

1 **Bigger juveniles and smaller adults: changes in fish size correlate with**
2 **warming seas**

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6 **ABSTRACT**

- 7
- 8 1. Increasing sea temperatures are predicted to decrease body size of marine ectotherms
9 based on the Temperature Size Rule. This will impact fisheries yields but empirical
10 evidence of the process is still limited.
 - 11 2. We used fishery-independent bottom trawl survey data from 1970 to 2017 to examine
12 the trends of length-at-age of four commercially important demersal fish species (cod,
13 haddock, whiting and saithe) in two study areas facing increasing sea temperatures: the
14 West of Scotland and the North Sea. We then compared the trends of length-at-age with
15 annual bottom sea temperatures.
 - 16 3. The mean length-at-age of adults declined over the study period, in all species and in
17 both areas, except for cod in the West of Scotland. A common trend of decline in adult
18 length was inversely correlated with bottom sea temperatures. Correlations with
19 temperature at seven yearly time lags were significant and negative in the North Sea.
20 Correlations were only significant at lags of 1 and 2 years in the west of Scotland, where
21 sea temperature warming was twice as slow.
 - 22 4. The mean length-at-age of juveniles concurrently increased, which has not hitherto
23 been reported. This trend, shared by all species and both regions, correlated positively
24 with rising temperature, suggesting that our study species have a faster growth rate due
25 to increased temperatures.

26 5. *Synthesis and applications* We examined the body size of a range of commercially
27 exploited fish species, at different age groups, from two management regions. We found
28 that juvenile fish have been getting bigger and adults smaller in both regions. These
29 changes were correlated with rising seas temperatures, providing empirical evidence
30 that global warming is affecting the size of commercial fish species. The effects of these
31 changes on productivity of fish populations and fisheries yield now requires
32 investigation. Temperature changes should, therefore, be included into forecasts used
33 in fisheries science in order to mitigate the impact of global warming and maximize
34 sustainable yields.

35

36 **Keywords:** body size, demersal species, dynamic factor analysis, fisheries, global warming,
37 juveniles, length-at-age, rising temperatures.

38

39 INTRODUCTION

40

41 There is mounting evidence that climate change is affecting commercial fish species, as oceans
42 warm rapidly (Hoegh-Guldberg & Bruno, 2010; Field *et al.*, 2014; Chan *et al.*, 2019). Fish
43 populations are responding in numerous ways, including changes in productivity (Planque *et*
44 *al.*, 1999; Brander, 2007), shifts in distribution (Perry *et al.*, 2005; Rindorf & Lewy 2006; Nye
45 *et al.*, 2009; Baudron *et al.*, 2020), deepening of vertical distribution (Baudron *et al.*, 2019;
46 Helland *et al.*, 2007; Dulvy *et al.*, 2008), phenology (Asch, 2015; Engelhard; McQueen &
47 Marshall, 2017), and growth (Martins *et al.*, 2012; Winder & Schindler, 2004). Temperature
48 and body size are two fundamental factors which affect many biological rates and ecological
49 processes (Lindmark *et al.*, 2018). These rates are understood from the metabolic theory of
50 ecology, which predicts organisms' metabolic rate to scale with body mass and increase

51 exponentially with temperature (Gillooly *et al.*, 2001). A major concern of ocean warming is
52 the impact on the biological processes of aquatic organisms.

53 Laboratory experiments have demonstrated that ectotherms develop faster at warmer
54 temperature and reach smaller body sizes (Gardner *et al.*, 2011; van Rijn *et al.*, 2017). This
55 phenomenon has been termed the Temperature Size Rule (TSR). TSR was first observed in
56 ectotherms (Atkinson, 1995) but has since been observed in other animals, plants, protozoans
57 and bacteria (Angilletta & Dunham, 2003; Ghosh *et al.*, 2013) making it one of the most
58 taxonomically widespread “rules” in biology (Angilletta, Steury and Sears, 2004). Alongside
59 shifts in distribution and phenology, a reduction in body size has, therefore, been proposed as
60 the third universal response to global warming (Daufresne, Lengfellner & Sommer, 2009). In
61 fish, a few empirical studies have shown that increases in temperature resulted in faster growth
62 (Thresher *et al.*, 2007), but smaller adult body size (Baudron *et al.*, 2014), which is consistent
63 with the TSR.

64 The maximum body size a fish can reach (i.e., adult size), reflects the balance between
65 the supply and demand of limiting resources (DeLong, 2012). Oxygen supply can limit the
66 maximum body size of fishes (Forster, Hirst & Atkinson, 2012 ; Verberk & Bilton, 2015), and
67 warmer waters typically contain less oxygen (Breitburg *et al.*, 2018). In addition, warmer
68 waters result in higher metabolic rates and thus a higher demand for oxygen (Clarke &
69 Johnston, 1999). Oxygen uptake rate (mostly referred to as supply) largely depends on the gill
70 surface area, whereas the demand is a function of body mass. As individuals grow, the ratio of
71 gill surface area to body mass decreases. Therefore, individuals in warming waters may sooner
72 approach the size where they can no longer acquire the oxygen needed for maintaining
73 metabolic demands (Pauly, 1979), thereby resulting in a decrease in adult body size. Although
74 the physiological mechanisms driving TSR are still being debated (Audzijonyte *et al.*, 2019),

75 empirical support for the TSR occurring in aquatic organisms implies that, for many fish
76 species, warming seas may result in smaller adult body sizes.

77 Temperature changes may affect successive life stages of a fish differently. For
78 example, a slight change in the temperature experienced at the juvenile stage can have a large
79 impact on early life growth rate and subsequent growth trajectory, which can, in turn, determine
80 regional population dynamics (Houde, 2008). Likewise, the optimum temperature for growth
81 may change as individuals grow larger, and overall growth may decrease to offset the energetic
82 demand for gonadal growth and successful reproduction as fish mature (Hartman & Brandt,
83 1995). Yet, this age-specific factor has rarely been considered empirically. For instance,
84 Baudron *et al.* (2014) investigated TSR in the North Sea using asymptotic length and reported
85 a decline in adult body size resulting from warming. They did not, however, document any
86 concomitant size changes occurring at the juvenile stage. Empirical studies documenting trade-
87 offs between warming-induced size changes occurring at different life stages of commercial
88 fish species, and their consequences for fisheries, are lacking.

89 In addition to warming, other factors such as fishing can also lead to decreasing body
90 size of commercial fish species. Fishing typically removes larger individuals and truncates the
91 age and size structure of a fish population (Barnett *et al.*, 2017). This truncation could be
92 deleterious for the population and for community stability (Sugihara *et al.*, 2011). Although
93 the impact of fishing is likely to be species-specific, as opposed to temperature which is likely
94 to impact all species sharing the same habitat similarly, it is still crucial to account for it when
95 comparing size changes across species, since fished populations are generally more sensitive
96 to environmental variability than unfished populations (Hsieh *et al.*, 2006).

97 So far, most studies investigating growth using length-at-age data have used modelled
98 growth parameters (e.g. Baudron *et al.*, 2014) and focused on one life stage only (Rogers *et al.*,
99 2011) in a single region. Here we investigated the effect of temperature on fish sizes from age

100 1 (juvenile) to age 7 (adult stage) in two neighbouring regions displaying contrasting trends in
101 warming. More specifically, we tested whether a common trend in body size of adults and
102 juveniles, consistent with TSR, could be detected across commercial fish species, and whether
103 such a trend could be linked to rising sea temperatures and/or fishing mortality. To do so, we
104 analyzed fishery-independent bottom trawl survey data of length-at-age of four commercially-
105 important demersal species: cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*),
106 whiting (*Merlangius merlangus*) and saithe (*Pollachius virens*). We considered two of the
107 largest fisheries management areas of northern Europe, the West of Scotland and North Sea,
108 which have both experienced consistent warming since the 1970s (Genner, Freer and
109 Rutterford, 2017) although at different rates (Gonzalez-Pola et al., 2019). These areas are of
110 particular interest because they are heavily fished and represent major economic and social
111 issues for European fishing countries. They are, therefore, also intensively surveyed and data
112 are abundant, with a long time-series of length-at-age for all ages of the main species of interest.

113 MATERIALS AND METHODS

114

115 Our study focused on four commercially important fish species from two study areas exhibiting
116 different rates of warming: the West of Scotland (ICES Subarea VIa) and the North Sea (ICES
117 Subarea IV). Age-Length Keys (ALKs) and Catch-Per-Unit-Effort (CPUE) per 1 cm length
118 class data were obtained from International Bottom Trawl Surveys ([https://ices.dk/marine-
119 data/dataset-collections/pages/default.aspx](https://ices.dk/marine-data/dataset-collections/pages/default.aspx)) for both the West of Scotland (WC-IBTS) and the
120 North Sea (NS-IBTS) for cod, haddock, whiting and saithe. ALKs were obtained by sampling
121 fish in each 1 cm length class and estimating the age through otolith reading. ALK data ranged
122 from 1986 to 2016 for the West of Scotland and 1970 to 2017 for the North Sea. Since ALKs
123 were generated from length-stratified sampling, they did not accurately depict the length
124 distribution. To account for this, ALKs were weighted by the CPUE observed in each length

125 class (Baudron *et al.* 2014). The mean length-at-age per year was then estimated as the average
126 length for each year of each species in each study area.

127 A Dynamic Factor Analysis (DFA) was used to test for common trends in the mean
128 length of age classes one through to seven, for all species in both areas. DFA is a multivariate
129 time series analysis method for estimating underlying common patterns in a set of
130 nonstationary time series containing missing values (Zuur *et al.*, 2003). Prior to inclusion in
131 the DFA, the mean length-at-age estimates were first standardized by subtracting the mean and
132 dividing by the standard deviation. For each area, standardised mean length-at-age (\bar{l}_m) time
133 series (t) of the four species were each modelled as a combination of common trends (x), factor
134 loadings (Z) plus some offset (a) as shown below:

$$135 \quad \bar{l}_{m,s}(t) = Z_{1,s}x_{1,t} + \dots + Z_{i,s}x_{i,t} + a_s + \varepsilon_{s,t}$$

136 Where ε_t is the normally distributed error, s is the individual species considered and i is the
137 number of identified common trends in the time series. As recommended by Zuur, Ieno and
138 Smith (2007), we tested from one to two underlying common trends ($m = 1$ to 2), and four
139 different structures of the error covariance matrix: (i) same variances and no covariance
140 (“diagonal and equal”); (ii) different variance and no covariance (“diagonal and unequal”); (iii)
141 same variance and same covariance (“equalvarcov”); and (iv) different variance and covariance
142 (“unconstrained”). Various choices of the covariance matrix are possible in DFA (Liang and
143 Zeger, 1986), the adoption of the four different covariance matrix structures was to account for
144 all the possible error terms that could arise from data due to survey design (Zuur *et al.*, 2003).
145 Akaike Information Criterion (AIC) was used to compare models and identify the most
146 parsimonious, with the least number of common trends needed to describe the mean length-at-
147 age of the species considered. DFA with the lowest AIC value was considered as the optimal
148 model (Zuur *et al.*, 2003). This approach was repeated for each age class of each species in
149 both areas.

150 To assess the impact of temperature on the annual mean length-at-age variability,
151 annual in-situ mean sea bottom temperature (SBT) data from 1970 to 2018 and 1960 to 2018
152 for the West of Scotland and the North Sea respectively were obtained from ICES
153 (<https://ocean.ices.dk>). A locally weighted smoothing algorithm (LOESS) with a span of 0.2
154 was applied to the SBT time series to capture the underlying temperature trend. A linear model
155 was also fitted to the SBT time series for each area to determine the rate of change per year for
156 the SBT time series. The smoothed SBT for each area was then split into a total of 8 time-lags
157 (i.e., from lag 0 to 7), with time lag-0 representing the temperature experienced by the species
158 at age-7, and time lag-7 the temperature experienced seven years prior (at age-0). To better
159 assess how temperature impacted body size at different life stages, the predominant common
160 trend identified for each age class was then correlated with the temperature at each lag (e.g.,
161 the common trend for age class 1 was correlated with temperature at lag 0 and lag-1) in each
162 area. A significant correlation ($p \leq 0.05$) between the predominant common trend and
163 temperature would be consistent with TSR.

164 Finally, to test for the impact of fishing on mean length-at-age, fishing mortality
165 estimates were extracted from the corresponding stock assessment for each species in each
166 area. These fishing mortality estimates were obtained from 1986 to 2018 for the West of
167 Scotland and 1970 to 2018 for the North Sea (ICES, 2017b). The impact of fishing was tested
168 only for adults (ages 4 to 7) since fishing mainly targets larger individuals. Fishing impact may
169 also be lagged, so a five-year time lag was considered and the mean length-at-age of each for
170 adults for each species in each area was then correlated with the different lags of fishing
171 mortality. All statistical analyses were performed using the R software (R version 3.3.3;
172 <http://www.r-project.org/>); the MARSS package (Holmes, Ward and Wills, 2012) was used to
173 perform the DFA.

174 RESULTS

175

176 Mean length-at-age was highly variable between species and study areas but some
177 common trends could be identified (Fig. 1). In the West of Scotland, a variable but gradual
178 increase in mean length-at-age 1 and 2 was observed for all species from 1995 onward (fig. 1a-
179 d). In the North Sea, after a stable or decreasing mean length-at-age 1 and 2, a sharp increase
180 was observed for all four species in the early 1990s. Since then, the length-at-age of these
181 young age classes has remained relatively constant (Fig. 1e-h). In both areas a conspicuous
182 decrease in mean length-at-ages 5 to 7 was observed for haddock and whiting until 2010, after
183 which observed lengths began to increase (Fig. 1b, c, f, g). No clear trend in the mean length
184 of ages 4 to 7 was observed for cod in both areas. For saithe however, a decline in mean length-
185 at-ages 5 to 7 between 1990 and early 2000s was observed in the North Sea (Fig. 1h) but not
186 in the West of Scotland (Fig. 1d).

187 In both areas, DFA revealed an increasing common trend in mean length for young ages
188 (see Fig. S1a - S2b in Supporting Information), with a switch in the pattern at around age 3
189 (Fig. S3a and S3b) to a decreasing common trend at older ages (Fig. S4a – S7b). The trends for
190 juveniles (age 1-2; Fig. S1a – S2b) were consistent across species, as were those for adults (age
191 3-7; Fig. S3a – S7b). The common trends of two ages classes, age 1 as representative of
192 juveniles, and age 7 for the older adults, were selected to depict the contrasting patterns
193 between the two life stages (Fig. 2).

194 In the West of Scotland, the best DFA models (Table 1a) describing the mean length-
195 at-age 1 and 7 both had only one common trend. For age 1 classes (juveniles), the common
196 trend was found to be decreasing in the late 1980s until 1996, followed by a sharp increase
197 which reversed again from 2008 (Fig. 2a). For the adults (age-7), an increasing common trend
198 was shortly observed from the late 80s until early 90s. This was then followed by a declining

199 common trend from 1993 until about 2008 (Fig. 2b), after which it increased again. Factor
200 loadings for age 1 related positively with the increasing common trend for all species, although
201 the weak factor loading for saithe shows little support for the common trend identified (Fig.
202 2c). Likewise, the factor loadings for age 7 related positively to the declining common trend
203 except for cod, which related negatively to the identified common trend (Fig. 2d).

204 In the North Sea, for ages 1 and 7, two common trends were identified for both ages
205 (see Fig. S1a & S7a). As per Zuur, Ieno and Smith (2007), in order to identify the dominant
206 common trend for each age, we: (i) fitted a model with only one common trend; and (ii)
207 compared it to our best model with two common trends. Of the two common trends identified
208 with the best model, the one most similar to the trend obtained when forcing the model to fit
209 with only one common trend is the dominant common trend (Table 1; Fig. S1a & S7a). The
210 dominant trends for age one and seven are shown in Figure 2. A decrease in the dominant
211 common trend in mean length-at-age 1 was observed from the late 1970s until the late 1980s,
212 followed by a sharp increase from 1990 onward (Fig. 2e). For age 7, the dominant common
213 trend declined until the mid-2000s after which it started to increase (Fig. 2f). Factor loadings
214 for all four species were positively related to the dominant common trend at both age one and
215 seven (Fig. 2g-h), although the weak factor loading for cod at age 7 shows little support for the
216 common trend.

217 The warming rate of annual SBT in the West of Scotland from 1986 until 2016 was
218 $0.015 \pm 0.003^{\circ}\text{C} \cdot \text{year}^{-1}$ while in the North Sea a faster warming rate of $0.035 \pm 0.006^{\circ}\text{C} \cdot \text{year}^{-1}$
219 was recorded from 1970 until 2017. In the West of Scotland, SBT was variable from 1986 to
220 the mid 1990's, after which it rose until the mid-2000's, and then declined slightly (Fig. 2). In
221 the North Sea, a sudden rise in SBT occurred in the late 1980s after which it remained stable.

222 In both areas, the correlation of SBT with the dominant common trend for juveniles
223 was significantly positive for both time lags tested (lag 0 and 1). Conversely, in the North Sea
224 the correlations for adults were significantly negative for all lags tested (lag 0 to 7); whereas
225 those for the West of Scotland were only significant for lags 0 to 1 (Table 2). The correlation
226 between SBT and the dominant common trend was stronger in the North Sea which
227 experienced faster warming than the West of Scotland. No significant correlation between
228 fishing mortality and mean length at age 7 was observed at any of the lags tested in both the
229 West of Scotland and the North Sea.

230 DISCUSSION

231

232 Our empirical study documents, for the first time, contrasting trends in the mean length-at-age
233 of juvenile and adult fish, which both coincide with increasing sea temperatures and provide
234 additional empirical support for the Temperature Size Rule (TSR) affecting the body size of
235 commercial species in warming waters. Most importantly, we observed identical patterns in
236 both the fast warming North Sea, which is consistent with existing literature, and the slower
237 warming West of Scotland. This indicates that TSR may be occurring, and affecting
238 commercial fish sizes, even in ecosystems experiencing moderate warming.

239 The observed decline in mean length-at-age 7 was negatively correlated with increasing
240 SBT in both the West of Scotland and the North Sea, as expected under the TSR. These findings
241 are consistent with previous studies showing a decline in the average body-size of many fish
242 species and other organisms as a response to global warming (Todd *et al.*, 2008; Genner *et al.*;
243 2010; Cheung *et al.* 2013; Ohlberger, 2013, Shapiro *et al.*, 2019; van Rijn *et al.*, 2017; Heather
244 *et al.*, 2018). In the West of Scotland, the declining trend in adult size is comparable to the
245 changes documented by Hunter, Speirs and Heath, (2016). However, unlike Hunter, Speirs and
246 Heath, (2016), who did not attribute size changes to temperature, we observed significant

247 correlations between mean length-at-age 7 and in situ SBT. In fact, the common trend we
248 identified mirrored the trend in SBT: a decline in length-at-age 7 between the mid-1990 and
249 the mid-2000s as SBT increased, followed by a sudden increase from 2008 onwards as SBT
250 declined. In the North Sea, the declining trend in adult size coinciding with increasing SBT is
251 similar in nature to the declining common trend in asymptotic body size observed by Baudron
252 *et al.*, (2014), who attributed the decline in body size of six (of eight) species to rising
253 temperatures.

254 While our results for adults are consistent with the existing literature, we also identified
255 contrasting patterns between juvenile and adult life stages. In addition to the expected decrease
256 in mean length-at-age of adults, we also detected a concurrent increase in the mean length-at-
257 age of juveniles. To our knowledge, contrasting common trends in size between life stage
258 across species have not been documented before. The increase in juvenile size was detected for
259 all species in both areas with the exception of saithe in the West of Scotland. This exception
260 might be due to the poor quality of data collected for this species' juveniles age groups which
261 showed more variability than other species. The increasing common trend observed for mean
262 length-at-age 1 was positively correlated with rising SBT, suggesting a faster juvenile growth
263 rate as a result of increasing temperature. This observation is to be expected as warmer waters
264 results in faster metabolic rates and, therefore, faster growth (Audzijonyte *et al.* 2019). Our
265 findings are consistent with Rogers *et al.*, (2011) who observed in-situ that warmer springs lead
266 to larger juvenile cod sizes, although they did observe a negative impact of warmer summers
267 which suggests that growth may be reduced if warming exceeds the optimum temperature for
268 growth. The correlation was stronger in the North Sea, most likely due to the higher warming
269 rate compared to the West of Scotland. Overall, our in situ observations corroborate laboratory
270 findings showing that ectotherms reared under warm conditions grow faster and reach smaller
271 adult body sizes, as opposed to larger body sizes when reared under cold conditions (Atkinson,

272 1994; Atkinson, 1995b; Atkinson and Sibly, 1997 & Atkinson, Ciotti and Montagnes, 2003).
273 Our observations are consistent with the expectation of the TSR which predicts faster growth
274 at young ages, and, therefore, larger juvenile body sizes as reported here, but a smaller size at
275 old ages (Angilletta & Dunham 2003; Walters and Hassall, 2017; Aguilar-Alberola and
276 Mesquita-Joanes, 2014). They are also in line with common physiological knowledge of
277 increased warming on ectotherms (Lindmark *et al.*, 2018 ; Forster & Hirst, 2012).

278 The correlation between the dominant common trend in length-at-age 1 and SBT was
279 significantly positive in both the North Sea and the West of Scotland for both lags 0 and 1. This
280 suggests that juvenile (age 1) body size is positively impacted by the warming temperature
281 experienced during the first two years (age 0 and age 1) of life; not only in fast warming
282 situations, but also in areas experiencing more moderate warming. In contrast, the correlation
283 between the dominant common trend in length-at-age 7 and SBT was significantly negative for
284 lags 0 to 7 in the North Sea, but only for lags 0 and 1 in the West of Scotland. This suggests
285 that under fast warming, as observed in the North Sea, adult body size is negatively impacted
286 by the warming temperature experienced through life (age 0 though to age 7), including early
287 life stages. Baudron *et al.* (2014) reported similar findings in the North Sea where they noted a
288 negative correlation between the common trend in asymptotic body size and the temperature
289 experienced in the early years of life. However, this also suggests that under moderate
290 warming, as observed in the West of Scotland, adult body size is only negatively impacted by
291 the warming temperature experienced recently (current and previous year) and may indicate
292 that other factors impacting growth (e.g., density-dependence) prevent the effect of temperature
293 from being detected throughout life stages.

294 Out of the four species considered, the boreal species cod and haddock have a lower
295 temperature optimum compared to the temperate species saithe and the Lusitanian species
296 whiting (Kaschner *et al.* 2016). Haddock showed the greatest reduction in adult body size in

297 response to warming, a finding similar to that of Baudron *et al.* (2014). However, cod did not
298 conform to the declining common trend in mean length-at-age 7 observed for other species. In
299 the West of Scotland, the negative factor loading indicated that the trend in cod's adult size
300 was negatively related to the common trend, while in the North Sea, cod's factor loading was
301 negligible. The negative factor loading in the West of Scotland could result from poor survey
302 data quality for this age group in the study area as there is evidence for domed shaped size
303 fishing selectivity for this species (Cook, 2019) which may also occur in the survey. In the
304 North Sea a possible explanation for the low factor loading could be the high thermal range of
305 cod, usually between -1.5 and 19°C, compared to other species (Freitas *et al.*, 2016). These
306 observations are consistent with Baudron *et al.* (2014)'s findings who did not observe a decline
307 in asymptotic length for North Sea cod. However, contrary to Baudron *et al.* (2014), we did
308 find support for the TSR impacting cod body size. Although we did not observe a decline with
309 adult size, we did observe an increase in juvenile size concomitant with SBT increase,
310 supporting the common trends in mean length-at-age 1 observed in both areas. In fact, in the
311 West of Scotland cod was the most strongly related to the common trend in juvenile size.
312 Despite their higher optimum temperature, both saithe and whiting did conform to the general
313 pattern of larger juvenile sizes and smaller adult sizes. However, it is interesting to note that
314 these two species show the quickest reversal of this pattern once temperature starts to decrease,
315 as in the West of Scotland, or stabilizes, as in the North Sea, which suggests that the effect of
316 the TSR may bounce back quicker for species with a higher thermal optimum.

317 Our study provides additional empirical support suggesting that, for commercial fish
318 species in northern European waters, warming seas have altered growth trajectories, resulting
319 in faster juvenile growth but detrimental to adult body size. These opposite trends in juveniles
320 and adults appear to be consistent, as even a slower warming in the West of Scotland is
321 sufficient to induce a significant response in the different fish species. A decline in adult body

322 size could lead to lower fecundity (Heinimaa & Heinimaa, 2004) and increase predation
323 mortality. This may result in reductions in fish populations recruitment success (Rijnsdorp *et*
324 *al.*, 2009) and productivity, which could in turn lead to declines in commercial fisheries yield
325 (Cheung *et al.*, 2012; Teplitsky and Millien, 2014). Baudron *et al.* (2014), who also linked
326 warming temperatures to smaller adult body sizes, estimated TSR to result in an average 23.1%
327 loss in yield-per-recruit for North Sea commercial species. They did not, however, report the
328 larger juvenile sizes documented here which could offset some of the negative impacts of
329 smaller adult sizes. For instance, faster growing juveniles may experience a reduction in natural
330 mortality due to being larger and less susceptible to predation. Likewise, a faster growth and
331 earlier maturation may increase turn over time and productivity. Whether the impact of larger
332 juveniles sizes would compensate for the decline in adult sizes remains unclear without
333 appropriate analyses, but this is worthy of investigation to fully assess the impact of the TSR
334 on commercial fish species.

335 Although fishing mortality is often associated with declines in fish sizes, as trawling
336 usually targets medium to large individuals, in this instance we did not find any significant
337 relationships between fishing mortality and mean length-at-age of adults. As such, our findings
338 contrast with Hunter, Speirs and Heath (2016) who concluded that high fishing pressure was
339 likely responsible for the fast decline observed in the mean length at age of gadoids in the
340 historically heavily exploited Firth of Clyde, although they did not find evidence for this
341 occurring across the wider West of Scotland shelf covered in our study. Fishing mortality in
342 the West of Scotland has been strongly reduced for demersal species from the early 1990s
343 except for cod (ICES, 2017a). Under such circumstances, if fishing was driving changes in
344 adult fish sizes, one would expect an increase in size while in fact we observed a declining
345 common trend in mean length-at-age 7 throughout the 1990s.

346 Cheung, *et al.* (2013) predicted a global decline of 14 – 24% between 2000 and 2050
347 in adult size for most fish species due to warming oceans. This could jeopardise coastal nations
348 relying mainly on fishing as an affordable source of protein and means of livelihood. Projected
349 global warming of 1.1 – 6.4°C by 2100 has been predicted to result in a 10 – 75% rise in
350 ectotherms metabolic rates (Bickford *et al.*, 2010). Our study brings additional evidence that
351 increasing temperature may reduce adult body size for fish species, which may possibly
352 translate to lower fisheries yield unless organisms can compensate with more food intake which
353 might not be the case for most fish species (Jennifer & David, 2011). Most importantly, our
354 study suggests that even slow warming, as observed in the West of Scotland, is sufficient to
355 elicit a response in fish size. Therefore, it is possible that fish size could be similarly affected
356 in other marine areas of the world, even under moderate warming.

357 In their study of 235 fish populations, Free *et al.*, (2019) estimated that the maximum
358 sustainable yield decreased by 4.1% from 1930 to 2010, with five ecoregions experiencing
359 severe losses of 15 to 35%, and 19 populations responding significantly negatively to warming.
360 Warming has also been shown to reduce species abundance by negatively affecting
361 physiological processes, thus reducing growth and survival (Neuheimer *et al.*, 2011). Global
362 warming may, however, have regional variations. The slowing of the Atlantic Meridional
363 Overturning Circulation (AMOC), for example, is forecast to reduce temperatures in the sub-
364 polar gyre by 1° over the next 80 years (Caesar *et al.*, 2018). This region is adjacent to the West
365 of Scotland which may explain the weaker warming we measured in this area. This may, in the
366 long term, mitigate some of the warming impact of fish body sizes we have detected in the
367 West of Scotland.

368 In conclusion, the decline in mean length-at-age for adults and increase in mean length-
369 at-age for juveniles observed in four commercially-important demersal fish species in the West
370 of Scotland and North Sea and coinciding with increasing temperatures provide strong

371 empirical support for the TSR, and indicates that the TSR may affect commercial fish sizes and
372 fisheries yields even under moderate warming. This brings additional evidence of the impacts
373 of warming oceans on fish physiology and metabolism, although the consequences may vary
374 among regions. Given the consequences that the fishery sector would face as a result of global
375 warming, it would be worth incorporating temperature forecasts into fisheries management
376 strategy evaluations. Currently, reference points are quantified based on biological and
377 economic characteristics of the fishery with the aim to maximize yield. This can only be robust
378 if crucial environmental variables affecting fish growth rate, such as temperature, are included.
379

380 **AUTHORS CONTRIBUTIONS**

381 PGF and ARB conceived the study. IEK compiled the data used. IEK performed the analysis
382 and wrote the paper with support from ARB and AP. All authors contributed to substantial
383 revisions of the manuscript.

384

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391 **DATA AVAILABILITY STATEMENT**

392 All data used are publicly available on ([https://www.ices.dk/data/data-](https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx)
393 [portals/Pages/DATRAS.aspx](https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx)) the Database of Trawl Surveys (DATRAS) maintained and
394 managed by the International Council on the Exploration of the Seas.

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563

564

565 **Figure 1.** Variability in annual mean length-at-age 1 (lowest blue line in each panel) through
566 age 7 (uppermost red line) for West of Scotland (left column) and North Sea (right) of four
567 important commercial fish species. Grey lines show LOESS smoothers fitted through each
568 time-series at age.

569

570

571 **Figure 2.** Common trends (black) given by best DFA model (a, b, e, f) describing the variations
572 in mean length-at-age 1 (top row) and age 7 (bottom row), along with temperature (red), for
573 West of Scotland (a, b) and North Sea (e, f) species and their corresponding factor loadings
574 (panels c, d, g, h).

575

576

577 **Table 1a:** Statistics of the Dynamic Factor Analysis (DFA) models with 1 to 2 trends in the
578 West of Scotland. The model in bold was selected. Where: R is the error covariance matrix;
579 m is the number of trends detected; $\log\text{Lik}$ is the loglikelihood; ΔAIC is the change in Akaike
580 information criteria relative to the selected model; and Ak.wt and Ak.wt.cum are the Akaike
581 weight and cumulative weights respectively.

582

583

584 **Table 1b:** Statistics of the Dynamic Factor Analysis (DFA) models with 1 to 2 trends for the
585 North Sea. Table headings as per Table 1a

586

587

588 **Table 2:** Common trend correlation with sea bottom temperature (SBT, °C) at different
589 annual lags. p is the probability associated with the Pearson's correlation coefficient, with an
590 adjustment made for multiple hypotheses (Bonferroni correction). Significant values after the
591 Bonferroni correction are highlighted in bold.

592

Table 1a: Statistics of the Dynamic Factor Analysis (DFA) models with 1 to 2 trends in the West of Scotland. The model in bold was selected. Where: R is the error covariance matrix; m is the number of trends detected; logLik is the loglikelihood; Δ AIC is the change in Akaike information criteria relative to the selected model; and Ak.wt and Ak.wt.cum are the Akaike weight and cumulative weights respectively.

R	m	logLik	Δ AIC	Ak.wt	Ak.wt.cum
	Age 1				
equalvarcov	1	-102.55	0.00	0.70	0.70
diagonal and unequal	1	-101.93	3.36	0.13	0.83
unconstrained	1	-94.90	4.23	0.08	0.92
equalvarcov	2	-101.42	4.72	0.07	0.98
diagonal and unequal	2	-100.77	8.28	0.01	0.99
diagonal and equal	2	-105.20	9.91	0.00	1.00
unconstrained	2	-94.90	12.41	0.00	1.00
diagonal and equal	1	-110.96	14.59	0.00	1.00
	Age7				
diagonal and unequal	1	-128.89	0.00	0.46	0.46
unconstrained	1	-121.84	1.13	0.26	0.72
equalvarcov	1	-132.45	2.47	0.13	0.86
diagonal and equal	1	-133.71	2.73	0.12	0.98
diagonal and unequal	2	-129.12	7.82	0.01	0.98
unconstrained	2	-121.10	8.09	0.01	0.99
equalvarcov	2	-132.45	9.53	0.00	1.00
diagonal and equal	2	-133.71	9.64	0.00	1.00

Table 1b: Statistics of the Dynamic Factor Analysis (DFA) models with 1 to 2 trends for the North Sea. Table headings as per Table 1a

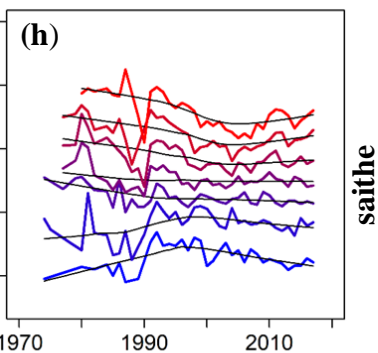
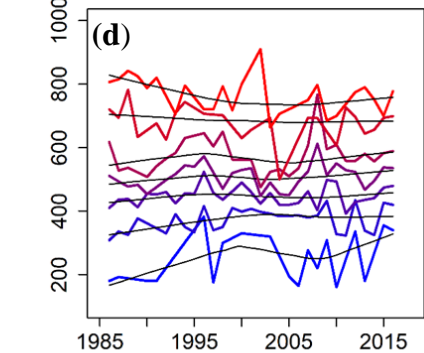
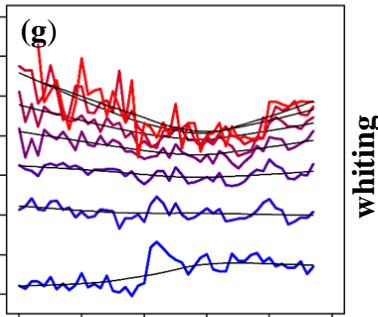
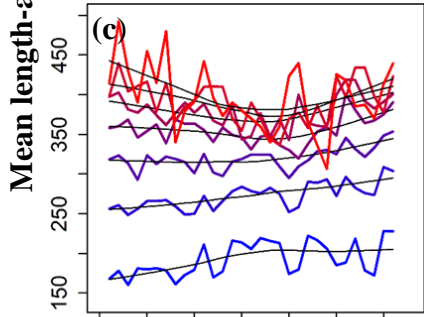
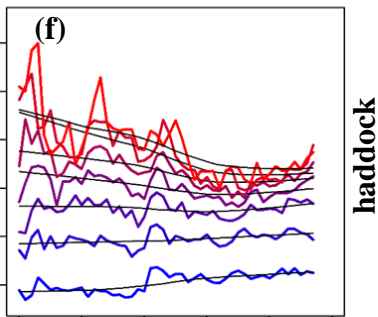
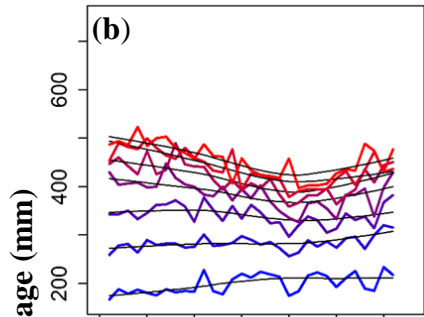
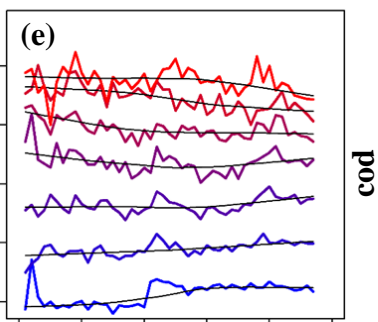
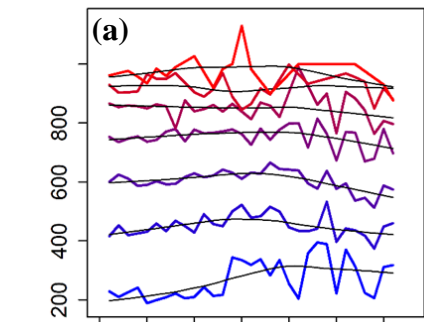
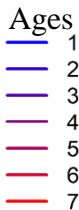
R	m	logLik	Δ AIC	Ak.wt	Ak.wt.c um
	Age 1				
diagonal and unequal	2	-158.13	0.00	0.59	0.59
unconstrained	2	-151.65	1.27	0.31	0.90
diagonal and equal	2	-163.69	4.39	0.07	0.97
equalvarcov	2	-163.59	6.40	0.02	0.99
unconstrained	1	-159.47	9.68	0.00	1.00
diagonal and unequal	1	-166.62	10.24	0.00	1.00
diagonal and equal	1	-176.15	22.81	0.00	1.00
equalvarcov	1	-176.13	24.92	0.00	1.00
	Age 7				
diagonal and unequal	2	-201.35	0.00	0.80	0.80
diagonal and unequal	1	-206.21	2.96	0.18	0.98
diagonal and equal	2	-209.01	8.56	0.01	0.99
equalvarcov	2	-208.45	9.67	0.01	0.99
unconstrained	2	-199.33	10.25	0.00	1.00
unconstrained	1	-204.19	12.69	0.00	1.00
diagonal and equal	1	-216.87	17.75	0.00	1.00
equalvarcov	1	-216.60	19.37	0.00	1.00

Table 2: Common trend correlation with sea bottom temperature (SBT, °C) at different annual lags. p is the probability associated with the Pearson's correlation coefficient, with an adjustment made for multiple hypotheses (Bonferroni correction). Significant values after the Bonferroni correction are highlighted in bold.

West of Scotland				North Sea		
Age-1				Age-1		
SBT (°C)	Correlation coefficient	p	Bonferroni correction	Correlation coefficient	p	Bonferroni correction
Lag 0	0.708	8.16E-06	1.632E-05	0.629	1.78E-06	3.56E-06
Lag 1	0.740	1.94E-06	3.88E-06	0.700	2.94E-08	5.87E-08
Age-7				Age-7		
Lag 0	-0.647	8.23E-05	0.000658	-0.667	2.25E-07	1.80E-06
Lag 1	-0.549	0.001363	0.010904	-0.707	1.98E-08	1.58E-07
Lag 2	-0.448	0.01151	0.09208	-0.743	1.50E-09	1.20E-08
Lag 3	-0.372	0.0392	0.3136	-0.753	6.87E-10	5.50E-09
Lag 4	-0.309	0.091	0.728	-0.736	2.61E-09	2.09E-09
Lag 5	-0.257	0.164	1	-0.699	3.38E-08	2.70E-07
Lag 6	-0.202	0.275	1	-0.668	2.08E-07	1.66E-06
Lag 7	-0.132	0.479	1	-0.659	3.57E-07	2.85E-06

West of Scotland

North Sea



Mean length-at-age (mm)

cod

haddock

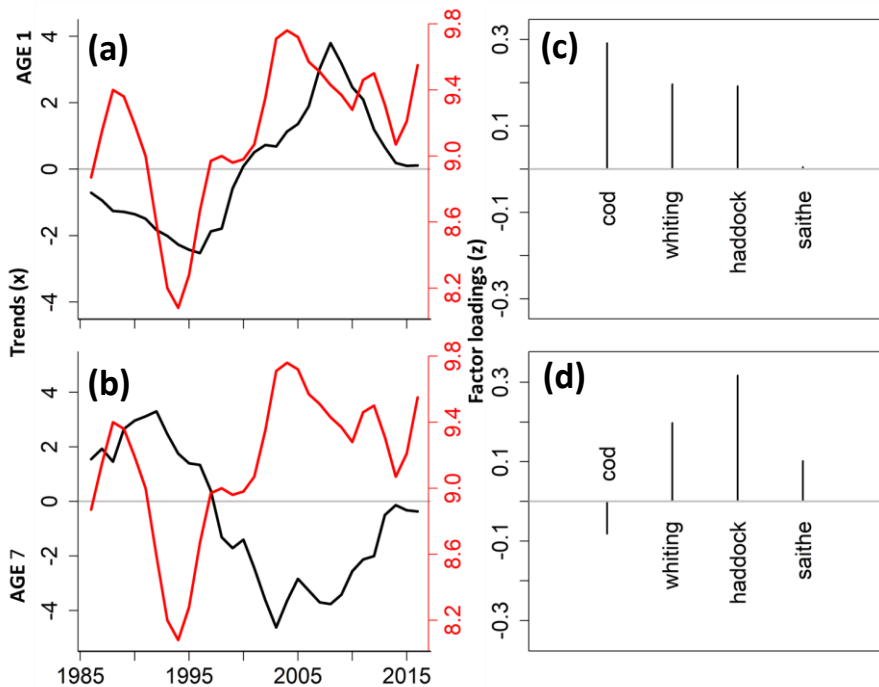
whiting

saithe

1985 1995 2005 2015

1970 1990 2010

WEST OF SCOTLAND



NORTH SEA

