_j + \beta_7 lml_j^2\right) * depth_i^{\beta_5} + npp_i^{\beta_5} * exp\left(lml_j + \beta_7 lml_j^2\right) * depth_i^{\beta_5} + npp_i^{\beta_5} * exp\left(lml_j + \beta_7 lml_j^2\right) * depth_i^{\beta_5} + npp_i^{\beta_5} * exp\left(lml_j + \beta_7 lml_j^2\right) * depth_i^{\beta_5} + npp_i^{\beta_5} + npp_i^{\beta_5$$

 $catch_{i,j}^{\beta_{8}} * aswept_{i}^{\beta_{9}} * mesh_{i}^{\beta_{11,j}}$

302

303 where α , the proportionality constant, subsumes the combined effects of the standardisation of the 304 Arrhenius expression to a reference temperature, and other pre-factors related to abundance, depth, 305 net primary production, the maximum length term, catch in numbers, area swept and mesh-size.

307 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:

312

313
$$\mu_{i,j} = \alpha * lat_i^{\beta_0} * lon_i^{\beta_1} * depth_i^{\beta_4} * \exp(lml_j + \beta_7 lml_j^2) * catch_{i,j}^{\beta_8} * aswept_i^{\beta_9} * mesh_i^{\beta_{11,j}}$$

314

315 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 S0).

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:

323

324
$$\mu_{i,j} = \alpha * \exp\left(\frac{-\beta_2}{k * temp_i}\right) * density_{i,j}^{\beta_3} * ml_j^{\beta_6} * catch_{i,j}^{\beta_8} * aswept_i^{\beta_9} * mesh_i^{\beta_{11,j}}$$

326 where β_2 is the 'activation energy of metabolism' (Gillooly & Allen, 2007), k is Boltzmann's constant, ml_i is the median maximum length of the species in log maximum length group j, and α , the 327 proportionality constant, accounts for the combined effects of the standardisation of the Arrhenius 328 329 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. 330

331

Neutral model 332

333 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 334 drift, counterbalanced by immigration of species from a larger surrounding meta-community where 335 336 random speciation takes place (Hubbell, 2001; Rosindell, Hubbell & Etienne, 2011) (see Appendix S0).

337

Following Reuman et al. (2014), we assume that species of similar log maximum length are 338 339 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 340 species in each survey stratum and log maximum length group. We also assume that the probability 341 342 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 343 344 on the number of species caught, we add number of individuals caught, total area swept and meshsize terms to the species richness model of Reuman et al. (2014) providing the following equation: 345 346

347
$$\mu_{i,j} \approx J_{M_j} * \left(\frac{\nu_i}{1-\nu_i}\right) * \log\left[1 - \frac{\lambda_j \log(\lambda_j)}{1-\lambda_j} * \left(\frac{abundance_{i,j}}{J_{M_j} * (\nu_i/(1-\nu_i))}\right)\right] * catch_{i,j}^{\beta_8} * aswept_j^{\beta_9} * mesh_i^{\beta_{11,j}}$$

Where J_{M_j} is absolute abundance in log maximum length group j in the meta-community, 350 $abundance_{i,j}$ is the absolute abundance of group j in the local community, and v_i is the per capita 351 speciation rate in area *i*. Note also that J_{M_i} and v_i are confounded in the $J_{M_i}(v_i/(1-v_i))$ term. 352 However, as the speciation rate is likely to be very small, the term can be approximated by the 353 fundamental biodiversity number, $\theta_{i,j} = J_{M_i}v_i$ (Rosindell et al., 2011). Because fish evolution is 354 affected by temperature (Wright, Ross, Keeling, McBride & Gillman, 2011), we follow Tittensor & 355 Worm (2016) and make v_i temperature dependent by adding the Arrhenius equation. Finally, we 356 approximate the change in J_{M_i} with log maximum length by a quadratic term as found in the 'best' 357 descriptive model and thus end up with: 358

359

360
$$J_{M_j}\left(\frac{\nu_{i,j}}{1-\nu_{i,j}}\right) \approx \theta_{i,j} = \alpha * \exp\left(lml_j + \beta_7 lml_j^2\right) * \exp\left(\frac{-\beta_2}{k * temp_i}\right)$$

361

362 where α again is an overall proportionality constant. Hence

363

364
$$\mu_{i,j} = \theta_{ij} * \log\left[1 - \frac{\lambda_j \log(\lambda_j)}{1 - \lambda_j} * \frac{abundance_{i,j}}{\theta_{ij}}\right] * catch_{i,j}^{\beta_8} * aswept_j^{\beta_9} * mesh_i^{\beta_{11,j}}$$

where, $j = 1 \dots 11$, 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.

369

370 Estimating model parameters

We use the non-linear model fitting R-package TMB (Kristensen, Nielsen, Berg, Skaug & Bell, 2015) to 371 estimate the parameters of the four non-linear models. Fitting each model to the number of species 372 373 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 374 plotted them against each co-variate to reveal potential heteroscedasticity. To compare the models 375 376 we calculated AIC-values (Burnham & Anderson, 2002), R² from observed and predicted number of 377 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 378 difference in deviance between a saturated model (with one parameter for each of the 550 379 observations) and the actual model, to the difference in deviance between a saturated model and a 380 model with only one parameter (Cameron & Windmeijer, 1996). To also illustrate how much of the 381 382 overall deviance each model term explained, we consecutively replaced each of the independent 383 variables by its overall average and calculated the relative increase in the proportion of deviance 384 explained when the actual 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 385 density data by fitting them to the 1000 separate estimates of density and abundance obtained from 386

387	the mixed effects catchability model, and calculated the mean and variance of the resulting
388	parameter estimates. We plotted the proportion of the deviance explained by each of the model
389	parameters in the 1000 runs, and used these to illustrate the sensitivity of our results to the
390	uncertainty in the catchability estimates. All analyses were undertaken in R version 3.4.4.
391	
392	
393	Results
394	
395	Observed number of species and density
396	The number of observed species, log average swept area density, and log average absolute density
397	follow almost symmetrical distributions when plotted against log maximum length (Figure 2). As
398	expected, the average number of species observed increases with temperature while log average
399	swept area density and log average absolute density change little except in areas with a mean annual
400	sea temperature below 7.5°C where the densities are significantly lower in the intermediate length
401	range.
402	
403	GAM model
404	Fitting the GAM to the survey data reveals a strong and highly significant unimodal effect of log
405	maximum length on log number of species observed, a significant effect of absolute fish abundance,
406	significant non-linear positive effects of average temperature in the upper 200 m of the water column
407	and area swept, and a significant positive linear effect of net primary production. Log number of

408 species caught declines significantly with depth and, for the smaller length groups, with increasing 409 mesh-size (Figure 3). Stratum area, vertical opening, temperature range and catch in numbers were all insignificant or generated a too high concurvity. The model explains 85% of the deviance, and has a 410 411 lower AIC than model versions in which abundance is replaced by density and average temperature 412 by either sea surface temperature, bottom temperature, or latitude and longitude. Although there are survey strata that produce significant negative residuals, such as the 50-200m stratum in Guinea 413 414 which features the lowest number of hauls of all strata, there are no clear patterns in the residuals across survey strata. This suggests that the model provides an equally good description of fish species 415 416 richness in the Atlantic, Arctic and Mediterranean Seas (Figure 4). Further model diagnostics are 417 shown in Appendix S4, Figures S4.1 and S4.2).

418

Some of the smooth relationships suggested that the AIC value could be further reduced by using the 419 420 logarithm or the inverse of the independent variable, and for log maximum length, in particular, that 421 the smoother could be replaced by a second-order term, corresponding to a log-normal like 422 distribution of richness versus maximum length. Replacing the independent variables in the GAM by 423 inverse temperature, log abundance, log depth, net primary production, log area swept, an interaction between mesh-size and log maximum length, and the exponential of a second-order 424 polynomial in log maximum length, reduced the AIC-value from 2090 to 1860 and increased the 425 426 percentage of deviance explained to 91%.

427

428 Non-linear models

429 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 430 abundances we initially used variance ratio tests to determine whether the bias correcting terms 431 $(catch_{i,j}^{\beta_8}, aswept_j^{\beta_9})$ and $mesh_i^{\beta_{11,j}}$ contributed significantly to the fit. We found that 432 $catch_{i,j}^{\beta_8}$ did not improve the fit of the 'best' and neutral models significantly, improved the 433 metabolic model marginally, but contributed highly significantly to the fit of the environmental 434 model. The total area swept, $aswept_i^{\beta_9}$, contributed significantly to all models, except the 435 436 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 , 437 were not significantly different from zero; and were therefore replaced by a single overall λ for all log 438 439 maximum length groups (see Appendix S4 Table S4.1).

440

Fitting the 'best' model to the average of the absolute abundances explains 90% of the deviance 441 (Table 1). The neutral model provides the second-best fit (Δ AIC=38) followed by the metabolic model 442 (Δ AIC=40) and the environmental model (Δ AIC=46). Note that the difference between the metabolic 443 444 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 445 mesh-size, $\beta_{11,i}$, is thus negative for the smaller species in all models, implying a general decline in 446 the number of small species caught as mesh-size increases. In all models log maximum length and 447 either temperature or latitude account for most of the deviance explained (Figure 5). The parameter 448 estimates of 'best', metabolic and neutral models are robust to the uncertainty in the modelled 449

450 catchabilities as shown by the limited distribution of deviance around the mean value of the 1000 451 estimates. The standard deviations of the parameter estimates are also small (see Appendix S4 Table S4.1). Additional model diagnostics are presented in the Supplementary Information (Appendix S4 452 Figures S4.4 & S4.5). 453 454 455 456 Discussion 457 Our study reveals strong consistent patterns in the number of demersal and benthopelagic fish 458 459 species across the northern Atlantic. As in previous investigations, we find body size, depth and either 460 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 461 462 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 463 with depth and latitude. Adjusting for differences in area swept and mesh-size, the 'best' descriptive 464 465 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 466 inverse temperature, a parabolic relationship with log maximum length, area swept and mesh-size are 467 468 significant, explains 89% of the deviance, and so does the metabolic model. Our analyses furthermore show that both the neutral and metabolic models provide significantly better fits than the 469

470 environmental model in which local richness is described as a function of log maximum length, catch,
471 latitude, longitude and depth.

472

In all four non-linear models more than half of the deviance is explained by a combination of log 473 474 maximum length and either temperature or latitude (Figure 5). In the data the distribution of the number of species observed across maximum length groups is approximately lognormal (Figure 2). 475 476 Similar distributions have been obtained for marine bivalves (Roy, Jablonsky & Martien, 2000), terrestrial snakes (Boback & Guyer, 2003), and insects (Siemann, Tilman & Haarstad, 1996), while 477 more right-skewed distributions have been found for birds and mammals (Purvis, Orme & Dolphin, 478 479 2003; Smith & Lyons, 2013). A lognormal distribution also provided a highly significant fit in the best, 480 neutral and environmental models (Table 1). Contrary to this, metabolic theory predicts that species richness should scale with body mass raised to a power of 0.75, hence maximum length to a power of 481 482 2.25. This prediction was not confirmed by our analysis where the power was estimated to -1.00 (±0.48 conf. lim.) and thus highly significantly different from the expected. 483

484

The average water column temperature from 0-200 m is a better predictor of the observed number of fish species than bottom temperature, surface temperature and latitude. 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

491 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 492 metabolic and neutral models. This range is not far from the average activation energy of metabolism 493 494 of 0.65 eV predicted by metabolic theory (Gillooly & Allen, 2007; Bailly et al., 2014), and close to 495 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 496 497 metabolism of fish and temperature, and independently estimated the activation energy as 0.43 eV. 498 Barneche et al. (2014) used a model with a temperature optimum to account for metabolic 499 inactivation at high temperatures and found an activation energy of 0.59 eV. How temperature 500 influences the rates of speciation and extinction is not completely known, and other co-varying 501 factors may be involved (see e.g. Rabosky et al., 2018).

502

503 The 'best' and neutral models contain positive relationships between abundance and the number of 504 species observed. The 'best' model also includes a significant positive relationship with net primary 505 production. Areas of high productivity have been hypothesised to have higher species richness 506 because they harbor more individuals able to maintain a higher number of viable populations (Brown, 507 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 508 509 reduced by fishing, primary production may better reflect fish abundance and density in the unexploited state and hence be a better predictor of richness. Without primary production included in 510 511 the model, the three largest positive differences between the observed and predicted number of

species were generated by the data from Mauretania, which features the highest primary production, but has been subject to marked overexploitation (Meissa & Gascuel, 2014). Note however, that abundance or density never accounted for more than 10% of the total deviance in the 'best', neutral and metabolic models, explaining the robustness of these models to the uncertainty in the catchabilities (Figure 5).

517

518 Tittensor & Worm (2016) and Worm & Tittensor (2018) used a neutral model to simulate species 519 richness in the ocean and allowed speciation rate and generation time to depend on temperature. 520 Thermal effects on speciation rate generated a stable but weak latitudinal richness gradient in their 521 model, while thermal effects on generation time produced a transient latitudinal richness gradient 522 that eventually disappeared. Combining the effect of an increase in abundance caused by the increase in ocean area towards the equator and a temperature-dependent speciation rate produced the most 523 524 realistic gradient in richness. Fitting a neutral model to the survey data we found a strong effect of temperature on species richness and a weaker influence of fish abundance. Furthermore, the shelf 525 areas in the eastern Atlantic down to 200 m, the depth range where our fish species have their 526 527 maximum abundance, increases with latitude from the Equator to the Arctic (Pilson & Seitzinger, 528 1996). A consistent decline in habitat area with latitude is therefore unlikely to explain our results.

529

The parameter describing the probability of immigration in the neutral model could not be estimated
with sufficient precision. The known functional dependency between per capita immigration
probability and the speciation rate in the surrounding meta-community makes it difficult to estimate

533 both parameters simultaneously (Jabot & Chave, 2011). The immigration probability may depend on temperature and size, as assumed by Reuman et al. (2014), but the evidence for temperature related 534 535 differences in larval dispersal is lacking (Leis et al., 2013), and when immigration probability was 536 assumed to be size dependent, none of the estimates of λ_i were significant. Additional analysis of species distributions and information on the genetic divergence of subpopulations is necessary to 537 538 fully understand the relationship. The neutral model has been criticised for predicting unrealistically long species ages for common species and too short species ages for new species with few individuals 539 540 (Chisholm & O'Dwyer, 2014). Recent work has shown that more realistic species ages are generated when protracted speciation and weak selection caused by small differences in hereditary fitness are 541 incorporated in the model (Rosindell et al., 2015), but no approximate solution for the number of 542 543 species in each community is yet available for this model.

544

Despite the large sample sizes and good geographical coverage of the survey data, several problems 545 may be associated with using bottom trawl survey data to study fish species richness and density 546 patterns. The main aim of a scientific bottom trawl survey is often to provide reliable estimates of the 547 relative abundance and year-class strength of commercially important fish species, and less attention 548 549 may therefore be given to identifying species that are rare or of little or no commercial value. Trawl-550 survey catches may furthermore provide biased estimates of the actual fish species composition and 551 density due to species and size-specific differences in the probability of the individuals to be retained by the trawl (Arreguín-Sánchez, 1996). Some species and sizes are herded into the path of the trawl 552 by the action of the otter doors and trawl sweeps, others avoid the trawl by escaping under the 553

554 fishing line or over the headline, others are able to outswim the trawl, and among those entering the 555 trawl the smaller individuals and species may escape through the meshes. Factors that have been reported to influence the catch efficiency of survey trawls include time of day, light intensity, 556 557 turbidity, current strength and direction, depth, sweep length, net spread and vertical opening, trawl 558 speed, haul duration, and the size and type of the ground gear (Arreguín-Sánchez, 1996; Fraser, Greenstreet & Piet, 2007). Although we corrected our analysis for differences in species catchability, 559 560 we were unable to fully account for all of the factors that may lead to species and size specific differences in catchability. This was due to the sparsity of spatially and temporally overlapping stock 561 assessments, the absence of individual length measurements for many of the non-commercial 562 563 species, and our use of average catch rates rather than individual hauls. However, as seen in Figure 5, density or abundance only explain less than 10% of the deviance. The sensitivity of our overall 564 conclusions to the uncertainty in the catchabilities is therefore modest, and the parameter estimates 565 566 and the relative importance of the variables only change little in the different models. Finally, our use of a single estimate of maximum length for each species hides the fact that maximum body length in 567 fish is likely to vary from area to area (Rypel, 2013). However, the maximum length of a species in a 568 569 given area is difficult to estimate as it depends on local fishing mortality and sampling effort.

570

We base our analysis on the number of fish species and individuals observed over a recent period of time in different regions of the northern Atlantic, Arctic and Mediterranean Seas. It is now well documented that changes in fish distributions have occurred over the last decade or two in many regions of the North Atlantic and that these are significantly associated with changes in temperature,

575 (Perry, Low, Ellis & Reynolds, 2005; Hiddink & Ter Hofstede, 2008; Batt, Morley, Selden, Tingley & 576 Pinsky, 2017). We have fitted our models to data from a period when temperatures have been increasing, but where regulatory processes generally seem to maintain existing patterns in species 577 578 richness (Gotelli et al., 2017). Future analyses should investigate whether these patterns will persist 579 over longer time periods and how our model parameters will be modified by temperature change, for example by conducting the analyses on different time periods characterised by different mean 580 581 temperatures. Such analyses could provide insight into the relative importance of temperature having a direct effect on metabolic processes vs. its effects on other ecosystem features that affect species 582 richness. For example, Marbá, Jordà, Augustí, Girard & Duarte (2015) showed that the activation 583 584 energy for many biological responses in the Mediterranean Sea is far higher than the reported 585 activation energy for metabolism, suggesting that temperature increases are having additional ecosystem effects on biotic responses beyond their effect on metabolic processes and speciation 586 587 rates. The effects of global warming on fish communities have been predicted from stacked species distribution models (SSDMs; e.g. Jones & Cheung, 2015), but these models have so far largely ignored 588 589 the regularity in the distribution of fish species richness and abundance with log maximum length. 590 This regularity accounts for a third or more of the deviance explained by our models (Figure 5) and 591 may thus be used to improve the predictive capability of the SSDMs significantly. But while the righthand side of the richness versus log maximum length distribution, consisting of species with a 592 593 maximum length larger than app. 50 cm, has been explained by size spectrum theory (Reuman et al., 594 2014), little is known about the processes shaping the left-hand side.

595

596 Numerous hypotheses have been put forward to explain the latitudinal pattern in species richness 597 (Brown, 2014; Fine, 2015). Finding log maximum length, temperature, absolute fish abundance, depth and net primary production to explain 90% of the deviance in the distribution of demersal fish species 598 599 richness across the northern Atlantic, and both neutral and metabolic equilibrium models to explain 600 close to 89%, conveys an important message. When 89% of the deviance in the extant species richness can be explained by two competing mechanistic hypotheses, and by a model based on 601 602 latitude, longitude and depth, and when many of the independent variables are significantly 603 correlated, it seems relevant to question how much more the present patterns in species richness and 604 abundance can tell us about the underlying environmental, ecological and evolutionary processes 605 (Gotelli et al., 2009). We probably need dynamic mechanistic models with more realistic descriptions 606 of speciation, dispersal and extinction plus additional data to reveal how past changes in 607 environmental (e.g. temperature, currents, ice cover, shelf area) and biotic (e.g. primary production) 608 variables may have contributed to shaping the present distribution of species richness and the strong lognormal relationship between richness and maximum length (Fine, 2015; Descombes et al., 2018). 609 Such data should include information from paleo-geographical and climatological reconstructions of 610 611 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 612 et al., 2018). In addition to providing a baseline from which we can evaluate future change, our data 613 614 and results point to new possibilities for understanding demersal fish species biogeography in the northern Atlantic. 615

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618 References

- Alfaro, M.E., Faircloth, B.C., Harrington, R.C., Sorenson, L., Friedman, M., Thacker, ... Near, T.J., 2018.
- 620 Explosive diversification of marine fishes at the Cretaceous-Palaeogene boundary. *Nature*
- 621 *Ecology and Evolution*, 2, 688-696.
- Allen, A.P., Brown, J.H. & Gillooly, J.F., 2002. Global biodiversity, biochemical kinetics, and the
 energetic-equivalence rule. *Science*, 297, 1545-1548.
- Allen, A.P., & Gillooly, J.F., 2007. The mechanistic basis of the metabolic theory of ecology. *Oikos*,
 116, 1073-1077.
- Andersen, K.H., Berge, T., Gonçalves, R.J., Hartvig, M., Heuschele, J., Hylander, S., ... Olsson, K., 2016.
 Characteristic sizes of life in the oceans, from bacteria to whales. *Annual Review of Marine Science*, 8, 217-241.
- Arreguín-Sánchez, F., 1996. Catchability: a key parameter for fish stock assessment. *Reviews in Fish Biology and Fisheries*, 6, 221-242.
- Bailly, D., Cassemiro, F.A., Agostinho, C.S., Marques, E.E. & Agostinho, A.A., 2014. The metabolic
- theory of ecology convincingly explains the latitudinal diversity gradient of Neotropical
- 633 freshwater fish. *Ecology*, 95, 553-562.
- Barneche, D.R, Kulbicki, M., Floeter, S.R., Friedlander, A.M., Maina, J., & Allen, A.P., 2014. Scaling
- 635 metabolism from individuals to reef-fish communities at broad spatial scales. *Ecology Letters*,
- 636 **17**, 1067-1076.
- 637 Batt, R.D., Morley, J.W., Selden, R.L., Tingley, M.W. & Pinsky, M.L., 2017. Gradual changes in range
- 638 size accompany long-term trends in species richness. *Ecology Letters*, 20, pp.1148-1157.

639	Behrenfeld, M.J. & Falkowski, P.G., 1977. Photosynthetic rates derived from satellite-based
640	chlorophyll concentration. Limnology and Oceanography, 42, 1-20.

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

659	Descombes, P., Gaboriau, T., Albouy, C., Heine, C., Leprieur, F., & Pellissier, L., 2018. Linking species
660	diversification to palaeo-environmental changes: A process-based modelling approach. Global
661	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.
- 668 Fraser, H.M., Greenstreet, S.P. and Piet, G.J., 2007. Taking account of catchability in groundfish
- 669 survey trawls: implications for estimating demersal fish biomass. *ICES Journal of Marine*

670 *Science*, 64, 1800-1819.

- 671 Froese, R., & Pauly, D., (eds.), 2016. FishBase. World Wide Web electronic publication.
- 672 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.
- Gotelli, N.J., Anderson, M.J., Arita, H.T., Chao, A., Colwell, R.K., Connolly, S.R., ... Willig, M.R., 2009.
- 678 Patterns and causes of species richness: a general simulation model for macroecology. *Ecology*
- 679 *Letters,* 12, 873-886.

680	Gotelli, N. J., & Colwell, R. K., 2001. Quantifying biodiversity: procedures and pitfalls in the				
681	measurement and comparison of species richness. <i>Ecology Letters</i> , 4, 379-391.				

- 682 Gotelli, N.J., Shimadzu, H., Dornelas, M., McGill, B., Moyes, F., & Magurran, A.E., 2017. Community-
- level regulation of temporal trends in biodiversity. *Science advances*, 3, p.e1700315.
- Hiddink, J.G., & Ter Hofstede, R., 2008. Climate induced increase in species richness of marine fishes. *Global Change Biology*, 13, 453-460.
- 686 Hilbe, J.M., 2011. *Negative Binomial Regression*. 2nd ed. Cambridge University Press, 553pp.
- Hillebrand, H., 2004. Strength, slope and variability of marine latitudinal gradients. *Marine Ecology Progress Series*, 273, 251-267.
- Hubbell, S.P., 2001. *The unified neutral theory of biodiversity and biogeography*. Monographs in
 Population Biology, Vol. 32. Princeton University Press. 375pp.
- Jabot, F., & Chave, J., 2011. Analyzing tropical forest tree species abundance distributions using a
- 692 non-neutral model and through approximate Bayesian inference. *The American Naturalist*, 178,
 693 E37-E47.
- Jones, M.C., & Cheung, W.W.L., 2015. Multi-model ensemble projections of climate change effects
 on global marine biodiversity, *ICES Journal of Marine Science*, 72,741–752.
- Kristensen, K., Nielsen, A., Berg, C.W., Skaug, H., & Bell, B., 2015. TMB: automatic differentiation and
 Laplace approximation. *arXiv preprint arXiv:1509.00660*.
- Leis, J.M., Caselle, J.E., Bradbury, I.R., Kristiansen, T., Llopiz, J.K., Miller, M.J., ... Swearer, S.E., 2013.
- Does fish larval dispersal differ between high and low latitudes? *Proceedings of the Royal*
- 700 Society of London B: Biological Sciences, 280, p.20130327.

701	Locarnini, R. A., Mishonov, A. V., Antonov, J. I., Boyer, T. P., Garcia, H. E., Baranova, Seidov, D.,
702	2013. World Ocean Atlas 2013, Volume 1: Temperature. S. Levitus, Ed., A. Mishonov Technical
703	Ed.; NOAA Atlas NESDIS 73, 40pp.

- Macpherson, E., & Duarte, C. M., 1994. Patterns in species richness, size, and latitudinal range of
 East Atlantic fishes. *Ecography*, 17, 242-248.
- Marbà, N., Jordà, G., Agustí, S., Girard, C., & Duarte, C.M., 2015. Footprints of climate change on
 Mediterranean Sea biota. *Frontiers in Marine Science*, 2:56 doi: 10.3389/fmars.2015.00056.
- Meissa, B., & Gascuel, D., 2014. Overfishing of marine resources: some lessons from the assessment
 of demersal stocks off Mauritania. *ICES Journal of Marine Science*, 72, 414-427.
- 710 Mora, C., Tittensor, D.P., & Myers, R.A., 2008. The completeness of taxonomic inventories for
- 711 describing the global diversity and distribution of marine fishes. *Proceedings of the Royal*

712 Society of London B: Biological Sciences, 275, 149-155.

- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., ... Wagner, H., 2019. Vegan:
 Community Ecology Package. R package version 2.2-1.
- Perry, A.L., Low, P.J., Ellis, J.R., & Reynolds, J.D., 2005. Climate change and distribution shifts in
 marine fishes. *Science*, 308, 1912–1915.
- Pilson, M.E., & Seitzinger, S.P., 1996. Areas of shallow water in the North Atlantic. Biogeochemistry,
 35, 227-233.
- 719 Purvis, A., Orme, C.D.L., & Dolphin, K., 2003. *Why are Most Species Small-Bodied?* Macroecology:
- 720 Concepts and Consequences, pp.155–173. Oxford University Press, Oxford.

- Rabosky, D.L., Chang, J., Title, P.O., Cowman, P.F., Sallan, L., Friedman, ... Alfaro, M.E., 2018. An
- inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, 55, 392–395
- Reuman, D.C., Gislason, H., Barnes, C., Mélin, F., & Jennings, S., 2014. The marine diversity
 spectrum. *Journal of Animal Ecology*, 83, 963-979.
- Romano, C., Koot, M.B., Kogan, I., Brayard, A., Minikh, A.V., Brinkmann, W., ... Kriwet, J., 2016.
- 726 Permian–Triassic Osteichthyes (bony fishes): diversity dynamics and body size evolution.
- 727 *Biological Reviews*, 91, 106-147.
- Rosindell, J., Harmon, L.J., & Etienne, R.S., 2015. Unifying ecology and macroevolution with
 individual-based theory. *Ecology Letters*, 18, 472-482.
- Rosindell, J., Hubbell, S.P., & Etienne, R.S., 2011. The unified neutral theory of biodiversity and
 biogeography at age ten. *Trends in Ecology and Evolution*, 26, 340-348.
- Roy, K., Jablonski, D., & Martien, K.K., 2000. Invariant size-frequency distributions along a latitudinal
 gradient in marine bivalves. *Proc. Nat. Acad. Sci.*, 97, 13150–13155.
- Rypel, A.L., 2013. The cold-water connection: Bergmann's rule in North American freshwater fishes.
- 735 *The American Naturalist*, 183, 147-156.
- 736 Segura, A.M., Calliari, D., Kruk, C., Fort, H., Izaguirre, I., Saad, J.F., & Arim, M., 2015. Metabolic
- dependence of phytoplankton species richness. *Global Ecology and Biogeography*, 24, 472-482.
- Siemann, E., Tilman, D., & Haarstad, J., 1996. Insect species diversity, abundance and body size
 relationships. *Nature*, 380, 704-706.
- 740 Smith, F.A., & Lyons S.K., 2013. Animal Body Size: Linking Pattern and Process across Space, Time,
- 741 *and Taxonomic Group*. University of Chicago Press. 272pp.

742	Storch, D., Bodhalkvá, E., & Okie, J., 2018. The more-individuals hypothesis revisited: the role of
743	community abundance in species richness regulation and the productivity-diversity
744	relationship. <i>Ecology Letters</i> , 21, 920-937.
745	Tittensor, D.P., Mora, C., Jetz, W., Lotze, H. K., Ricard, D., Berghe, E. V., & Worm, B., 2010. Global
746	patterns and predictors of marine biodiversity across taxa. Nature, 466, 1098-1101.
747	Tittensor, D.P. & Worm, B., 2016. A neutral-metabolic theory of latitudinal biodiversity. Global
748	Ecology and Biogeography, 25, 630-641.
749	Walker, N. D., Maxwell, D. L., Le Quesne, W. J., & Jennings, S., 2017. Estimating efficiency of survey
750	and commercial trawl gears from comparisons of catch-ratios. ICES Journal of Marine Science,
751	74, 1448-1457.
752	Wood, S.N., 2006. Generalized additive models: an introduction with R. Boca Raton, Florida:
753	Chapman and Hall/CRC. 391pp.
754	Worm, B., & Tittensor, D.P., 2018. A Theory of Global Biodiversity. Monographs in Population
755	Biology 60. Princeton University Press, 214 pp.
756	Wright, S.D., Ross, H.A., Keeling, D.J., McBride, P., & Gillman, L.N., 2011. Thermal energy and the
757	rate of genetic evolution in marine fishes. <i>Evolutionary Ecology</i> , 25, 525-530.
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- 763 Data accessibility
- The data and R-code that support the findings of this study and were used to produce the figures and
- tables are deposited on GitHub (<u>https://github.com</u>) in the repository 'DTUAqua/biodiversity'.

Table 1. Parameter estimates from TMB-model fits using average absolute density and abundance.

769 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

771 Significant term removed from the model.

Parameter		Best descriptive model	Neutral	Metabolic	Environmental
Constant	(logα)	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	(logκ)	3.752 (0.402)***	3.058 (0.239)***	3.085 (0.247)***	3.049 (0.239)***
Proportion of de	viance				
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
ΔΑΙC			38	40	46



Longitude

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').



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780 Figure 2. Average number of species, log swept area density (No*km⁻²) and log absolute density

(No*km⁻²) (±95% conf. limits) versus maximum length (cm) in four different sea surface temperature
 intervals (°C).

Figure 3. Estimated smoothing curves from 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; color indicate geographic regions).



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Figure 5.Violin plots of the relative contribution of the parameters in each of the four models to the

total deviance explained by each model. Results from 1000 non-linear model runs with stochastic

catchabilities. Unexplained deviance: unexp. Models: a) 'best' descriptive, b) neutral, c) metabolic, d)
 environmental.