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1 **Climate change drives poleward increases**
2 **and equatorward declines in marine species**

3

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14 **Summary**

15

16 Marine environments have increased in temperature by an average of 1°C since pre-industrial
17 (1850) times [1]. Given that species ranges are closely allied to physiological thermal
18 tolerances in marine organisms [2], it may therefore be expected that ocean warming would
19 lead to abundance increases at poleward side of ranges, and abundance declines towards
20 the equator [3]. Here we report a global analysis of abundance trends of 304 widely distributed
21 marine species over the last century, across a range of taxonomic groups from phytoplankton
22 to fish and marine mammals. Specifically, using a literature database we investigate the extent
23 that the direction and strength of long-term species abundance changes depend on the
24 sampled location within the latitudinal range of species. Our results show that abundance
25 increases have been most prominent where sampling has taken place at the poleward side of
26 species ranges, while abundance declines have been most prominent where sampling has
27 taken place at the equatorward side of species ranges. These data provide evidence of
28 omnipresent large-scale changes in abundance of marine species consistent with warming
29 over the last century, and suggest that adaptation has not provided a buffer against the
30 negative effects of warmer conditions at the equatorward extent of species ranges. On the
31 basis of these results we suggest that projected sea temperature increases of up to 1.5°C
32 over pre-industrial levels by 2050 [4] will continue to drive latitudinal abundance shifts in
33 marine species, including those of importance for coastal livelihoods.

34 **Results and Discussion**

35

36 Marine organisms have a temperature range outside of which physiological processes cease
37 to be optimal. As such, species distributions often correspond closely with physiological
38 temperature limits [2, 5]. Cold tolerance can determine the position of the poleward edge of a
39 species range, and consequently, ocean warming is expected to increase organismal
40 performance, survival and reproductive success at higher latitudes of species ranges. It has
41 therefore been predicted that warming seas should also drive increases in the abundance of
42 species at their poleward range side [6]. Equally, warm tolerance is strongly associated with
43 the position of the equatorward edge of marine species ranges. Hence, as oceans warm we
44 may expect to find reductions in performance, survival and recruitment at lower latitudes of
45 species ranges, leading to reductions in abundance at equatorward range limits [4].

46

47 Importantly, however, space use by marine species is not simply determined by thermal
48 affinities. Species distributions and abundances are also dependent upon availability of core
49 ecological resources such as food and substrate, which are not homogeneously distributed
50 across species ranges. Consequently, distributions of species may not be fully predicted on
51 the basis of the thermal environment and physiological tolerances alone [7]. Moreover, the
52 temporal population-abundance response of species to warming at any position in their range
53 may not exclusively depend on their thermal physiology, but also the responses of the species
54 with which they interact [8]. An additional consideration is that regional temperature shifts are
55 not the only physical changes in the marine environment associated with climate change, as
56 parallel changes to storminess [9, 10], salinity [11], acidification [12] and sea ice conditions
57 [13] have also been reported. To fully understand abundance changes of populations requires
58 a comprehensive understanding of marine environmental change, as well as the physiological,
59 life history and ecological characteristics of study species [14].

60

61 Despite the intrinsic complexities of marine biological systems, analyses from local and
62 regional datasets suggest that thermal affinities are strong predictors of the responses of
63 marine species to increasing temperatures [15, 16]. In general, studies have reported that
64 within local communities warm-adapted species have increased in abundance, relative to
65 cool-adapted species that have declined in abundance [2, 6, 15, 16]. However, such studies
66 tend to be limited to a small number of species and a single locality or region. A more complete
67 understanding of large-scale patterns of climate-associated local abundance change requires
68 combining information from multiple studies across broad taxonomic diversity, and across
69 wider spatial scales that encompass the full realised latitudinal distributions of study species
70 [17]. In the most comprehensive analyses of marine species to date, abundance responses

71 have been interpreted as being at poleward and equatorward limits [2] or “consistent” or
72 “inconsistent” with climate change [17] based on the findings of the original authors. However,
73 a fully quantitative approach is required to test the strength of evidence for species-level
74 poleward abundance increases and equatorward abundance declines within marine
75 systems over the last century. Here, we consider abundance trends of marine species over
76 the last century within an explicit latitudinal and quantitative framework.

77

78 We extracted all single-species abundance change observations from a published meta-
79 database covering literature published from 1991 to 2012 [17], and added further records
80 published from 2012 to 2016. For each record we ensured the direction of abundance change
81 during the study was recorded (either positive or negative, with respect to time or
82 temperature), and ensured each record had an accompanying survey location (Figure 1A).
83 We then identified the relative latitudinal position of the survey location within the known
84 latitudinal distribution of the species, as determined from occurrence data within the Global
85 Biodiversity Information Facility (GBIF) database [18]. In total the complete dataset included
86 540 records of abundance change, across 304 species (average 1.67 records per species;
87 range 1 to 21) ranging from phytoplankton and macroalgae, to seabirds and marine mammals
88 (Figure 1B). We then used these data to generate linear models that examined how the
89 direction of abundance change was dependent on the latitudinal position of the survey, and if
90 there were any biases in responses associated with hemisphere of study or the survey
91 methods (i.e. time-span of study, and whether the study was a continuous time series, an
92 irregularly sampled study, or a two-point comparison).

93

94 Analyses based on our complete dataset of 540 sets of records demonstrated that the location
95 of sampling within the species range was a highly significant predictor of the direction of
96 abundance change (Table S1). Specifically, marine species were significantly more likely to
97 have increased in abundance if a study had been undertaken at the poleward range side than
98 at the equatorward range side. By contrast species were significantly more likely to have
99 declined in abundance if a study had been undertaken at the equatorward side than the
100 poleward range side (Figure 2A). We found no influence of survey methods or hemisphere of
101 the study (Table S1). We repeated analyses on a subset of the dataset where the original
102 authors report a statistically significant change in abundance over the study period (185 from
103 540 records), and again we found the position in the latitudinal range of the species to be the
104 most important predictor of the direction of abundance change (Figure 2B). Next, we explored
105 the strength of abundance responses to temperature (or year) using the reported correlation
106 coefficients (r values) that were available for 77 from 540 records. Again, we found greater

107 negative responses occurring at the equatorial range margins and more positive responses at
108 the polar side of species distributions (Figure 2C).

109

110 Our study relies on published abundance trends being unbiased representations of
111 abundance changes in the natural environment. However, there is a possibility that
112 observations of significant abundance change matching expectations from climate change are
113 more likely to be selected for publication [19]. This effect is plausibly strongest in single-
114 species studies [17], which comprised 68 records in our analysis, so we repeated analyses on
115 only the 472 records from multispecies studies. Our analyses were robust with respect to
116 potential publication bias, with position of the study within the latitudinal range again the
117 strongest predictor of the direction of abundance responses in the multispecies analysis (Table
118 S1). The reported observations in our dataset are spatially clustered, with the majority of
119 observations (448 of the 540 records) from the Northern Hemisphere, and were concentrated
120 in the temperate continental shelf waters of Europe, North America and Japan (Figure 1A). To
121 investigate potential influence of spatial bias we subsampled the data to exclude records that
122 were in close spatial proximity to other records from the same species (within the same 1
123 degree latitude × longitude grid cell). The analysis of this spatially thinned dataset (478 of the
124 540 records) again resolved latitudinal position of the study within the range of the species as
125 the most reliable predictor of the direction of abundance change. Taken together these
126 analyses indicate the data are robust to publication and spatial biases, however further work
127 is required across undersampled regions and taxonomic or functional groups to fully
128 understand the global extent of the observed pattern.

129

130 Addressing taxonomic bias, we explored if survey position in the species range was a
131 consistent predictor of species responses among each of the five taxonomic or functional
132 groups that were most well represented in the dataset, namely non-larval fishes, larval bony
133 fishes, seabirds, benthic invertebrates, and zooplankton (Figure 1B). Although we found that
134 the extent of the response varied significantly among these groups (Table S2), we found a
135 consistent pattern of observed abundance increases at the poleward side of species range,
136 and decline at equatorward sides in all taxonomic groups. This pattern was statistically
137 significant in individual analyses of non-larval fishes, larval bony fishes and seabirds ($P < 0.05$,
138 Table S2), with larval bony fishes having a more pronounced positive response at the
139 poleward side of their range relative to other groups (Table S2, Figure 3). This result highlights
140 variation among marine organisms (and potentially their varied life stages) in their responses
141 to warming. Differences among taxonomic or functional groups may be expected due to
142 variation in life history traits including reproductive rates, dispersal biology, migratory

143 behaviour and growth rates [14], which in turn affect opportunities to maximise on ecological
144 opportunity.

145

146 Clearly not all species and populations followed the general pattern, and such contrasts in
147 responses to warming may be predicted in situations where thermal constraints are not
148 necessarily the primary determinant of species ranges. Such situations can arise when the
149 other physiological (e.g. oxygen availability) or ecological (e.g. food availability) constraints
150 dominate, although such constraints often covary with temperature (e.g. [20]). Equally, there
151 are situations where the latitudinal limit of a species is determined by a geographic barrier
152 such as the presence of a continental landmass, or the absence of suitable substrate to
153 colonise [21], rather than the thermal environment. Finally, the abundance of many species
154 will also have been influenced by human activities in recent history, such as habitat
155 degradation and fisheries, which may have already influenced population sizes and limited
156 capacity for rapid response to climate warming [22].

157

158 We focused on latitudinal range limits of species, making the broad assumption that latitudinal
159 gradients correspond with the thermal gradients that species occupy. However, while global
160 thermal gradients are broadly colder towards the poles, a range of factors influence local
161 temperature variation across latitude, depth and time. For example, surface ocean currents
162 and upwelling can drive variation in associations between latitude and temperature [23].
163 Equally, the pace of climate change is not homogeneous and can be inconsistent with
164 latitudinal gradients [21, 24]. Although we found an overall association between time and
165 temperature across all survey locations in this dataset, it is possible that abundance changes
166 are more likely to be detected where the pace of climate change has been most rapid [25].

167

168 A notable result of this study was that populations at both polar and equatorial range margins
169 are undergoing abundance changes. This is consistent with expectations that marine species
170 have shifted abundance in line with their full thermal tolerance limits [2], and is important
171 because it is suggestive of thermal tolerance limits of species being relatively inflexible over
172 decadal timescales. Specifically, it also indicates that populations of marine organisms at the
173 equatorial sides of species ranges are unable to adapt at a sufficiently rapid pace to enable
174 them to thrive in warmer conditions. Evolutionary adaptation to warming conditions may be
175 particularly slow for species with relatively long generation times such as the marine fishes
176 [26] which dominate our dataset, but by contrast evolutionary adaptation may be expected to
177 be more rapid in taxonomic or functional groups with fast life histories such as phytoplankton
178 [27]. It is also plausible that differential responses of marine species to warming will result in

179 abundance shift mismatches between interdependent components of marine communities, for
180 example predators and their prey [28].

181

182 We included a wide breadth of studies from across the globe, but ideally more records would
183 be available from under-represented taxonomic or functional groups, including those of
184 ecological and commercial importance. Additionally, the available data was strongly biased
185 towards temperate latitudes and further work is needed to determine whether the same
186 patterns hold for tropical species. With increased recognition of the value of long-term and
187 resurvey data, increasing numbers of datasets are becoming available through initiatives to
188 study broader patterns of biodiversity change [29, 30]. There are also efforts to bring together
189 and standardise existing datasets over space and time, to enable abundance change
190 estimates to be made across vast expanses of marine habitat [31]. Thus, it is possible that
191 future analyses will be able to evaluate temporal abundance changes across much larger
192 proportions of species ranges than are considered here, enabling a more thorough evaluation
193 of how physiological, ecological, and life history traits interact with environmental variation to
194 drive abundance changes within individual species.

195

196 In conclusion, the analyses presented here clearly demonstrate a pattern of local abundance
197 change that is widespread in marine systems, most likely due to the combination of
198 physiologically-determined thermal niches and changes in climatic variables. Thus, our study
199 builds on evidence of climate-associated local abundance changes and sits alongside climate-
200 driven changes in other biological parameters such as the overall distributions of species, and
201 shifts in the timing of life history events [2]. Average sea surface temperatures are set to rise
202 further over the course of this century [4] and the frequency of marine heatwaves is increasing
203 [32]. It therefore seems plausible that local abundance changes linked to physiological and
204 ecological tolerances will continue to take place at both the poleward and equatorward sides
205 of species ranges impacting further on local marine assemblages and the coastal industries
206 that depend on them.

207

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212

213 **Author Contributions**

214 Conceptualization, M.J.G.; Data compilation, L.A.R., J.J.F. and R.A.H.; Methodology, R.A.H.,
215 L.A.R., R.A.C and M.J.G.; Formal analysis, R.A.H., L.A.R., R.A.C and M.J.G.; Writing -

216 Original Draft, L.A.R., R.A.H. and M.J.G.; Writing - Review & Editing, L.A.R., J.J.F., R.A.C.,
217 S.D.S., M.J.G.; Funding Acquisition, M.J.G. and S.D.S.

218

219 **Declaration of Interests**

220 The authors declare no competing interests.

221

222 **Main text figure/table legends**

223

224 **Figure 1 – Spatial and taxonomic coverage of studies analysed.**

225 **A)** Global distribution of long-term abundance observations used in this analysis. **B)** Number
226 of temporal abundance records analysed in each of the nine taxonomic or functional groups
227 (total n=540). Map relief data from the ETOPO1 Global Relief Model [41]. Photos represent
228 species in the dataset undertaking responses at range margins consistent with ocean
229 warming: sea sparkle (*Noctiluca scintillans*) by M.A. Sampayo; common dolphin (*Delphinus*
230 *delphis*) original source anonymous; Australasian gannet (*Morus serrator*) by J.J. Harrison;
231 lined chiton (*Tonicella lineata*) by M. Knoth; Atlantic salmon (*Salmo salar*) by H.-P. Fjeld.
232 Photos from Wikimedia commons licensed under the Creative Commons Attribution licences
233 2.0 (chiton), 2.5 (salmon) or 3.0 (sea sparkle, dolphin, gannet).

234

235 **Figure 2. Long-term abundance changes depend on the position of sampling stations** 236 **within the latitudinal range of species.**

237 **A)** Abundance changes across all 540 records. **B)** Abundance changes recorded as significant
238 in original data sources, 185 records in total. **C)** Reported *r* values for abundance change over
239 time or temperature in original data sources, 77 records in total. The blue shaded area
240 indicates the 95% confidence interval, while vertical lines represent datapoints that reflect
241 either positive (1 in binomial model, shown as +1 on axis), or negative abundance changes (0
242 in binomial model, shown as -1 on axis). See Table S1 for full model details.

243

244 **Figure 3. Associations between relative position in latitudinal range and direction of** 245 **the abundance change within each taxonomic/functional group.**

246 Abundance changes over the study time periods for A) Fish, B) Larval bony fish, C)
247 Invertebrates (other), D) Seabirds, E) Zooplankton. These species groups represent the five
248 most well represented groups within the main dataset. The blue shaded area indicates the
249 95% confidence interval, while vertical lines represent datapoints that were either positive (1
250 in binomial model, shown as +1 on axis), or negative (0 in model, shown as -1 on axis). See
251 Table S2 for full model details.

252

253 **STAR★Methods**

254

255 **Lead Contact and Materials Availability**

256 Further information and requests for resources should be directed to and will be fulfilled by the
257 Lead Contact, Martin Genner (M.Genner@bristol.ac.uk). This study did not generate new
258 unique reagents.

259

260 **Method Details**

261 We sourced data on the abundance changes of marine species from two sources. First, we
262 used the database generated by Poloczanska, et al. [17] that covered literature published
263 between 1991 to 2012, and we extracted the records where abundance was the response
264 variable. We then checked original papers to ensure observations were from fully marine
265 species or species dependent on the ocean, and then also checked and assigned direction of
266 the abundance response over the studied time interval. Secondly, we compiled observations
267 from literature published between 2012 and 2016 using the same methodology as
268 Poloczanska et al. [17]. For both sets of records we retained only those where abundance
269 trends could clearly be attributed to individual species. Each study was defined as a
270 continuous time series, an irregularly sampled study or a two-point comparison, as determined
271 from the original paper. Studies were categorised as single-species (reporting trends for one
272 species only) or multispecies (abundance trends for multiple species reported).

273

274 We included cases where abundance changes were correlated against time and cases
275 where abundance changes were correlated against temperature. We quantified the
276 association between time and temperature at study locations using the correlation coefficient
277 (r) between year and mean annual sea surface temperature (SST). Mean annual SST was
278 obtained for each latitude and longitude cell from monthly HadISST data, across every year
279 of a study period [39]. This was performed for 139 of 157 unique locations, based on
280 availability of consistent mean annual temperature data for the full study period. Overall,
281 temperature and time were positively correlated in the locations and durations of the original
282 studies, with an average correlation coefficient $r = 0.34$.

283

284 To assign positive or negative abundance trends for species at their study location, we used
285 a three-step sequential process. First, and preferentially, where a study reported a
286 statistically-significant abundance change, we used those records. Second, where significant
287 responses were not recorded, but the direction of change was quantitatively described in the
288 text, then those records were used. Third, where no quantitative assessment was provided
289 in the text, but a visual image of the abundance data was available, we determined the trend

290 from the plotted data. In cases where abundance responses to both temperature and time
291 were recorded, only the association with temperature analysis was included in analyses.
292 Where the environmental variable reported was not explicitly temperature or time (e.g. sea
293 ice), we ensured that the environmental variable was clearly associated with temperature or
294 time by the original authors.

295

296 Occurrence data for each species were obtained from GBIF [18] via the ModestR tool [33]. A
297 taxonomy for each species, from species to class rank is required for ModestR, and this was
298 constructed using taxonomic information from the World Register of Marine Species (WoRMS)
299 [38]. Any species that had been re-classified since the publication of the paper that the
300 observation originated from were renamed in line with the accepted WoRMS taxonomy.
301 ModestR was used to collate, visualise and check species occurrences from GBIF and to
302 export the geographical coordinates associated with these records as text files (one file per
303 species). We excluded 0,0 coordinates, occurrences falling on land, and duplicate coordinates
304 to two decimal places. Where studies were conducted outside the recognised GBIF range
305 they were assigned 1 for more poleward and 0 for closer to the equator to reflect the extreme
306 range edge of the particular survey location.

307

308 Some species had occurrence records in both the northern and southern hemispheres. If the
309 original survey location for a species in the database was undertaken in the Northern
310 Hemisphere, we deleted from the dataset all coordinates from the Southern Hemisphere for
311 that species, and vice versa. Species that were the focus of studies in both hemispheres were
312 treated as two discrete entities, for example being referred to as "*Species name N*" and
313 "*Species name S*". To avoid erroneous points or outliers having an undue influence on the
314 species ranges, we removed 2% of the most extreme latitudinal records, 1% from each side
315 of the range. We then checked resultant records visually for any remaining outliers, which
316 were then deleted. To ensure latitudinal ranges were well characterised and reliable, any
317 species left with fewer than 50 observations were excluded from further analysis. After these
318 checks and deletions, we retained 540 abundance trend records from 304 species. Of these
319 540 trend records 185 were reported as significant in the original studies, and we generated
320 a subset comprising only these significant record for some analyses due to the potential for
321 non-significant trends to introduce type II errors in results.

322

323 To generate a spatially-thinned subset, we subsampled the 540 abundance trend records by
324 removing repeat data for the same species within each 1° latitude and longitude grid cell. The
325 dataset was first sorted by species and grid cell, and where two or more records of abundance
326 change were reported the longest time series was retained (if records covered the same time

327 period, we systematically removed the first record in the data list). In total 62 records were
328 removed from the full dataset to generate this spatially thinned subset of the data.

329

330 **Quantification and Statistical Analysis**

331 We calculated the relative latitudinal position of each study sampling location within the range
332 of the focal species using the formula:

333

$$334 \quad \text{Sampling position} \in \text{species range} = \frac{\text{study latitude} - \text{equatorward extreme}}{\text{poleward extreme} - \text{equatorward extreme}}$$

335

336 Where equatorward and poleward extremes were identified from the cleaned GBIF records,
337 we modelled the association between the direction of the abundance change and predictor
338 variables using Generalized Linear Mixed-Effects Model (GLMER-Model 1) with a binomial
339 response with a link logit using the lme4 package in R 3.6.0 [34, 40]. We used these models
340 to analyse several data subsets including: the full dataset, only records with significant trends,
341 only multispecies studies and spatially thinned data. In these models fixed effects included:
342 sampling position in species range, study hemisphere, study timespan, and study type
343 (continuous time series, irregular or two-point). Random effects included: taxonomic group
344 (fishes, benthic invertebrates, larval fishes, macroalgae, mammals/reptiles, phytoplankton,
345 seabirds, seagrass, zooplankton) and study (as multiple observations were typically reported
346 in individual studies). Generalised linear models (GLM-Model 2) were subsequently used to
347 generate simpler models with sampling position in species range as the sole predictor variable.

348

349 We modelled the association between reported r -values (including square-root transformed r^2
350 values) and the same set of predictor variables reported above using linear mixed-effects
351 models (Model 3). We then used linear models (Model 4) with sampling position in species
352 range as the sole predictor variable. The lmerTest package was used to extract output from
353 mixed models. Model outputs were plotted using the effects package [36] (Fig. 2). R^2 values
354 were obtained using the r2glmm package [35].

355

356 **Data and Code Availability**

357 *All datasets and code are available at <https://doi.org/10.6084/m9.figshare.11848152>*

358

359 **References**

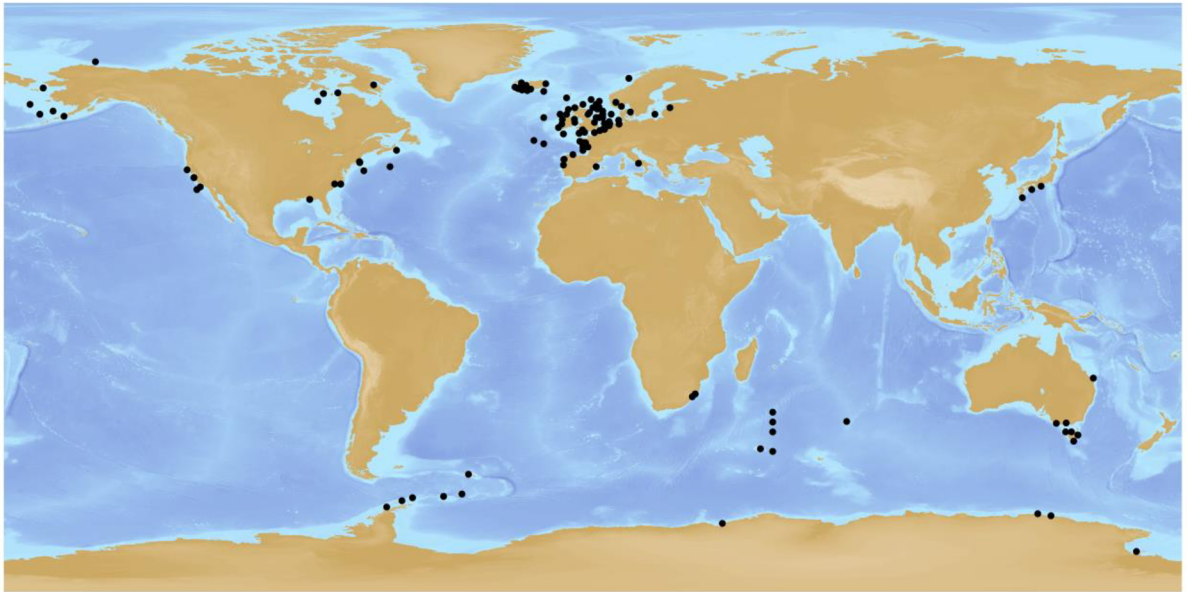
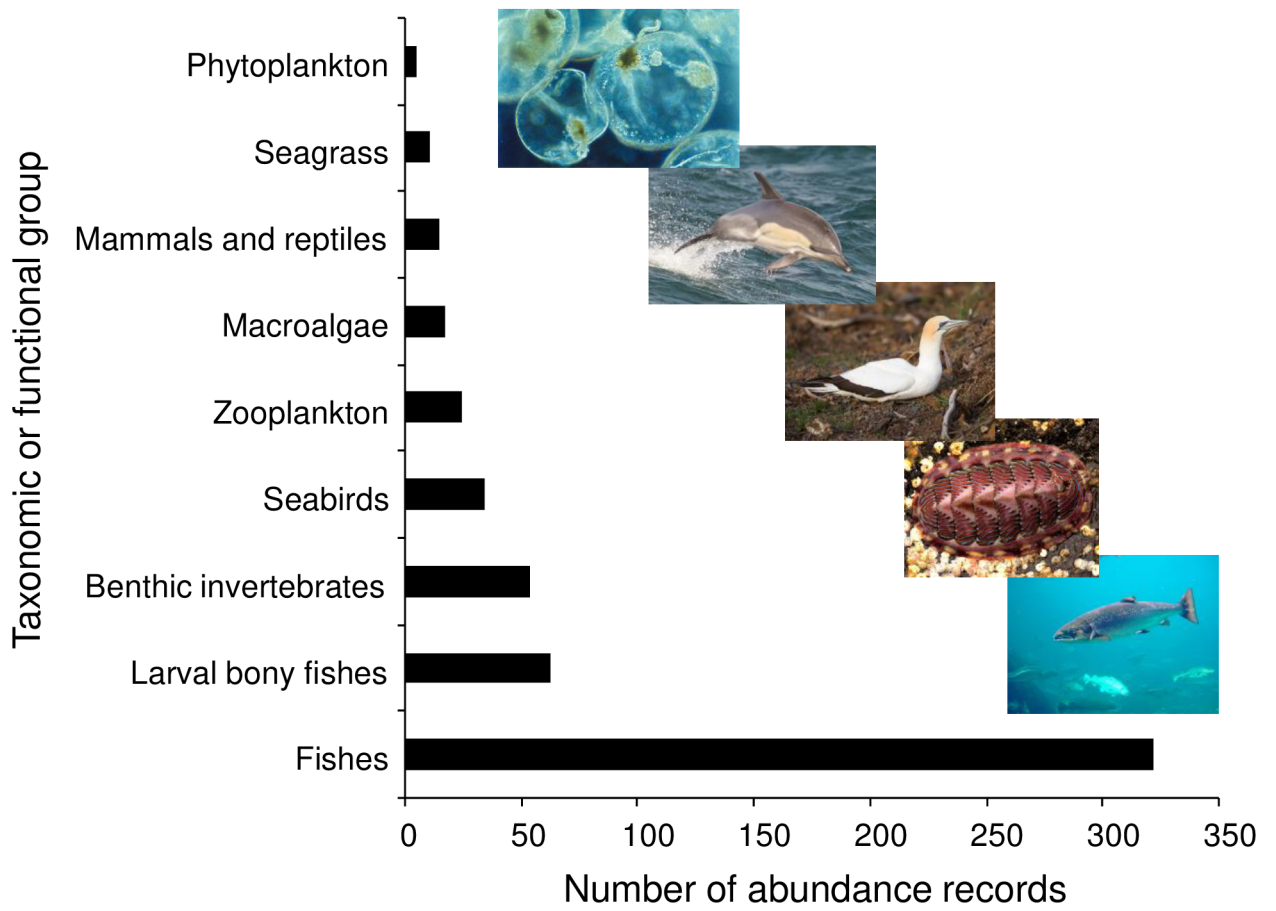
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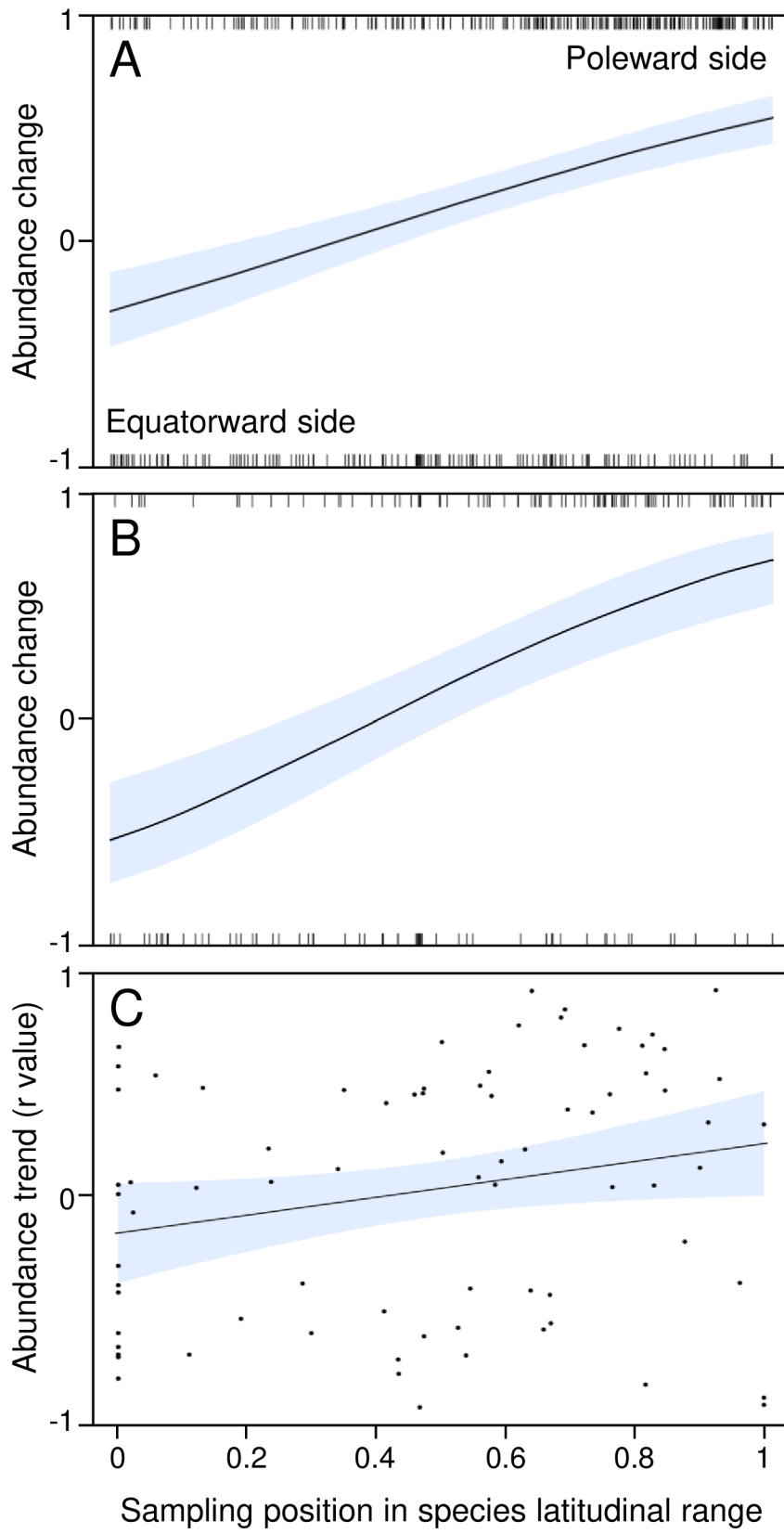
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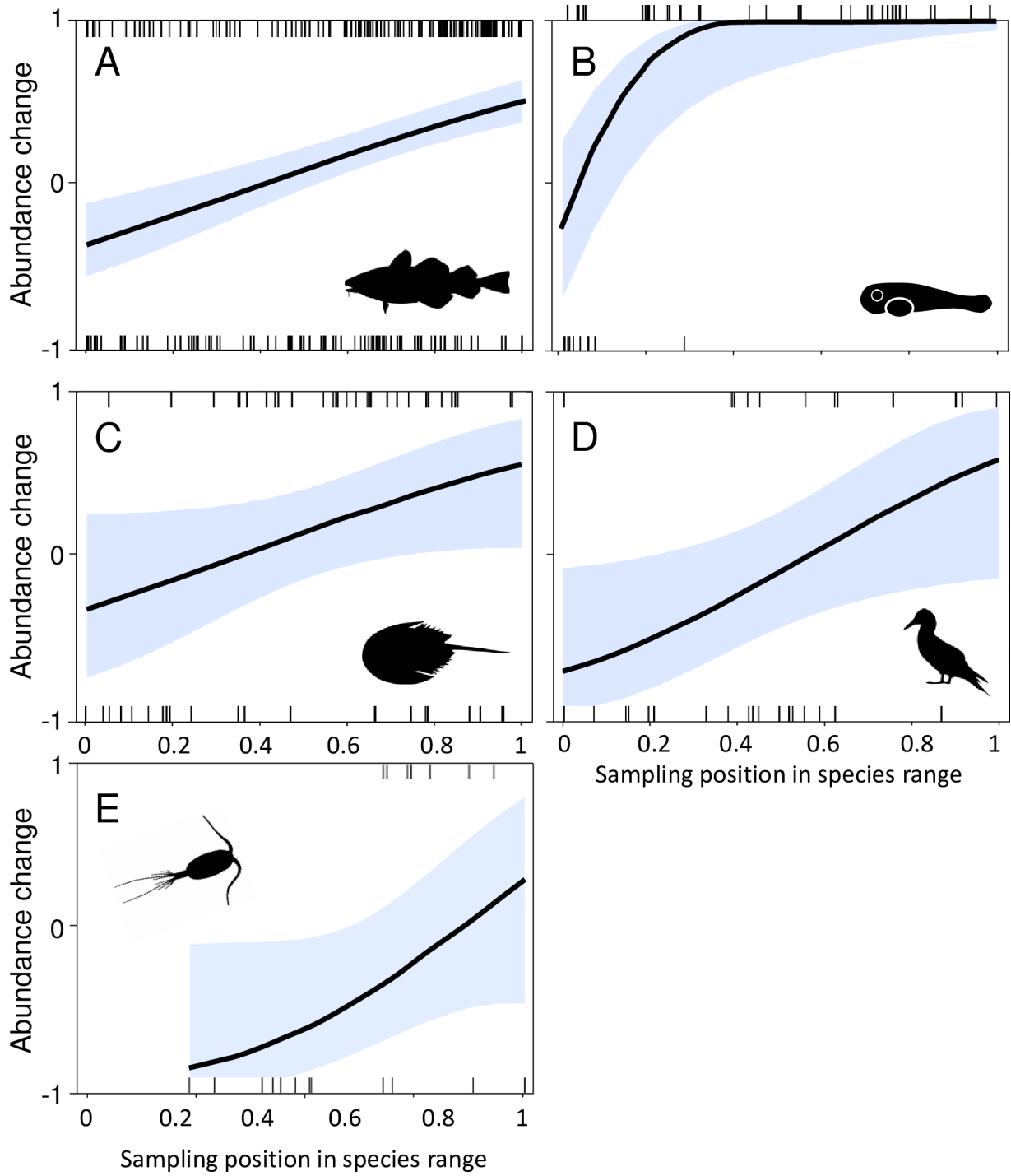
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A**B**





Key Resources Table

RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Data analysed and analysis code	This paper	https://doi.org/10.6084/m9.figshare.11848152
Software and Algorithms		
R	R Core team	https://www.r-project.org/
ModestR	[33]	http://www.ipez.es/ModestR/
lme4 package	[34]	https://github.com/lme4/lme4/
r2glmm package	[35]	https://www.rdocumentation.org/packages/r2glmm
effects package	[36]	https://www.rdocumentation.org/packages/effects/versions/4.1-3/topics/effects-package
lmerTest package	[37]	https://www.rdocumentation.org/packages/lmerTest/versions/3.1-1
glm	R Core team	https://www.r-project.org/
Other		
Referenced dataset	[17]	doi.org/10.1038/nclimate1958
GBIF	[18]	https://www.gbif.org/
WoRMS	[38]	http://marinespecies.org/
HADISST	[39]	www.metoffice.gov.uk/hadobs/hadisst/

Full dataset analysis

	Estimate	Std. Error	z value	P	r ²
Model 1: glmer(AbundanceChange ~ Position + (1 taxa_gp) + Timespan + Sampling + Hemisphere + (1 DOI_Record), family=binomial("logit"))					
(Intercept)	-1.169	0.638	-1.833	0.067	-
Position (in species range)	2.665	0.406	6.57	<0.001	0.088
Timespan (of study)	0.002	0.007	0.347	0.728	0.000
Sampling (type timeseries)	-0.261	0.416	-0.626	0.532	0.001
Sampling (type twopoint)	-1.717	1.121	-1.531	0.126	0.004
Hemisphere	0.59	0.512	1.151	0.250	0.006
Model 2: glm(AbundanceChange ~ Position, family=binomial("logit"))					
(Intercept)	-0.6381	0.1865	-3.421	0.001	-
Position (in species range)	1.8748	0.2858	6.561	<0.001	0.075

Records with statistically significant abundance shifts only

	Estimate	Std. Error	z value	P	r ²
Model 1: glmer(AbundanceChange ~ Position + (1 taxa_gp) + Timespan + Sampling + Hemisphere + (1 DOI_Record), family=binomial("logit"))					
(Intercept)	-1.99735	1.190	-1.678	0.093	-
Position (in species range)	3.70236	0.713	5.194	<0.001	0.153
Timespan (of study)	0.01215	0.017	0.735	0.462	0.004
Sampling (type timeseries)	-0.30405	0.804	-0.378	0.705	0.002
Sampling (type twopoint)	-1.86467	1.424	-1.31	0.190	0.012
Hemisphere	0.50667	0.998	0.508	0.612	0.003
Model 2: glm(AbundanceChange ~ Position, family=binomial("logit"), data=dat)					
(Intercept)	-1.1933	0.3193	-3.738	0.000	-
Position (in species range)	2.9493	0.5479	5.383	0.000	0.14

Multispecies studies only

	Estimate	Std. Error	z value	P	r ²
Model 1: glmer(AbundanceChange ~ Position + (1 taxa_gp) + Timespan + Sampling + Hemisphere + (1 DOI_Record), family=binomial("logit"))					
(Intercept)	-1.101763	0.751	-1.467	0.143	-
Position (in species range)	2.513356	0.420	5.988	<0.001	0.087
Timespan (of study)	0.001139	0.008	0.142	0.887	0.000
Sampling (type timeseries)	-0.094943	0.471	-0.202	0.840	0.000
Sampling (type twopoint)	-1.863263	1.120	-1.663	0.096	0.006
Hemisphere	0.759877	0.580	1.31	0.190	0.010
Model 2: glm(AbundanceChange ~ Position, family=binomial("logit"))					
(Intercept)	-0.4646	0.1965	-2.365	0.018	-
Position (in species range)	1.727	0.2985	5.785	0.000	0.650

Spatially-thinned records

	Estimate	Std. Error	z value	P	r ²
Model 1: glmer(AbundanceChange ~ Position + (1 taxa_gp) + Timespan + Sampling + Hemisphere + (1 DOI_Record), family=binomial("logit"))					
(Intercept)	-1.173461	0.63802	-1.839	6.59E-02	-
Position (in species range)	2.661017	0.405128	6.568	5.09E-11	0.960
Timespan (of study)	0.002592	0.007177	0.361	0.718	0.001
Sampling (type timeseries)	-0.252619	0.41595	-0.607	0.5436	0.001
Sampling (type twopoint)	-1.720151	1.120568	-1.535	0.1248	0.011
Hemisphere	0.585845	0.511921	1.144	0.2525	0.007

Model 2: glm(AbundanceChange ~ Position, family=binomial("logit"))

(Intercept)	-0.6824	0.2033	-3.357	0.001	-
Position (in species range)	1.8748	0.2858	6.561	<0.001	0.075

Records with r values reported

	Estimate	Std. Error	df	t	P	r ²
Model 3: lmer(r ~ Position + (1 taxa_gp) + Timespan + Sampling + Hemisphere + (1 DOI_Record))						
(Intercept)	-0.111502	0.588	18.397889	-0.190	0.852	-
Position (in species range)	0.437045	0.156	61.224134	2.808	0.007	0.062
Timespan (of study)	-0.002105	0.006	21.001368	-0.336	0.740	0.002
Sampling (type timeseries)	-0.168088	0.414	18.68575	-0.406	0.689	0.003
Sampling (type twopoint)	-0.11274	0.650	13.713493	-0.174	0.865	0.001
Position (in species range)	-0.414449	0.607	17.763703	-0.682	0.504	0.008

	Estimate	Std. Error	t	P	r ²
Model 4: lm(r ~ Position)					
(Intercept)	-0.1526	0.1039	-1.468	0.146	-
Position (in species range)	0.3738	0.1795	2.083	0.041	0.055

Table S1: Summary of model fixed effects, related to Figure 2.

Generalized Linear Mixed-Effects Model (Model 1) for association between the response variable (direction of the abundance change) and predictor variables and generalised linear model results for the reduced model (Model 2). A linear mixed-effect model was used for r value analysis as the values were continuous (Model 3) and a linear model for the reduced model (Model 4).

Position*Group

	Estimate	Std. Error	z value	P	r ²
AbundanceChangeN ~ Position* taxa_gp, family=binomial("logit")					
(Intercept)	-0.73505	0.26062	-2.82	0.0048	-
Position (in species range)	1.88364	0.36516	5.158	2.49E-07	0.013
taxa_gp Invertebrates	0.07137	0.66351	0.108	0.9143	0.000
taxa_gp Larval fish	0.0791	0.65053	0.122	0.9032	0.007
taxa_gp Seabirds	-0.96201	0.83925	-1.146	0.2517	0.000
taxa_gp Zooplankton	-2.52858	1.6025	-1.578	0.1146	0.010
Position * taxa_gp Invertebrates	0.04586	1.11113	0.041	0.9671	0.000
Position * taxa_gp Larval fish	11.13908	4.94277	2.254	0.0242	0.221
Position * taxa_gp Seabirds	1.16963	1.48568	0.787	0.4311	0.000
Position * taxa_gp Zooplankton	1.98631	2.19916	0.903	0.3664	0.005

Group-specific models

glm(Abundance Change~ Position, family = binomial("logit"))

	Estimate	Std. Error	z value	P	r ²
Zooplankton					
(Intercept)	-3.264	1.581	-2.064	0.039	-
Position (in species range)	3.870	2.169	1.785	0.074	0.316
Seabirds					
(Intercept)	-1.697	0.798	-2.127	0.033	-
Position (in species range)	3.053	1.440	2.120	0.034	0.118
Benthic Invertebrates					
(Intercept)	-0.664	0.610	-1.088	0.277	-
Position (in species range)	1.930	1.049	1.839	0.066	0.052
Fish					
(Intercept)	-0.735	0.261	-2.820	0.005	-
Position (in species range)	1.884	0.365	5.158	<0.001	0.079
Larval bony fish					
(Intercept)	-0.656	0.596	-1.100	0.271	-
Position (in species range)	13.023	4.931	2.641	0.008	0.335

Table S2. Summary of model fixed effects, related to Figure 3.

Generalized linear models for testing for dependence of the response variable (direction of the abundance change) on both the position in range and taxonomic/functional group. The analysis included only the five most well represented groups within the main dataset.