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Ecological and methodological drivers of species' distribution and phenology responses to climate change

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Abstract

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

Keywords: fishing, global warming, marine ecosystem, meta-analysis, publication bias, range edge, range shift, season, time series, tropics

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Introduction

A large number of marine (Poloczanska *et al.*, 2013) and terrestrial (Parmesan & Yohe, 2003) species have shifted their distributions and phenology in recent decades, indicating that climate change is driving a global

biological response. For example, recent climate change has: driven the invasion of pest species (Ling *et al.*, 2008), contributed to declines in commercially important fish species (Beaugrand & Kirby, 2010) and appears to be increasing mismatch in the seasonal timing between predators and their prey (Edwards & Richardson, 2004; Barbraud & Weimerskirch, 2006).

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

Measurements of distribution and phenology are influenced by a suite of decisions that are made in two stages of all studies: their sampling design and data analysis (Brown *et al.*, 2011; Bates *et al.*, 2014a). In the sampling design phase, researchers decide how species' variables are measured. For example, distribution can be measured as mean latitude of a populations' geographical extent (e.g. Perry *et al.*, 2005) or by measuring the most extreme latitudes where a species is found (e.g. Robinson *et al.*, 2015). Similarly, the phenology of breeding events can be measured by censusing a population throughout a season to determine the peak breeding date, or as the first and last individuals to breed (e.g. Fitter & Fitter, 2002; Barbraud & Weimerskirch, 2006). Measures of distribution and phenology based on the most extreme individuals rather than variables that represent the distribution of individuals within a population may lead to very different estimates of climate change response rates. For example, single individuals may by chance have extreme responses (Brown *et al.*, 2011), and measurements using single individuals are susceptible to detection biases (Cook *et al.*, 2012; Bates *et al.*, 2015).

In the analysis phase, most marine climate change studies include only a single predictor – temperature – to explain changes in distribution or phenology and thus do not explicitly consider other drivers of change (Brown *et al.*, 2011). It is unknown whether studies that do not account for other potential anthropogenic

drivers, such as fishing, eutrophication and habitat loss, could lead to higher estimates of impacts of climate change. For example, an investigation of changes in the distribution of North Sea cod showed fishing pressure explains part of the observed biological changes (Engelhard *et al.*, 2014).

A greater understanding of how different methodological approaches affect the detection of observed responses to climate change will benefit climate change ecology in four main ways. First, studies that analyse existing data sets to test for climate impacts need to account for historical choices made about field data collection that could limit the ability to detect species' responses to climate change. For instance, uneven sampling effort along coasts means museum records of species occurrences may misrepresent historical range boundaries (Shoo *et al.*, 2006; Przeslawski *et al.*, 2012). Second, many regional studies compare rates of change with other studies in their discussions of how ecological traits influence a species' response (e.g. Richardson, 2008). Comparisons of change may also need to consider differences in methodological approaches across studies, such as how occurrence data are used to estimate ranges. Third, new time series are being initiated with the aim of measuring future distribution and phenology change (e.g. Robinson *et al.*, 2015). Greater understanding of how different methodological approaches can affect measured responses to climate change could assist the design of new time series. For instance, inconsistent sampling effort through time may bias measured rates of change (Bates *et al.*, 2015). Finally, meta-analyses of existing studies will produce more accurate estimates if they standardize for study differences, or constrain comparisons to be among studies with similar methods (Parmesan, 2007; Przeslawski *et al.*, 2012). For instance, differences in rates of range shifts among European butterflies, birds and plants could be a consequence of taxonomic identity, geographical biases or differences in the metrics used (Parmesan & Yohe, 2003).

Here, we examine the potential causes of variability in observed marine species distribution and phenology responses to climate change using a meta-analysis. First, we ask whether measurements of distribution and phenology change from the peer-reviewed literature are representative of different taxa, oceans and methodological approaches. Then, we conduct a meta-analysis on rates of response, to ask how ecological traits, study design and measurement approaches influence rates of distribution and phenology change. This enables us to ask how study measurement approaches may bias measured rates of change and affect inferences about the biological drivers of change. Finally, we investigate how different measurement approaches

are used for different taxa and discuss the implications of measurement biases on the global understanding of climate change responses.

Materials and methods

Database

We analysed the database of peer-reviewed studies of observed impacts of climate change on marine organisms compiled by Poloczanska *et al.* (2013). We used a subset of 61 studies where rates of range change in phenology or distribution were reported or could be calculated and updated the database with a further 18 studies published in 2011–2014, for a total of 79 studies (Tables S1 and S2). In the original database and the update, we made every effort to include every data set and study that met our criteria; thus, we believe this to be a comprehensive data set rather than a small subset of available data.

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

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

Analysis of rates of change

First, we summarize measurements of distribution and phenology change by methodological attributes, taxon, latitude, and for phenology, season. We then conducted analyses to examine how rates of change were influenced by ecological traits and methodological approaches. Rates of change, in kilometres per decade or days per decade, were obtained from individual studies in the database, either directly as reported in the text, calculated from figures, or

by contacting the study's authors. Distribution changes were recorded as positive where they were consistent with a response to climate change (generally polewards, but see Burrows *et al.*, 2011) and negative if they were not consistent with climate change. Phenology changes were recorded as negative for shifts to earlier dates and positive for shifts to later dates.

We related rates of change to a suite of predictors using a generalized linear modelling approach. The response variables were the rate of change in either distribution or phenology. Predictors were divided into two categories: methodological approaches and ecological traits. For methodological attributes, we considered the frequency of sampling (continuous, irregular or comparison of two periods). Fewer sampling points for studies that compare two periods of time (e.g. repeating a historical survey) may mean less accurate (either higher or lower) rates of change, because intervening fluctuations are ignored. We considered the number of species in a study; studies reporting on more species were expected to have lower rates of change because they are less likely to be influenced as strongly by publication bias (Parmesan, 2007). We also considered whether non-climatic drivers of change were accounted for in the study. We expect slower rates of change in studies with non-climatic drivers because confounding influences on the response could explain some of the observed variation. For distribution, we considered whether rates were generated from abundance (or relative abundance) metrics or from present data on species occurrence at sites. Occurrence-based data were expected to have higher rates of change because they are more susceptible to the outlying influences of a single individual. Similarly for phenology, we considered whether the magnitude of change in timing was related to whether the measure was an abundance metric, or the timing of the most extreme individual (e.g. first or last arrival – the temporal analogue of single sightings on a range edge). Extreme timings were expected to have higher rates of change (Moussus *et al.*, 2010).

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

We also included climate predictors in analyses: the velocity of climate change (km per decade) for distribution and seasonal shift (days per decade) for phenology. The climate predictors measure the expected rate of response if species are tracking thermal niches in space and time (Loarie *et al.*, 2009; Burrows *et al.*, 2011). The indices were calculated for each study following Burrows *et al.* (2011). In brief, we used a global database of monthly sea surface temperatures, at a resolution of 1° (Rayner *et al.*, 2003). First, we spatially matched every species observation to a grid square. Where studies had a larger extent than a single grid square, we matched them to a grid square at the centroid of a study's location, or the nearest ocean cell if the centroid fell on land. We then calculated the decadal rate of temperature change for each study's centroid using linear regressions of mean annual temperatures. The time period was chosen to match each study's duration. For distribution, we additionally calculated the spatial gradient in temperature ($^{\circ}\text{C km}^{-1}$) by taking the mean temperature in each grid square across the each study's time span, then calculating the spatial gradient in temperature as the vector sum of the north-south and east-west components of spatial change. For phenology, we additionally calculated the seasonal gradient in temperature over the dates of each study, as the mean of the monthly temperature differences over each season. Velocities were then calculated as the spatial or seasonal gradient in temperature divided by the interannual trend (Burrows *et al.*, 2011).

We used linear mixed-effects models to relate rates of change to the suite of methodological and ecological predictors [‘LME4’ package in the R programming language (Bates *et al.*, 2014b)]. Taxon was treated as a random effect because our main interest was to characterize rates of change by ecological traits and measurement type, which are correlated with taxa. For distribution and phenology, we developed separate full models including all physical, ecological and measurement predictors. Models were simplified using a stepwise selection process, removing the variable that caused the greatest reduction in the Bayes information criteria (BIC) at each step. The selection process stopped when no further predictors could be removed without increasing the BIC. We chose to use the BIC over the Akaike information criteria because the BIC is less likely to include spurious predictors and it controls for sample size (Burnham & Anderson, 2002). Thus, the final models could be considered conservative in that they include only the strongest predictors of rates of response to climate change.

We plotted effect sizes for predictors included in the final models on term plots. Term plots illustrate the modelled effects of a predictor relative to the mean of all predicted values. Term plots are an appropriate way to display effect sizes when there is no control treatment, because comparisons can be made across all predictions. A positive value for an effect on the term plot indicates that a predictor increases the rate of an organism's response to climate change. A negative value indicates the effect slows an organism's response to climate change. Terms were presented with confidence intervals, which were estimated using bootstrapping [using the ‘BOOT’ package in R, see Canty & Ripley (2014)].

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

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

Results

Summary of distribution and phenology observations

Across all the distribution and phenology studies, there were many biases in study attributes and methodologies (Fig. 1). Of 47 distribution studies and 32 phenology studies, only 15 and 6, respectively, had more than one species, although only 2 distribution studies and no phenology studies had >10 species (Fig. 1a). Of 485 distribution measurements, occurrence-based measures of distribution were slightly more common than abundance-based measures (Fig. 1b). For 156 phenology observations, abundance-based measures were more common than measurements of extreme individuals (Fig. 1b). 38% of distribution responses compared two points in time, whereas 85% of phenology responses were measured from continuous time series (Fig. 1c). Most distribution and phenology data were collected in mid-to-high latitudes, with phenology records, in particular biased towards the Northern Hemisphere and a remarkable paucity of observations for tropical species (Fig. 1d). There was considerable bias in taxonomic representation; 41% of distribution records were for bony fish and 19% for benthic algae (Fig. 1e), whereas 33% of phenology records were for seabirds and 51% for phyto- and zooplankton, which were both poorly represented in distribution records (3% and 1%, respectively). Most benthic taxa had distribution observations, but few phenology observations. Measurements of phenology tended to be made in spring and summer, but rarely in autumn or winter (Fig. 1f).

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

The final model for the rate of distribution change included one ecological trait and two methodological approaches (Table 1, Fig. 2). Estimates of change

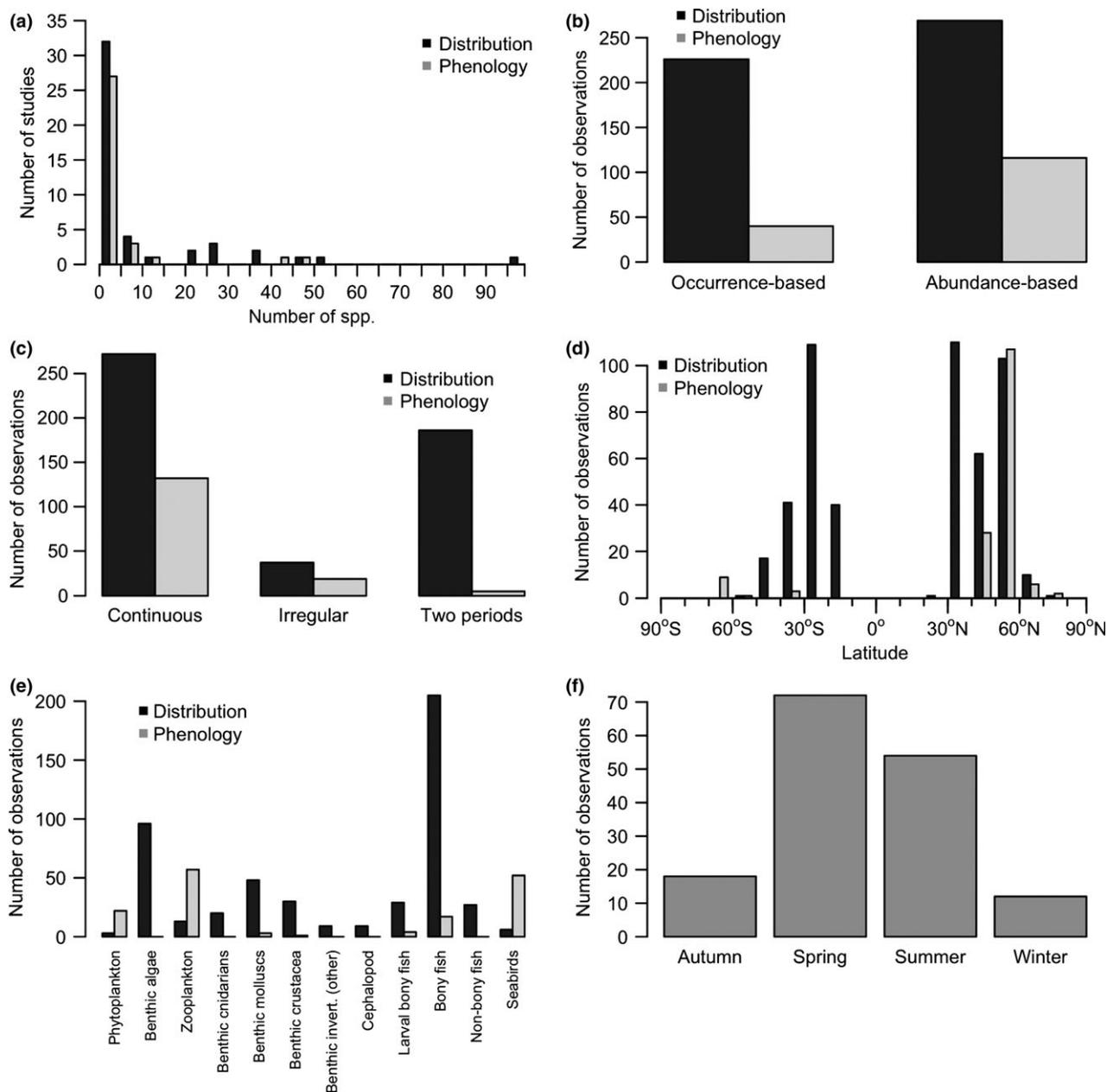


Fig. 1 Frequency of different factors in studies of distribution and phenology: (a) number of species in a study; (b) occurrence-based or abundance-based measures of distribution and phenology; (c) sampling frequency; (d) latitude; (e) broad taxonomic groupings; and (f) season, for phenology.

derived from irregular time series or those that were calculated by comparing two points in time tended to be faster than continuous time series (Fig. 2). Occurrence-based measures of distribution change were also faster than abundance-based measures. Demersal and pelagic species moved faster than coastal species (intertidal species and seabirds). A model including these top-ranked predictors suggests that phytoplankton have changed distributions faster than other taxa, whereas benthic cnidarians and seabirds have changed

the slowest (Fig. 2). The reduced model explained 28% of the variance, with methodological approaches (sampling frequency and type of measure) accounting for 22% of the variation in rates of change and ecological variables (depth zone) accounting for 7.8% (there was shared variance across methodological and ecological variables, so the individual variables did not add up to the total variance explained).

Ecological traits that were excluded from the final model included the range edge, which was not a

Table 1 Analysis of rates of distribution and phenology change, with the Δ BIC calculated by adding (for non-significant variables) or removing (for significant variables) each variable from the reduced model

Factor	Variable class	Distribution data set Δ BIC	Phenology data set Δ BIC
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. of spp. in study	Methodological approach	-5.4	-4.0
Time span 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 dispersal type	Ecological trait	-2.5	-5.6
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

Variables with negative Δ BIC were not included in the reduced models. N.A., not applicable.

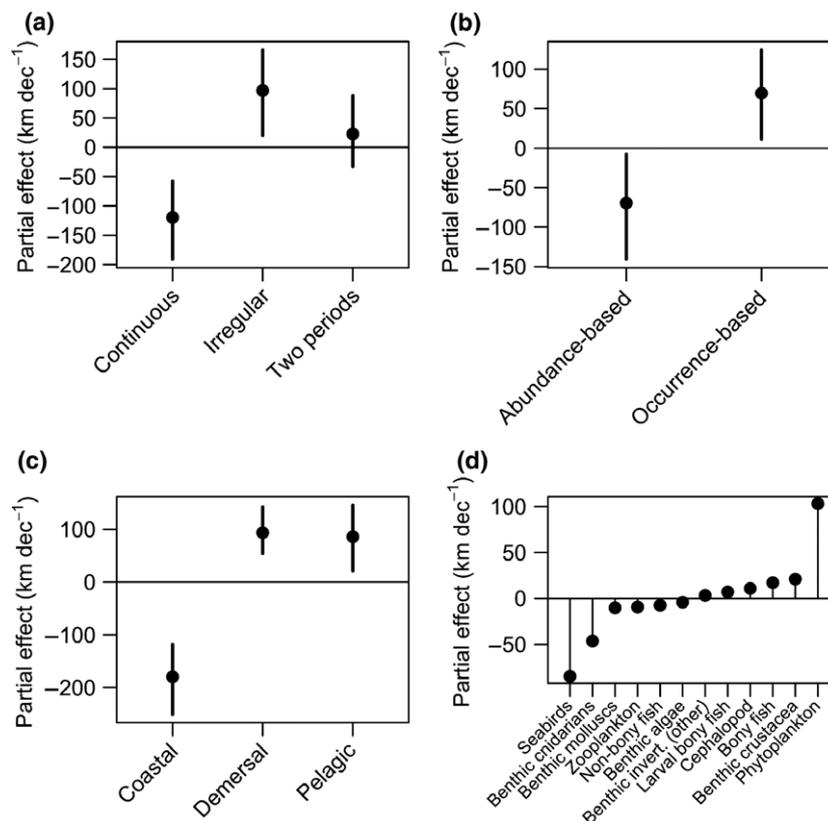


Fig. 2 Term plot for the analysis of rates of change in distribution using the final mixed-effects model, showing the final model (selected using BIC, full model BIC = 5713, reduced model BIC = 5686). For the fixed effects, points indicate mean predicted effects and bars represent 95% confidence intervals.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

parsimonious predictor of distribution change (Table 1). The velocity of climate change was also excluded from the final model, while the model estimated a positive

effect of higher velocities on distribution change, the velocity effect was weak. The number of species in each study, a methodological variable, was also

excluded from the final model, suggesting there is no strong effect of publication bias in this analysis.

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

The final reduced model for phenology change explained 14% of the variance in the data and included four factors, time span, season, inclusion of non-climatic factors and latitude (Table 1, Fig. 3). It excluded sampling frequency, depth range, life-history development type, exploitation status, seasonal climate shift, measurement type and the number of species in a study. Studies that used shorter time series were more likely to report earlier timings, suggesting a slight publication bias, although the effect size was small. However, counter to our expectations, studies that considered non-climatic factors estimated faster rates of change than studies that did not. Phenological events at midlatitudes were more likely to be slower than those at higher latitudes. The phenology of autumnal events typically shifted later, rather than earlier. Overall, the

effects of ecological traits and methodological attributes were small (8% and 4% of the variance, respectively) compared to the random effect of taxa on rates of change. Larval bony fish were most likely to be shifting events earlier, whereas seabirds had small changes in phenology or were likely to be shifting later.

Differences in how responses are measured across taxa

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

For distribution, occurrence-based measures (that tended to report larger distribution changes) predominated over abundance-based measures. Most abun-

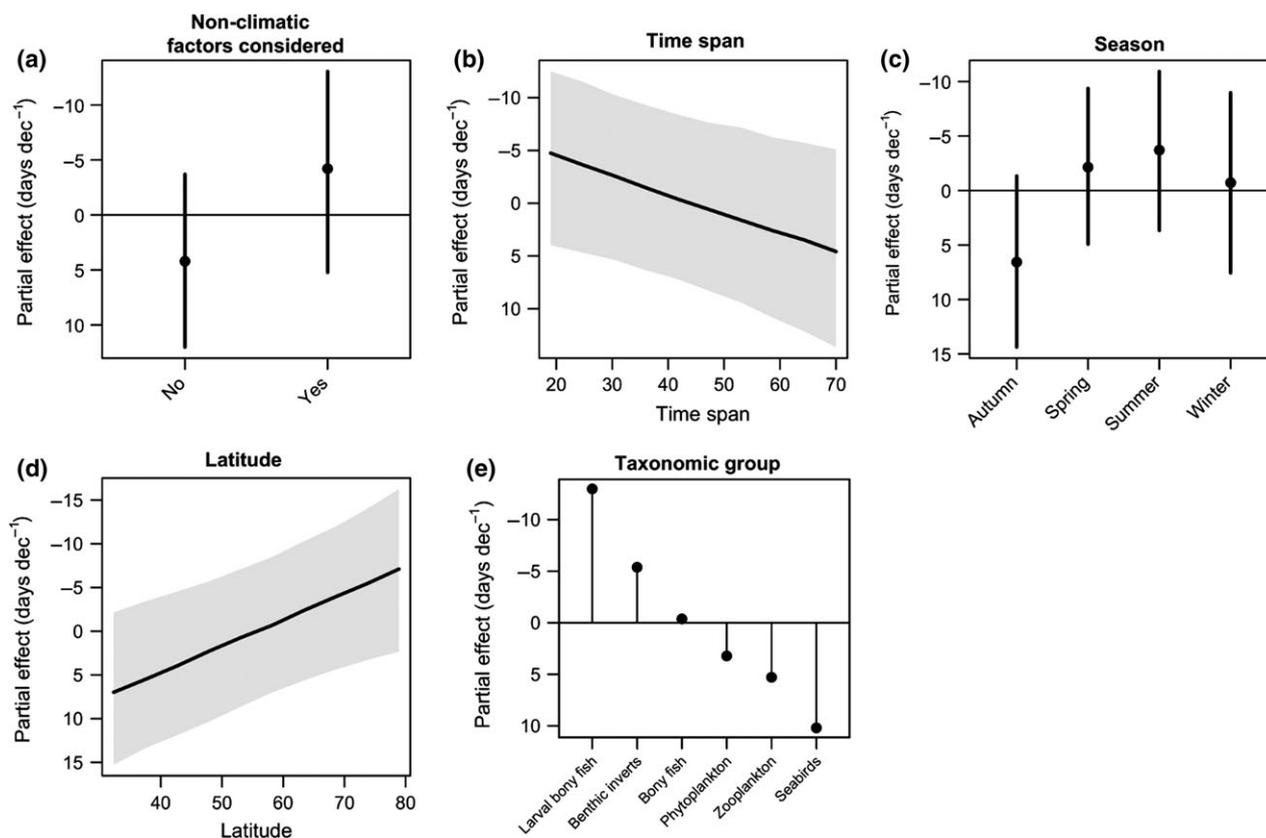


Fig. 3 Term plot for the analysis of rates of change in phenology using the final mixed-effects model, showing the final model (selected using BIC, full model BIC = 1153, reduced model BIC = 1112). Points indicate mean predicted effects and bars the 95% confidence intervals. Taxa were treated as a random effect. Effects are standardized to the overall mean, so negative effects (upwards on the *y*-axis) indicate a tendency towards phenology change that is earlier and consistent with climate change, whereas positive effects indicate a tendency towards smaller date changes or changes that are not consistent with warming. Note the varying scales for the *y*-axes.

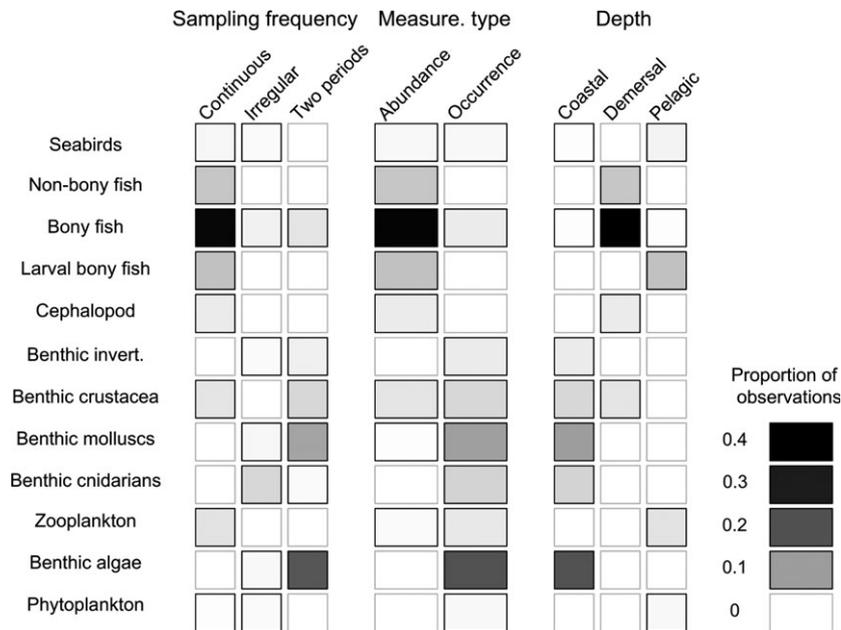


Fig. 4 Proportion of distribution observations by taxa and each covariate used in the final model for distribution rate of change. The maximum proportion of observations in any category was 0.4.

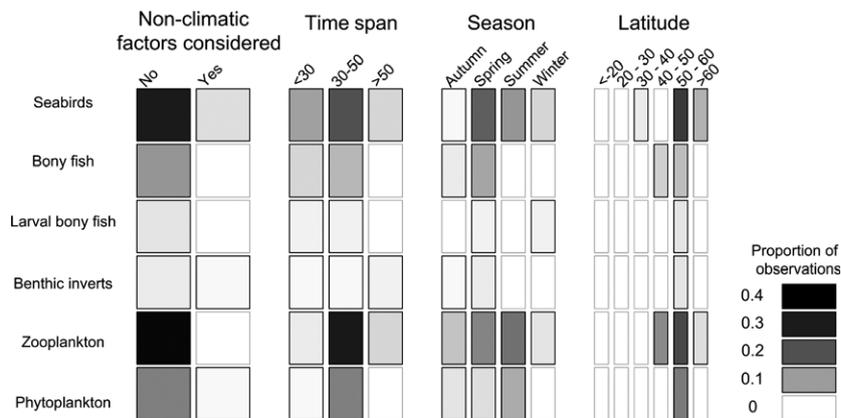


Fig. 5 Proportion of phenology observations by taxa and each covariate used in the final model for distribution rate of change. The maximum proportion of observations in any category was 0.4.

dance-based measures came from fish and larval fish studies, which typically use nets to sample species in fishery-related surveys (Fig. 4). Occurrence-based measures were predominant in other taxa. Fishery-related surveys also had many more continuous time series, rather than comparisons of two points in time. In particular, benthic molluscs, benthic cnidarians, macroalgae and other invertebrates had no continuous time series.

Although measurements of phenology change were faster in studies that considered non-climatic factors (Fig. 3a), there were very few studies (only 7) that considered non-climatic factors in their analyses (Fig. 5). Observations that come from studies that considered

non-climatic factors were mostly for seabirds, but there was also a small proportion for phytoplankton and benthic crustaceans. All taxa were represented in data sets with time spans of up to 50 years. Autumn and spring were also well represented; however, many taxa did not have phenological measurements in summer and winter. Most phenology records for most species were at latitudes $>40^{\circ}$, and only seabirds had measurements closer to the equator.

Discussion

The methodology used to standardize studies for meta-analyses can have considerable effects on estimates for

rates of response to climate change (Parmesan, 2007; Przeslawski *et al.*, 2012). Typically, meta-analyses exclude some studies to achieve consistency, such as excluding studies of single species to avoid publication bias (Parmesan & Yohe, 2003; Parmesan, 2007; Poloczanska *et al.*, 2013). Rather than excluding studies, we used linear models to standardize for differences in approaches across studies. By including studies that used different methods to measure change, we have quantified the size and direction of methodological effects on estimates of distribution and phenology responses to climate change. We found methodological differences explained 22% of the variation in range shifts, more than the 7.8% of the variation explained by ecological traits. For phenology change, methodological approaches accounted for 4% of the variation in measurements, whereas 8% of the variation was explained by ecological traits. Our study bolsters other recent findings that different approaches to observing a single pattern (e.g. a geographical distribution) can lead to different estimates of change over time (Moussus *et al.*, 2010; Wolkovich *et al.*, 2012; Bates *et al.*, 2015). Below, we discuss the implications of differences in study design and biological traits on estimated rates of change.

Study design

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

Historical comparisons (i.e. resurveying) are an important way to create long-term studies, where there has not been funding to support long-term sampling (e.g. Southward *et al.*, 2004; Przeslawski *et al.*, 2012; Robinson *et al.*, 2015). Studies of fish were more likely to have continuous time series, presumably because of their economic importance, whereas observations for other taxa often came from comparisons of two points in time. We encourage authors to look for and publish resurveys of historical sampling, regardless of whether

there have been considerable changes in distribution, to help overcome potential publication biases. Efforts to digitize and publish historical data sets (e.g. Engelhard *et al.*, 2014), combined with the growth of data journals with the mandate that data generated using public funds must be made available, may lead to many such data sets surfacing in the future, providing a richer and less biased basis to assess responses to climate change.

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

Studies with single species or short time series are often excluded from meta-analyses because of perceived publication bias towards publishing results consistent with climate change (Parmesan & Yohe, 2003; Parmesan, 2007). Based on the analysis of length of study as a predictor, we found no publication bias in distribution studies and only a small bias in phenology studies. Publication bias may be less prevalent in marine than terrestrial studies because overall there are more multispecies studies in marine ecosystems where sampling methods tend to collect numerous organisms (e.g. fish and plankton) by nets (Richardson *et al.*, 2012).

We found that inclusion of non-climatic factors in the analysis increased the estimated rates of phenology change, but had no effect on rates of distribution

change. However, few studies included non-climatic factors, so further investigation of how climate responses interact with factors such as fishing pressure and eutrophication is important. Phenology is sensitive to multiple human impacts, and it may be that in the studies analysed here, those impacts are also causing seasonal timings to occur earlier. Given the paucity of studies, further work is required to assess the interaction between climate change and other variables (Parmesan *et al.*, 2013).

Ecological traits

We found that pelagic and demersal species tended to move faster than coastal (inshore) species. Coastal species such as kelps and rocky shore invertebrates may be less able to track warming because their distributions are restricted to the coast, and hence subject to non-climatic biogeographical barriers to simple latitudinal shifts (Broitman *et al.*, 2008). For instance, limited availability of hard substrates on Australia's east coast may limit poleward migration of rocky intertidal organisms (Poloczanska *et al.*, 2011).

Contrary to previous studies for terrestrial and marine ecosystems, we did not find that leading edges moved faster than trailing edges (Parmesan *et al.*, 1999; Sunday *et al.*, 2012; Poloczanska *et al.*, 2013). Range edges are more likely to be detected with occurrence-based measures, because species tend to be rarer at their range edges (Sagarin *et al.*, 2006); therefore, the measurement type and the position of measurements within a species' range may be confounded. In our analysis, sufficient measurements of species abundance at range edges were available to distinguish the effects of range position and measurement type on the rate of distribution shift. We found that occurrence-based measurements were generally faster than abundance-based measurements. Thus, if measurement differences are not accounted for, studies may overestimate the rate of shift at range edges, because of the bias towards measuring edges using single individuals.

Gaps in climate change ecology studies

Our analyses revealed that many gaps remain in our understanding of distribution and phenology responses to climate change. Gaps are a consequence of not only geographical biases in sampling effort, but also how different taxa are studied. In particular, a strong geographical bias exists towards temperate regions, where data collection efforts have historically been the greatest. Tropical regions, grossly under-represented in current studies (Lenoir & Svenning, 2015), are expected to display some of the highest rates of distribution change,

particularly in marine systems (Burrows *et al.*, 2014), and the distributions of tropical taxa may be particularly susceptible to warming (Sunday *et al.*, 2012; Molinos *et al.*, 2015). Moreover, the subtropical and tropical ocean represents ~70% of the global ocean surface, implying that the current paucity of studies of distribution and phenology shifts in the tropics affects our capacity to extrapolate available data to global rates. Global rates of distribution change estimated here are therefore likely lower than those that would be inferred if the studies were randomly distributed across latitudes.

There were few long-term phenology studies in the tropics. While seasonality in temperature is weaker in the tropics and our results suggest phenology change is slower towards lower latitudes, warming can still drive temporal changes in species abundance, for instance blooms of dangerous jellyfish (Jacups, 2010). In addition to warming, seasonality along tropical coastlines can be driven by precipitation (Van Schaik *et al.*, 1993; Chambers *et al.*, 2013). For example, the timing of juvenile prawn migrations from rivers to the ocean is related to cumulative rainfall in tropical river basins (Staples & Vance, 1986). Phenological response to precipitation is more difficult to predict than warming-related responses because species may shift earlier or later (Chambers *et al.*, 2013). Impacts of climate change on tropical seasonality have historically been neglected and warrant further studies.

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

Few observations of marine phenology were available from autumn or winter, a potential temporal bias that also occurs in terrestrial studies of phenology (Gallinat *et al.*, 2015). The lack of data on phenology from autumn and winter could partially reflect the fact that many species perform many of their most important processes (e.g. feeding and reproduction) predominantly in spring and summer. There are also many more spring than autumn observations for terrestrial ecosystems (Parmesan & Yohe, 2003). But unlike marine systems, terrestrial systems do have a few very long-term (e.g. grape harvests over 800 years (Menzel, 2005)) and iconic (e.g. fall colour indexes in New England, USA (Gallinat *et al.*, 2015)) autumn measurements. We found evidence that autumnal events were shifting later, rather than earlier, which is consistent with lengthening seasons. Measuring autumn phenology in higher latitudes is therefore an important knowledge gap in both marine and terrestrial systems. Because of this gap, we have little information on how growing seasons may be extended by warming (for an example see Moore *et al.*, 2011).

Recommendations for measuring change

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

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

Covariates, particularly those not related to climate, are key to consider when analysing time series. A typical test is to ask whether warming is driving an observed change, with the null hypothesis being warming is not a factor. Greater consideration of other alternatives is important (Brown *et al.*, 2011), including non-climate drivers of distribution and phenology. For instance, changes in depth range of an organism could be driven by warming, but the potentially confounding effect of fishing pressure changing with depth should

also be considered in such an analysis (Dulvy *et al.*, 2008; Engelhard *et al.*, 2014).

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

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

Meta-analyses of species responses to climate change. It is especially important for meta-analyses of species responses across many studies to include the influence of different variables explicitly in a statistical model. Important covariates include measurement and ecological variables. Past studies have either ignored these differences (Poloczanska *et al.*, 2013) or tried to remove non-similar studies (Parmesan & Yohe, 2003; Parmesan, 2007; Przeslawski *et al.*, 2012). While including additional measurement variables in analysis did not significantly change our results when compared to previous analyses (Poloczanska *et al.*, 2013), it did shed important light on factors affecting distribution and phenology change. Removing studies from analyses focuses on a subset of potential biases (e.g. only including studies on multiple species or time series greater than a certain length) and is a blunt approach that does not consider other potential sources of bias (e.g. measurement type, latitude, non-climate factors). Thus, removing studies from analysis reduces the power to detect real biological effects and therefore should be avoided where possible.

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

When designing a study, abundance-based measures therefore offer more explanatory power because they can be used to measure both colonization and establishment. Further, abundance-based measures will be less influenced by extreme occurrences of individuals, so may be a more robust measure of change (Brown *et al.*, 2011). However, there may be trade-offs in sampling effort that warrant consideration. Occurrences are cheaper to measure than abundances, particularly for rare species, so occurrence surveys may cover larger areas and a greater range of species than abundance-based surveys could for the same cost. Further, occurrence-based measures are easier to obtain from non-experts, such as through citizen science programmes or from observations from fishers (Robinson *et al.*, 2015). Occurrence-based measures could therefore provide a more useful early warning of invasion of new species, but do not necessarily indicate establishment of a new population.

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

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

We found that measurement biases can have a substantial effect on inferences about the impacts of climate

change on distribution and phenology. Greater consideration of measurement bias in climate impact studies will improve our understanding of how measurement methods affect observations and ultimately contribute to a more representative view of the impacts of climate change on organisms.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Distribution studies, rates of change and factors used in the analysis.

Table S2. Phenology studies, rates of change and factors used in the analysis.