

1 Title: Ecological and methodological drivers of species' distribution and phenology responses
2 to climate change

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4 Running head: Species' responses to climate change

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44 **Abstract**

45 Climate change is shifting species' distribution and phenology. Ecological traits, such as
46 mobility or reproductive mode, explain variation in observed rates of shift for some taxa.
47 However, estimates of relationships between traits and climate responses could be influenced
48 by how responses are measured. We compiled a global dataset of 651 published marine
49 species' responses to climate change, from 47 papers on distribution shifts and 32 papers on
50 phenology change. We assessed the relative importance of two classes of predictors of the
51 rate of change, ecological traits of the responding taxa and methodological approaches for
52 quantifying biological responses. Methodological differences explained 22% of the variation
53 in range shifts, more than the 7.8% of the variation explained by ecological traits. For
54 phenology change, methodological approaches accounted for 4% of the variation in
55 measurements, whereas 8% of the variation was explained by ecological traits. Our ability to
56 predict responses from traits was hindered by poor representation of species from the tropics,
57 where temperature isotherms are moving most rapidly. Thus, the mean rate of distribution
58 change may be underestimated by this and other global syntheses. Our analyses indicate that
59 methodological approaches should be explicitly considered when designing, analysing and
60 comparing results among studies. To improve climate impact studies, we recommend that: (1)
61 re-analyses of existing time-series state how the existing datasets may limit the inferences
62 about possible climate responses; (2) qualitative comparisons of species' responses across
63 different studies be limited to studies with similar methodological approaches; (3) meta-
64 analyses of climate responses include methodological attributes as covariates and; (4) that
65 new time series be designed to include detection of early warnings of change or ecologically
66 relevant change. Greater consideration of methodological attributes will improve the accuracy
67 of analyses that seek to quantify the role of climate change in species' distribution and
68 phenology changes.

69 **Introduction**

70 A large number of marine (Poloczanska *et al.*, 2013) and terrestrial (Parmesan & Yohe,
71 2003) species have shifted their distributions and phenology in recent decades, indicating that
72 climate change is driving a global biological response. For example, recent climate change
73 has driven the invasion of pest species (Ling *et al.*, 2008), contributed to declines in
74 commercially important fish species (Beaugrand & Kirby, 2010) and appears to be increasing
75 mismatch in the seasonal timing between predators and their prey (Edwards & Richardson,
76 2004, Barbraud & Weimerskirch, 2006).

77 Despite an overall broad consistency in species' responses to climate change, there is
78 considerable variability in magnitudes and patterns of responses (Parmesan, 2007,
79 Poloczanska *et al.*, 2013, Sunday *et al.*, 2015). Variability poses a challenge to ecological
80 science and management of species impacted by climate change, because it hinders
81 predictions of future responses. Analyses across many species have examined how
82 combinations of taxonomic identity, ecological traits and local environmental variables may
83 explain variability in responses (Perry *et al.*, 2005, Wolkovich *et al.*, 2012, Pinsky *et al.*,
84 2013, Poloczanska *et al.*, 2013, Sunday *et al.*, 2015). All of these approaches base their
85 inferences on standardised measures of distribution and phenology, yet observed responses to
86 climate change may also depend on how distribution and phenology are measured
87 (Wolkovich *et al.*, 2012).

88 Measurements of distribution and phenology are influenced by a suite of decisions that are
89 made in two stages of all studies: their sampling design and data analysis (Brown *et al.*, 2011,
90 Bates *et al.*, 2014a). In the sampling design phase researchers decide how species' variables
91 are measured. For example, distribution can be measured as mean latitude of a populations'
92 geographic extent (e.g. Perry *et al.*, 2005) or by measuring the most extreme latitudes where
93 a species is found (e.g. Robinson *et al.*, 2015). Similarly, the phenology of breeding events

94 can be measured by censusing a population throughout a season to determine the peak
95 breeding date, or as the first and last individuals to breed (e.g. Fitter & Fitter, 2002, Barbraud
96 & Weimerskirch, 2006). Measures of distribution and phenology based on the most extreme
97 individuals rather than variables that represent the distribution of individuals within a
98 population may lead to very different estimates of climate change response rates. For
99 example, single individuals may by chance have extreme responses (Brown *et al.*, 2011) and
100 measurements using single individuals are susceptible to detection biases (Cook *et al.*, 2012,
101 Bates *et al.*, 2015).

102 In the analysis phase, most marine climate change studies include only a single predictor –
103 temperature – to explain changes in distribution or phenology, and thus do not explicitly
104 consider other drivers of change (Brown *et al.*, 2011). It is unknown whether studies that do
105 not account for other potential anthropogenic drivers, such as fishing, eutrophication and
106 habitat loss, could lead to higher estimates of impacts of climate change. For example, an
107 investigation of changes in the distribution of North Sea cod showed fishing pressure explains
108 part of the observed biological changes (Engelhard *et al.*, 2014).

109 A greater understanding of how different methodological approaches affect detection of
110 observed responses to climate change will benefit climate change ecology in four main ways.
111 First, studies that analyse existing data sets to test for climate impacts, need to account for
112 historical choices made about field data collection that could limit the ability to detect
113 species' responses to climate change. For instance, uneven sampling effort along coasts
114 means museum records of species occurrences may misrepresent historical range boundaries
115 (Shoo *et al.*, 2006, Przeslawski *et al.*, 2012). Second, many regional studies compare rates of
116 change with other studies in their discussions of how ecological traits influence a species'
117 response (e.g. Richardson, 2008). Comparisons of change may also need to consider
118 differences in methodological approaches across studies, such as how occurrence data are

119 used to estimate ranges. Third, new time-series are being initiated with the aim of measuring
120 future distribution and phenology change (e.g. Robinson *et al.*, 2015). Greater understanding
121 of how different methodological approaches can affect measured responses to climate change
122 could assist the design of new time-series. For instance, inconsistent sampling effort through
123 time may bias measured rates of change (Bates *et al.*, 2015). Finally, meta-analyses of
124 existing studies will produce more accurate estimates if they standardise for study differences,
125 or constrain comparisons to be among studies with similar methods (Parmesan, 2007,
126 Przeslawski *et al.*, 2012). For instance, differences in rates of range shifts among European
127 butterflies, birds and plants could be a consequence of taxonomic identity, geographic biases
128 or differences in the metrics used (Parmesan and Yohe 2003).

129 Here we examine potential causes of variability in observed marine species distribution and
130 phenology responses to climate change using a meta-analysis. First, we ask whether
131 measurements of distribution and phenology change from the peer-reviewed literature are
132 representative of different taxa, oceans and methodological approaches. Then we conduct a
133 meta-analysis on rates of response, to ask how ecological traits, study design and
134 measurement approaches influence rates of distribution and phenology change. This enables
135 us to ask how study measurement approaches may bias measured rates of change and affect
136 inferences about the biological drivers of change. Finally, we investigate how different
137 measurement approaches are used for different taxa and discuss the implications of
138 measurement biases on the global understanding on climate change responses.

139 **Methods**

140 *Database*

141 We analysed the database of peer-reviewed studies of observed impacts of climate change on
142 marine organisms compiled by Poloczanska *et al.* (2013). We used a subset of 61 studies
143 where rates of range change in phenology or distribution were reported or could be calculated,

144 and updated the database with a further 18 studies published in 2011-2014, for a total of 79
145 studies (Supplemental online tables). In the original database and the update, we made every
146 effort to include every dataset and study that met our criteria; thus we believe this to be a
147 comprehensive dataset rather than a small subset of available data.

148 Three criteria were applied for inclusion of peer-reviewed studies in the database: (1) Authors
149 must have inferred or directly tested for trends in marine ecological and climate variables
150 from field observations; (2) observations spanned at least 19 years; and (3) studies included
151 data after 1990. Studies relying purely on modelling or experimental data were excluded.
152 Data spanning at least twenty years is a common cut-off used in syntheses of climate change
153 impacts (Rosenzweig *et al.*, 2008). This length of time gives confidence that biological
154 changes might be driven by long-term climate change rather than yearly climate variability.
155 We chose to use nineteen years as the minimum time span, since several large studies had
156 durations of 19 years. Requiring studies to also have data after 1990 ensures that there are
157 observations in recent decades when the anthropogenic climate signal has been strongest.

158 Inclusion of all peer-reviewed studies resulted in some pseudo-replication of observations. In
159 some cases, multiple studies analysed the same raw dataset, and in other cases multiple
160 metrics of change were reported for a single species in a region. In such cases, only the most
161 recent study for a given data-set was included in the main database. Non-independent
162 observations were removed from the database, using a decision tree based on data and
163 analysis quality (Poloczanska *et al.*, 2013). Following this process 47 distribution studies with
164 485 observations of change and 32 phenology studies with 156 observations of change
165 remained and were included in our analyses.

166 *Analysis of rates of change*

167 First, we summarize measurements of distribution and phenology change by methodological
168 attributes, taxon, latitude, and for phenology, season. We then conducted analyses to examine

169 how rates of change were influenced by ecological traits and methodological approaches.
170 Rates of change, in kilometres per decade or days per decade, were obtained from individual
171 studies in the database, either directly as reported in the text, calculated from figures, or by
172 contacting the study's authors. Distribution changes were recorded as positive where they
173 were consistent with a response to climate change (generally polewards, but see Burrows *et*
174 *al.*, 2011) and negative if they were not consistent with climate change. Phenology changes
175 were recorded as negative for shifts to earlier dates and positive for shifts to later dates.

176 We related rates of change to a suite of predictors using a generalised linear modelling
177 approach. The response variables were the rate of change in either distribution or phenology.
178 Predictors were divided into two categories: methodological approaches and ecological traits.
179 For methodological attributes we considered the frequency of sampling (continuous, irregular
180 or comparison of two periods). Fewer sampling points for studies that compare two periods of
181 time (e.g. repeating a historical survey), may mean less accurate (either higher or lower) rates
182 of change, because intervening fluctuations are ignored. We considered the number of species
183 in a study; studies reporting on more species were expected to have lower rates of change
184 because they are less likely to be influenced as strongly by publication bias (Parmesan, 2007).
185 We also considered whether non-climatic drivers of change were accounted for in the study.
186 We expect slower rates of change in studies with non-climatic drivers because confounding
187 influences on the response could explain some of the observed variation. For distribution, we
188 considered whether rates were generated from abundance (or relative abundance) metrics or
189 from presence data on species occurrence at sites. Occurrence-based data were expected to
190 have higher rates of change because they are more susceptible to the outlying influences of a
191 single individual. Similarly for phenology, we considered whether the magnitude of change in
192 timing was related to whether the measure was an abundance metric, or the timing of the most
193 extreme individual (e.g. first or last arrival – the temporal analogue of single sightings on a

194 range edge). Extreme timings were expected to have higher rates of change (Moussus *et al.*,
195 2010).

196 For ecological traits we considered whether life-history development type (direct
197 development with no larval phase, meroplanktonic, planktonic), exploitation status
198 (commercially targeted or not), the mean latitude of the observations for a species and the
199 depth range of the organism (coastal, demersal or pelagic) could influence the rates of change
200 measured (Poloczanska *et al.*, 2013). For the depth range, species were classified based on the
201 life-history stage that was studied and coastal species where those constrained to terrestrial
202 (seabirds), intertidal (e.g. barnacles) or near-shore (e.g. anemones) habitats (Poloczanska *et*
203 *al.*, 2013). Additionally, for distribution we considered whether the measurement was made
204 for a leading (poleward) or trailing (equatorward) edge, or for the population centre. For
205 phenology, we considered the season of the measurement. Where available, ecological traits
206 were extracted during the review of each study, based on what the individual studies reported.
207 Latitude, range edge and season could also be considered as methodological approaches,
208 however we classified them as ecological traits because ecological expectations can be given
209 for their effect on climate responses (Davis *et al.*, 2010).

210 We also included climate predictors in analyses: the velocity of climate change (km/decade)
211 for distribution and seasonal shift (days/decade) for phenology. The climate predictors
212 measure the expected rate of response if species are tracking thermal niches in space and time
213 (Loarie *et al.*, 2009, Burrows *et al.*, 2011). The indices were calculated for each study
214 following Burrows *et al.* (2011). In brief, we used a global database of monthly sea-surface
215 temperatures, at a resolution of 1° (Rayner *et al.*, 2003). First, we spatially matched every
216 species observation to a grid square. Where studies had a larger extent than a single grid-
217 square, we matched them to a grid square at the centroid of a study's location, or the nearest
218 ocean cell if the centroid fell on land. We then calculated the decadal rate of temperature

219 change for each study's centroid using linear regressions of mean annual temperatures. The
220 time-period was chosen to match each study's duration. For distribution, we additionally
221 calculated the spatial gradient in temperature (degrees Celsius per kilometre) by taking the
222 mean temperature in each grid square across the each study's timespan, then calculating the
223 spatial gradient in temperature as the vector sum of the north-south and east-west components
224 of spatial change. For phenology, we additionally calculated the seasonal gradient in
225 temperature over the dates of each study, as the mean of the monthly temperature differences
226 over each season. Velocities were then calculated as the spatial or seasonal gradient in
227 temperature divided by the inter-annual trend (Burrows *et al.*, 2011).

228 We used linear mixed-effects models to relate rates of change to the suite of methodological
229 and ecological predictors ('lme4' package in the R programming language (Bates *et al.*,
230 2014b)). Taxon was treated as a random effect because our main interest was to characterise
231 rates of change by ecological traits and measurement type, which are correlated with taxa. For
232 distribution and phenology we developed separate full models including all physical,
233 ecological and measurement predictors. Models were simplified using a step-wise selection
234 process, removing the variable that caused the greatest reduction in the Bayes Information
235 Criteria (BIC) at each step. The selection process stopped when no further predictors could be
236 removed without increasing the BIC. We chose to use the BIC over the Akaike Information
237 Criteria because the BIC is less likely to include spurious predictors and it controls for sample
238 size (Burnham & Anderson, 2002). Thus, the final models could be considered conservative
239 in that they include only the strongest predictors of rates of response to climate change.

240 We plotted effect sizes for predictors included in the final models on term plots. Term plots
241 illustrate the modelled effects of a predictor relative to the mean of all predicted values. Term
242 plots are an appropriate way to display effect sizes when there is no control treatment,
243 because comparisons can be made across all predictions. A positive value for an effect on the

244 term plot indicates that a predictor increases the rate of an organism's response to climate
245 change. A negative value indicates the effect slows an organism's response to climate change.
246 Terms were presented with confidence intervals, which were estimated using bootstrapping
247 (using the 'boot' package in R, see Canty and Ripley (2014)).

248 We estimated the relative importance of methodological approaches when compared to
249 ecological traits by comparing the proportions of variance explained by each set of predictors.
250 We estimated variance explained by either measurement approaches or ecological traits as the
251 difference between the marginal R^2 statistic (Nakagawa & Schielzeth, 2013) for the model
252 with all significant predictors and a model without the respective variables.

253 Following the analysis, we examined in more detail how inferences drawn from analysis of
254 the database may be influenced by the available studies. Specifically, we plot the frequency of
255 measurement for the variables that were significant predictors of distribution and phenology
256 change by taxa.

257 **Results**

258 *Summary of distribution and phenology observations*

259 Across all the distribution and phenology studies there were many biases in study attributes
260 and methodologies (Fig. 1). Of 47 distribution studies and 32 phenology studies, only 15 and
261 6 respectively had more than one species, although only 2 distribution studies and no
262 phenology studies had >10 species (Fig. 1a). Out of 485 distribution measurements,
263 occurrence-based measures of distribution were slightly more common than abundance-based
264 measures (Fig. 1b). For 156 phenology observations, abundance-based measures were more
265 common than measurements of extreme individuals (Fig 1b). 38% of distribution responses
266 compared two points in time, whereas 85% of phenology responses were measured from
267 continuous time series (Fig. 1c). Most distribution and phenology data were collected in mid-

268 to-high latitudes, with phenology records, in particular, biased towards the northern
269 hemisphere and a remarkable paucity of observations for tropical species (Fig. 1d). There was
270 considerable bias in taxonomic representation; 41% of distribution records were for bony fish
271 and 19% for benthic algae (Fig. 1e), whereas 33% of phenology records were for seabirds and
272 51% for phyto and zoo-plankton, which were both poorly represented in distribution records
273 (3% and 1% respectively). Most benthic taxa had distribution observations, but few
274 phenology observations. Measurements of phenology tended to be made in spring and
275 summer, but rarely in autumn or winter (Fig. 1f).

276 *Effects of ecological traits and methodological attributes on distribution rates of change*

277 The final model for the rate of distribution change included one ecological trait and two
278 methodological approaches (Table 1, Fig 2). Estimates of change derived from irregular time-
279 series or those that were calculated by comparing two points in time tended to be faster than
280 continuous time-series (Figure 2). Occurrence-based measures of distribution change were
281 also faster than abundance-based measures. Demersal and pelagic species moved faster than
282 coastal species (intertidal species and seabirds). A model including these top-ranked
283 predictors suggests that phytoplankton have changed distributions faster than other taxa,
284 whereas benthic cnidarians and seabirds have changed the slowest (Fig. 2). The reduced
285 model explained 28% of the variance, with methodological approaches (sampling frequency
286 and type of measure) accounting for 22% of the variation in rates of change, and ecological
287 variables (depth zone) accounting for 7.8% (there was shared variance across methodological
288 and ecological variables, so the individual variables did not add up to the total variance
289 explained).

290 Ecological traits that were excluded from the final model included the range edge, which was
291 not a parsimonious predictor of distribution change (Table 1). The velocity of climate change
292 was also excluded from the final model, while the model estimated a positive effect of higher

293 velocities on distribution change, this effect was not strong. The number of species in each
294 study, a methodological variable, was also excluded from the final model, suggesting there is
295 no strong effect of publication bias in this analysis.

296 *Effects of ecological traits and methodological attributes on phenology rates of change*

297 The final reduced model for phenology change explained 14% of the variance in the data and
298 included four factors, timespan, season, inclusion of non-climatic factors and latitude (Table
299 1, Fig 3). It excluded sampling frequency, depth range, life-history development type,
300 exploitation status, seasonal climate shift, measurement type and the number of species in a
301 study. Studies that used shorter time-series were more likely to report earlier timings,
302 suggesting a slight publication bias, although the effect size was small. However, counter to
303 our expectations, studies that considered non-climatic factors estimated faster rates of change
304 than studies that did not. Phenological events at mid-latitudes were more likely to be slower
305 than at higher latitudes. The phenology of autumnal events typically shifted later, rather than
306 earlier. Overall, the effects of ecological traits and methodological attributes were small (8
307 and 4% of the variance respectively) compared to the random effect of taxa on rates of
308 change. Larval bony fish were most likely to be shifting events earlier, whereas, seabirds had
309 small changes in phenology or were likely to be shifting later.

310 *Differences in how responses are measured across taxa*

311 Next we examined how observations are distributed across taxa, ecological traits and
312 methodological approaches to explore the representativeness of climate research. We focus on
313 the ecological traits and methodological approaches that were significant predictors of rates of
314 change. Importantly, not all taxa had measurements with every methodological approach
315 (Figs 4 & 5). Lack of measurements indicates caution should be taken when extrapolating the
316 results of meta-analyses to poorly sampled taxa.

317 For distribution, occurrence-based measures (that tended to report larger distribution changes)
318 predominated over abundance-based measures. Most abundance-based measures came from
319 fish and larval fish studies, which typically use nets to sample species in fishery-related
320 surveys (Fig. 4). Occurrence-based measures were predominant in other taxa. Fishery-related
321 surveys also had many more continuous time-series, rather than comparisons of two points in
322 time. In particular, benthic molluscs, benthic cnidarians, macro-algae and other invertebrates
323 had no continuous time-series.

324 Although measurements of phenology change were faster in studies that considered non-
325 climatic factors (Fig. 3a), there were very few studies (only 7) that considered non-climatic
326 factors in their analyses (Fig. 5). Observations that come from studies that considered non-
327 climatic factors were mostly for seabirds, but there was also a small proportion for
328 phytoplankton and benthic crustaceans. All taxa were represented in data-sets with timespans
329 of up to 50 years. Autumn and spring were also well represented, however many taxa did not
330 have phenological measurements in summer and winter. Most phenology records for most
331 species were at latitudes $>40^{\circ}$, only seabirds had measurements closer to the Equator.

332 **Discussion and recommendations**

333 The methodology used to standardize studies for meta-analyses can have considerable effects
334 on estimates for rates of response to climate change (Parmesan, 2007, Przeslawski *et al.*,
335 2012). Typically, meta-analyses exclude some studies to achieve consistency, such as
336 excluding studies of single species to avoid publication bias (Parmesan & Yohe, 2003,
337 Parmesan, 2007, Poloczanska *et al.*, 2013). Rather than excluding studies, we used linear
338 models to standardize for differences in approaches across studies. By including studies that
339 used different methods to measure change, we have quantified the size and direction of
340 methodological effects on estimates of distribution and phenology responses to climate
341 change. We found methodological differences explained 22% of the variation in range shifts,

342 more than the 7.8% of the variation explained by ecological traits. For phenology change,
343 methodological approaches accounted for 4% of the variation in measurements, whereas 8%
344 of the variation was explained by ecological traits. Our study bolsters other recent findings
345 that different approaches to observing a single pattern (e.g., a geographic distribution) can
346 lead to different estimates of change over time (Moussus *et al.*, 2010, Wolkovich *et al.*, 2012,
347 Bates *et al.*, 2015). Below we discuss the implications of differences in study design and
348 biological traits on estimated rates of change.

349 *Study design*

350 We found studies comparing two points in time or using irregularly sampled time-series
351 measured greater rates of change than studies using continuous time-series. Continuous time-
352 series should quantify rates of change more accurately than infrequent sampling, because
353 infrequent samples confound short-term variability with long-term trends (Moussus *et al.*,
354 2010, Brown *et al.*, 2011). Further, range shifts in response to climate change can be
355 confounded by inconsistent sampling effort when a species is unlikely to be detected at every
356 sampling event (Bates *et al.*, 2015). Studies in our database that had infrequent sampling often
357 resurveyed sites that were sampled historically, so our result may also suggest some
358 publication and study-site selection bias towards places where ecological change has been
359 greatest.

360 Historical comparisons (i.e. resurveying) are an important way to create long-term studies,
361 where there has not been funding to support long-term sampling (e.g. Southward *et al.*, 2005,
362 Przeslawski *et al.*, 2012, Robinson *et al.*, 2015). Studies of fish were more likely to have
363 continuous time-series, presumably because of their economic importance, whereas
364 observations for other taxa often came from comparisons of two points in time. We encourage
365 authors to look for and publish resurveys of historical sampling, regardless of whether there
366 have been considerable changes in distribution, to help overcome potential publication biases.

367 Efforts to digitise and publish historical datasets (e.g. Engelhard *et al.*, 2014), combined with
368 the growth of data journals with the mandate that data generated using public funds must be
369 made available, may lead to many such data sets surfacing in the future, providing a richer
370 and less-biased basis to assess responses to climate change.

371 Abundance-based estimates of distribution change were slower than occurrence-based
372 measures. Occurrence-based measures can be influenced by responses of single individuals or
373 by detectability of a species, so we expected their observed rate of change to be greater
374 (Brown *et al.*, 2011, Bates *et al.*, 2015). Occurrence-based measures may be more likely to
375 detect change, but also more susceptible to spurious affects. Occurrence and abundance
376 measures also reflect different aspects of distribution change (Bates *et al.*, 2014a).
377 Occurrence-based measures are sensitive to range expansion, whereas abundance-based
378 measures better reflect population establishment. As such, our analysis suggests that
379 population establishment occurs much more slowly than range expansion – taking the
380 difference in rate of change between abundance and occurrence-based measures, the analysis
381 suggests on average a lag of about 140 km/decade, which is of greater magnitude than rates of
382 change in individual species' range centres (Poloczanska *et al.*, 2013). Further, this result
383 indicates that caution should be taken when extrapolating rates of change across different
384 locations. Ranges may expand rapidly as few individuals of a species occupy areas it was
385 previously absent from, but population establishment may follow more slowly (Bates *et al.*,
386 2014a). The pattern of range expansion and population establishment is particularly important
387 when managing ecosystems dynamically as communities move into novel configurations with
388 climate change (Graham *et al.*, 2014).

389 Studies with single species or short time-series are often excluded from meta-analyses
390 because of perceived publication bias toward publishing results consistent with climate
391 change (Parmesan & Yohe, 2003, Parmesan, 2007). Based on the analysis of length of study

392 as a predictor, we found no publication bias in distribution studies and only a small bias in
393 phenology studies. Publication bias may be less prevalent in marine than terrestrial studies
394 because overall there are more multi-species studies in marine ecosystems where sampling
395 methods tend to collect numerous organisms (e.g. fish and plankton) by nets (Richardson *et*
396 *al.*, 2012).

397 We found that inclusion of non-climatic factors in the analysis increased the estimated rates of
398 phenology change, but had no effect on rates of distribution change. However, few studies
399 included non-climatic factors, so further investigation of how climate responses interact with
400 factors like fishing pressure and eutrophication is important. Phenology is sensitive to
401 multiple human impacts, and it may be that in the studies analysed here, those impacts are
402 also causing seasonal timings to occur earlier. Given the paucity of studies, further work is
403 required to assess the interaction between climate change and other variables (Parmesan *et al.*,
404 2013).

405 *Ecological traits*

406 We found that pelagic and demersal species tended to move faster than coastal (inshore)
407 species. Coastal species such as kelps and rocky shore invertebrates may be less able to track
408 warming because their distributions are restricted to the coast, and hence subject to non-
409 climatic biogeographic barriers to simple latitudinal shifts, and their requirements for specific
410 largely rule out depth shifts (Broitman *et al.*, 2008). For instance, limited availability of hard
411 substrates on Australia's East coast may limit pole-wards migration of rocky intertidal
412 organisms (Poloczanska *et al.*, 2011).

413 Contrary to previous studies for terrestrial and marine ecosystems, we did not find that
414 leading edges moved faster than trailing edges (Parmesan *et al.*, 1999, Sunday *et al.*, 2012,
415 Poloczanska *et al.*, 2013). Range edges are more likely to be detected with occurrence-based
416 measures, because species tend to be rarer at their range edges (Sagarin *et al.*, 2006),

417 therefore, the measurement type and the position of measurements within a species' range
418 may be confounded. In our analysis sufficient measurements of species abundance at range
419 edges were available to distinguish the effects of range position and measurement type on the
420 rate of distribution shift. We found that occurrence based measurements were generally faster
421 than abundance based-measurements. Thus if measurement differences are not accounted for,
422 studies may overestimate the rate of shift at range edges, because of the bias toward
423 measuring edges using single individuals.

424 *Gaps in climate change ecology studies*

425 Our analyses revealed that many gaps remain in our understanding of distribution and
426 phenology responses to climate change. Gaps are a consequence of not only geographical
427 biases in sampling effort, but also of how different taxa are studied. In particular a strong
428 geographic bias exists towards temperate regions, where data-collection efforts have
429 historically been the greatest. Tropical regions, grossly underrepresented in current studies
430 (Lenoir & Svenning, 2015), are expected to display some of the highest rates of distribution
431 change, particularly in marine systems (Burrows *et al.*, 2014) and the distributions of tropical
432 taxa may be particularly susceptible to warming (Sunday *et al.*, 2012, Molinos *et al.*, 2015).
433 Moreover, the subtropical and tropical ocean represents ~70% of the global ocean surface,
434 implying that the current paucity of studies of distribution and phenology shifts in the tropics
435 affects our capacity to extrapolate available data to global rates. Global rates of distribution
436 change estimated here are therefore likely lower than those that would be inferred if the
437 studies were randomly distributed across latitudes.

438 There were few long-term phenology studies in the tropics. While seasonality in temperature
439 is weaker in the tropics and our results suggest phenology change is slower toward lower
440 latitudes, warming can still drive temporal changes in species abundance, for instance blooms
441 of dangerous jellyfish (Jacups, 2010). In addition to warming, seasonality along tropical

442 coastlines can be driven by precipitation (van Schaik *et al.*, 1993, Chambers *et al.*, 2013). For
443 example, the timing of juvenile prawn migrations from rivers to the ocean is related to
444 cumulative rainfall in tropical river basins (Staples & Vance, 1986). Phenological response to
445 precipitation is more difficult to predict than warming-related responses because species may
446 shift earlier or later (Chambers *et al.*, 2013). Impacts of climate change on tropical seasonality
447 have historically been neglected and warrant further studies.

448 There was systematic differences in types of observations across taxa, which suggests that we
449 have major gaps in our understanding of climate impacts. For instance, seabird studies that
450 measured changes in phenology with climate change were common, whereas there were only
451 two seabird studies of distribution that met the criteria for inclusion in our database. This is
452 likely to be because seabirds are most easily sampled at breeding colonies where there have
453 been long-standing monitoring programs (e.g. Barbraud & Weimerskirch, 2006), rather than
454 during their extensive foraging forays. In the future, the extensive and ongoing tracking
455 information collected using satellite tags should provide long-term information on distribution
456 shifts in feeding distributions, and potentially on shifts in breeding sites. In contrast to seabird
457 studies, studies of fish distribution were common, and studies of fish phenology rare. Fish
458 studies in the database often used fisheries data-sets for analyzing climate patterns. Fisheries-
459 related surveys are large-scale, regular (usually annual) surveys of abundance indices. They
460 are typically annual so cannot be used to measure phenology, but they do often cover large
461 geographic areas, so are very suitable for distribution studies.

462 Few observations of marine phenology were available from autumn or winter, a potential
463 temporal bias that also occurs in terrestrial studies of phenology (Gallinat *et al.*, 2015). The
464 lack of data on phenology from autumn and winter could partially reflect the fact that many
465 species perform many of their most important processes (e.g. feeding and reproduction)
466 predominantly in spring and summer. There are also many more spring than autumn

467 observations for terrestrial ecosystems (Parmesan & Yohe, 2003). But unlike marine systems,
468 terrestrial systems do have a few very long-term (e.g. grape harvests over 800 year, (Menzel,
469 2005)), and iconic (e.g. fall color indexes in New England, USA (Gallinat *et al.*, 2015))
470 autumn measurements. We found evidence that autumnal events were shifting later, rather
471 than earlier, which is consistent with lengthening seasons. Measuring autumn phenology in
472 higher latitudes is therefore an important knowledge gap in both marine and terrestrial
473 systems. Because of this gap, we have little information on how growing seasons may be
474 extended by warming (for an example see Moore *et al.*, 2011).

475 *Recommendations for measuring change*

476 Based on the findings of our meta-analysis, we make several recommendations for measuring
477 responses of organisms to climate change when analysing past studies of climate change
478 impacts or designing new studies.

479 (1) Re-analysis of existing time-series

480 A critical question is whether the time-series can be used to address the study's aim. For
481 instance, a database of species occurrences across space and time can be used to examine
482 colonisation of new areas, but is more limited in supporting inferences about the
483 establishment and persistence of new populations. Similarly for phenology, a time-series of
484 the most extreme individuals breeding timing does not necessarily reflect significant change
485 in a whole population, although changes in a few individuals may be an early warning for
486 population level change. Therefore, researchers should be careful to consider the potential
487 limitations and biases in data when conducting re-analyses

488 Covariates, particularly those not related to climate, are key to consider when analysing time-
489 series. A typical test is to ask whether warming is driving an observed change, with the null
490 hypothesis being warming is not a factor. Greater consideration of other alternatives is

491 important (Brown *et al.*, 2011), including non-climate drivers of distribution and phenology.
492 For instance, changes in depth range of an organism could be driven by warming, but the
493 potentially confounding effect of fishing pressure changing with depth should also be
494 considered in such an analysis (Dulvy *et al.*, 2008, Engelhard *et al.*, 2014).

495 Broadening the scope of climate change studies to include other drivers will require greater
496 accessibility of data on human impacts – such as fishing and eutrophication at appropriate
497 time and space scales. Climate time-series data are widely available as free downloads,
498 whereas, data on other drivers are often less-easily available or do not exist at all. Efforts to
499 share currently closed databases, such as those on fishing and efforts to collect more data, for
500 instance using satellite images to map eutrophication, will enable better discrimination of
501 climate from other signals and thus more robust climate attribution.

502 (2) Qualitative comparisons with other studies

503 Qualitative comparisons among rates of change are common in regional or taxon-specific
504 studies of climate change (e.g. Richardson, 2008). The usual aim of qualitative comparisons is
505 to give context for an observed rate of change being faster or slower than typical, and to
506 speculate about the ecological or environmental drivers of a difference. However, differences
507 will also be strongly influenced by measurement biases. Where possible, qualitative
508 comparisons should be made with similar metrics used to measure observed change. For
509 instance measurements of distribution based on occurrence at sites should not be compared
510 with measurements based on abundance averages, which are typically slower. As the number
511 of climate studies grows, it will become easier to compare studies that use similar methods.

512 (3) Meta-analyses of species responses to climate change

513 It is especially important for meta-analyses of species responses across many studies to
514 include the influence of different variables explicitly in a statistical model. Important

515 covariates include measurement and ecological variables. Past studies have either ignored
516 these differences (Poloczanska *et al.*, 2013) or tried to removed non-similar studies (Parmesan
517 & Yohe, 2003, Parmesan, 2007, Przeslawski *et al.*, 2012). While including additional
518 measurement variables in analysis did not significantly change our results when compared to
519 previous analyses (Poloczanska *et al.*, 2013), it did shed important light on factors affecting
520 distribution and phenology change. Removing studies from analysis focuses on a subset of
521 potential biases (e.g. only including studies on multiple species or time series greater than a
522 certain length) is a blunt approach that does not consider multiple other potential sources of
523 bias (e.g. measurement type, latitude, non-climate factors) that are needed to provide more
524 robust estimates of climate change on species. Removing studies from analysis reduces the
525 power to detect real biological effects, and therefore should be avoided where possible.

526 (4) Design of new studies

527 Numerous time-series are currently being started, with the aim of monitoring effects of
528 climate change (e.g. Robinson *et al.*, 2015). Our findings provide some advice on designing
529 sampling protocols. The aims of measuring the time-series should be explicitly defined and a
530 protocol designed to address them. For example, a study that seeks to monitor invasion of pest
531 species may focus on monitoring for occurrences, to obtain early warnings of ranges shifts. In
532 contrast, a study that aims to detect ecologically significant might focus on monitoring
533 abundance.

534 When designing a study, abundance-based measures therefore offer more explanatory power
535 because they can be used to measure both colonisation and establishment. Further,
536 abundance-based measures will be less influenced by extreme occurrences of individuals, so
537 may be a more robust measure of change (Brown *et al.*, 2011). However, there may be trade-
538 offs in sampling effort that warrant consideration. Occurrences are cheaper to measure than
539 abundances, particularly for rare species, so occurrence surveys may cover larger areas and a

540 greater range of species than abundance-based surveys could for the same cost. Further,
541 occurrence-based measures are easier to obtain from non-experts, such as through citizen
542 science programs or from observations from fishers (Robinson *et al.*, 2015). Occurrence-
543 based measures could therefore provide a more useful early warning of invasion of new
544 species, but do not necessarily indicate establishment of a new population.

545 A common approach to detecting climate change impacts is to resurvey sites that had
546 historical measurements of climate change. Such resurveys are important to fill data gaps, yet
547 our results suggest some selection bias for sites with greater change, at least for distribution
548 studies. It is important that resurvey sights that are selected randomly (or comprehensively) to
549 provide a less biased global view of climate change impacts, for instance by systematically
550 sampling across a species' entire range.

551 Large gaps remain in our knowledge of climate change responses in both terrestrial and
552 marine systems. Key amongst these is that there is three times as much information on
553 changes in distribution than phenology in the ocean, whereas on land there is 100 times more
554 information on phenology than on distribution change (comparing Poloczanska *et al.* 2013
555 with Rosenzweig *et al.*, 2008). Expanding terrestrial studies of species' distribution change
556 and marine studies of phenology change, particularly in autumn and winter, is important to
557 give a comprehensive view of life's responses to climate change.

558 *Conclusion*

559 We found that measurement biases can have a substantial effect on inferences about the
560 impacts of climate change on distribution and phenology. Greater consideration of
561 measurement bias in climate impacts studies will improve our understanding for how
562 measurement methods affect observations and ultimately contribute to a more representative
563 view of the impacts of climate change on organisms.

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572

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- 695

696 **Tables**

697 **Table 1** Analysis of rates of distribution and phenology change, with the Δ BIC calculated by
 698 adding (for non-significant variables) or removing (for significant variables) each variable
 699 from the reduced model. Variables with negative Δ BIC were not included in the reduced
 700 models. N.A. Not applicable

Factor	Variable class	Distribution data-set ΔBIC	Phenology data-set ΔBIC
Abundance/occurrence based measure	Methodological approach	23	-4.5
Data sampling frequency	Methodological approach	64	-9.7
Non-climatic factors considered	Methodological approach	-6.1	2.8
No. spp. in study	Methodological approach	-5.4	-4.0
Timespan of study	Methodological approach	-5.4	0.2
Depth category	Ecological trait	47	-9.5
Exploitation status	Ecological trait	-4.0	-4.9
Latitude	Ecological trait	-1.2	2.8
Planktonic larval	Ecological trait	-2.5	-5.6

dispersal type			
Range edge/centre	Ecological trait	-6.9	N.A.
Season	Ecological trait	N.A.	10.4
Velocity of climate change	Ecological trait	-2.2	-4.6

701

702 **Figure legends**

703 **Fig 1** Frequency of different factors in studies of distribution and phenology: (a) number of
 704 species in a study; (b) occurrence-based or abundance-based measures of distribution and
 705 phenology; (c) sampling frequency; (d) latitude; (e) broad taxonomic groupings; and (f)
 706 season, for

707 **Fig 2** Term plot for analysis of rates of change in distribution using the final mixed effects
 708 model, showing the final model (selected using BIC, Full model BIC = 5713, reduced model
 709 BIC = 5686). For the fixed effects, points indicate mean predicted effects and bars are 95%
 710 confidence intervals. Taxa were treated as a random effect. Effects are standardised to the
 711 overall mean, so positive effects indicate a tendency toward distribution change that is greater
 712 and consistent with climate change, whereas negative effects indicate a tendency toward
 713 smaller changes or changes that are not consistent with warming (though those two cannot be
 714 distinguished in this figure). Note the varying scales for the y-axes; larger ranges indicate
 715 larger effect sizes.

716 **Fig 3** Term plot for analysis of rates of change in phenology using the final mixed effects
 717 model, showing the final model (selected using BIC, Full model BIC = 1153, reduced model
 718 BIC = 1112). Points indicate mean predicted effects and bars the 95% confidence intervals.
 719 Taxa were treated as a random effect. Effects are standardised to the overall mean, so

720 negative effects (upwards on the y-axis) indicate a tendency toward phenology change that is
721 earlier and consistent with climate change, whereas positive effects indicate a tendency
722 toward smaller date changes or changes that are not consistent with warming. Note the
723 varying scales for the y-axes.

724 **Fig 4** Proportion of distribution observations by taxa and each covariate used in the final
725 model for distribution rate of change. The maximum proportion of observations in any
726 category was 0.4.

727 **Fig 5** Proportion of phenology observations by taxa and each covariate used in the final
728 model for distribution rate of change. The maximum proportion of observations in any
729 category was 0.4.

730

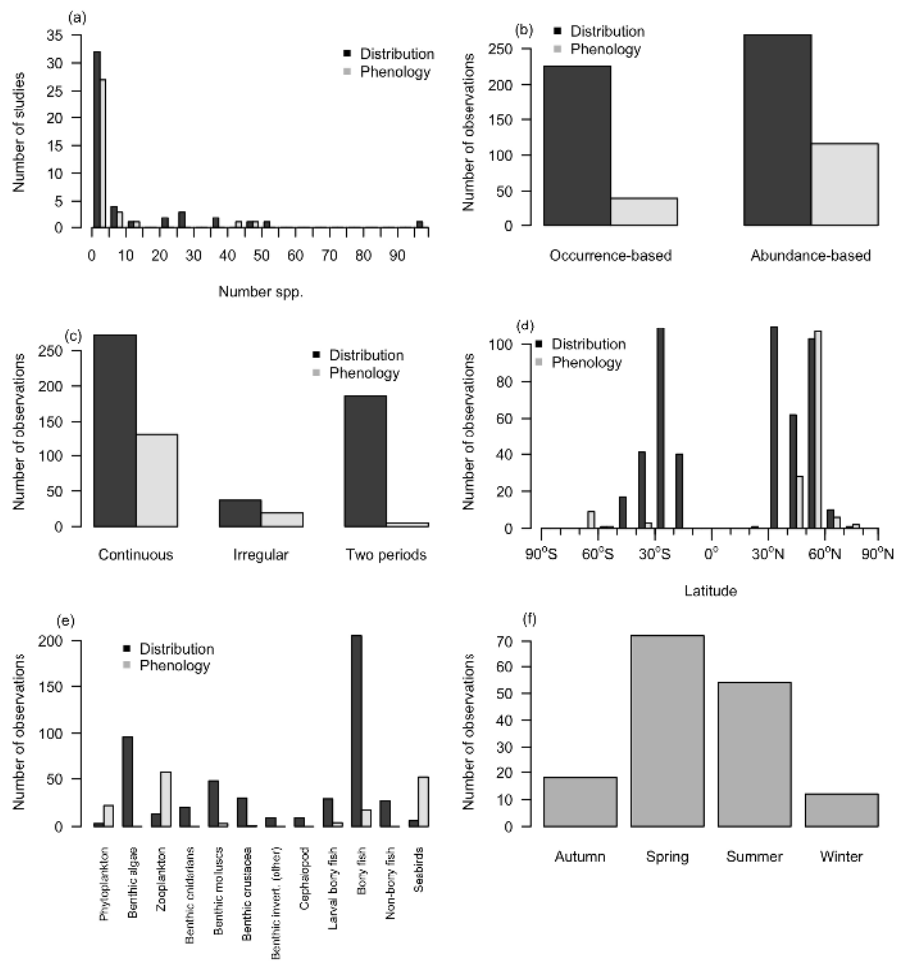


Fig 1 Frequency of different factors in studies of distribution and phenology: (a) number of species in a study; (b) occurrence-based or abundance-based measures of distribution and phenology; (c) sampling frequency; (d) latitude; (e) broad taxonomic groupings; and (f) season, for phenology.
704x939mm (72 x 72 DPI)

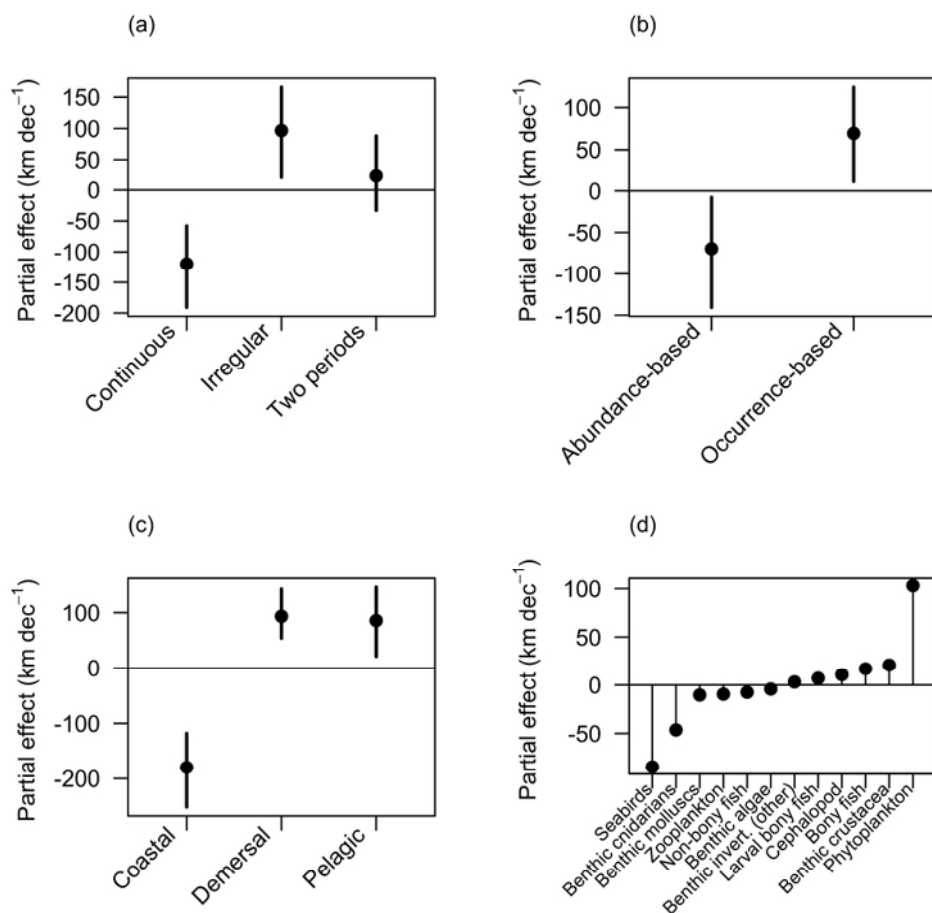


Fig 2 Term plot for analysis of rates of change in distribution using the final mixed effects model, showing the final model (selected using BIC, Full model BIC = 5713, reduced model BIC = 5686). For the fixed effects, points indicate mean predicted effects and bars are 95% confidence intervals. Taxa were treated as a random effect. Effects are standardised to the overall mean, so positive effects indicate a tendency toward distribution change that is greater and consistent with climate change, whereas negative effects indicate a tendency toward smaller changes or changes that are not consistent with warming (though those two cannot be distinguished in this figure). Note the varying scales for the y-axes; larger ranges indicate larger effect sizes.

80x80mm (300 x 300 DPI)

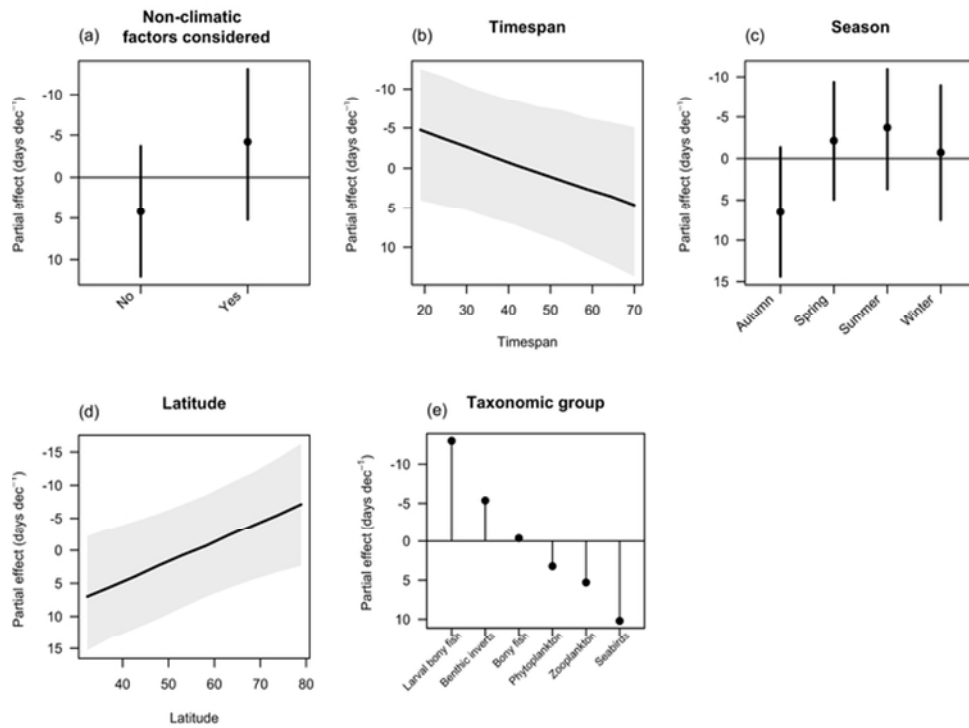


Fig 3 Term plot for analysis of rates of change in phenology using the final mixed effects model, showing the final model (selected using BIC, Full model BIC = 1153, reduced model BIC = 1112). Points indicate mean predicted effects and bars the 95% confidence intervals. Taxa were treated as a random effect.

Effects are standardised to the overall mean, so negative effects (upwards on the y-axis) indicate a tendency toward phenology change that is earlier, whereas positive effects indicate a tendency toward smaller date changes or to a later date. Note the varying scales for the y-axes.

59x44mm (300 x 300 DPI)

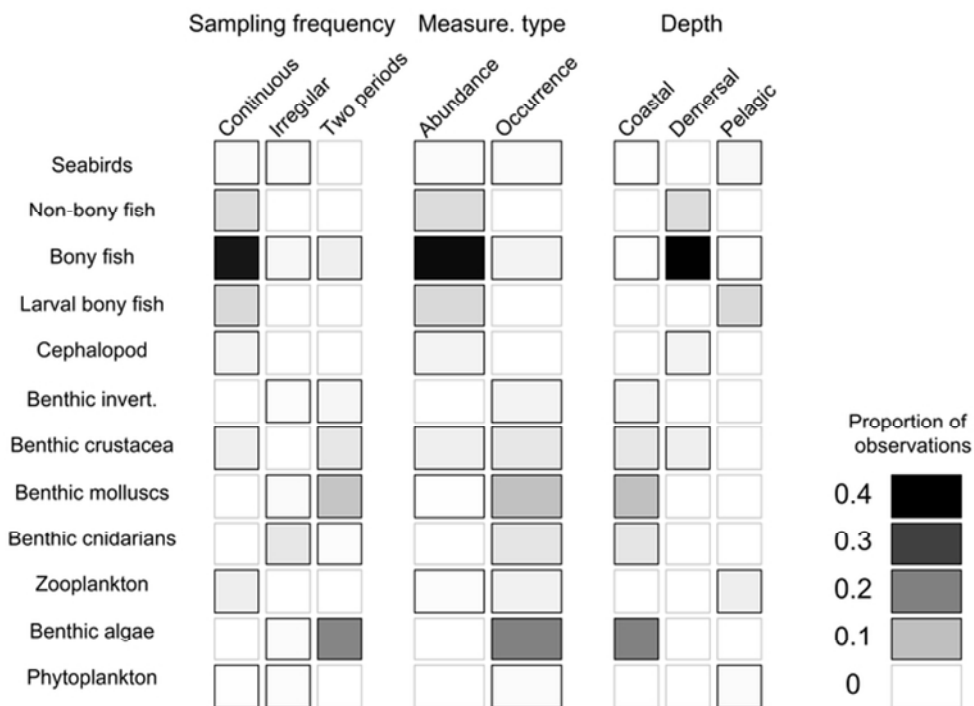


Fig 4 Proportion of distribution observations by taxa and each covariate used in the final model for distribution rate of change. The maximum proportion of observations in any category was 0.4.
59x44mm (300 x 300 DPI)

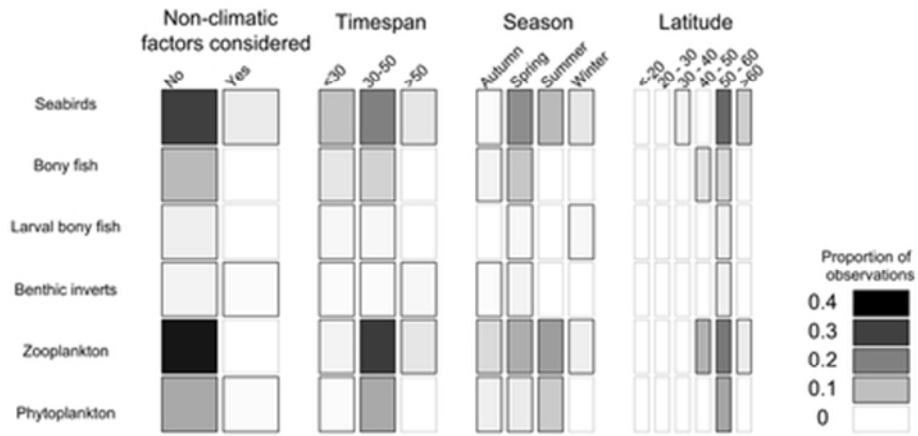


Fig 5 Proportion of phenology observations by taxa and each covariate used in the final model for distribution rate of change. The maximum proportion of observations in any category was 0.4.
39x19mm (300 x 300 DPI)