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

Brown, Christopher J.; O'Connor, Mary I.; Poloczanska, Elvira S.; Schoeman, David S.; Buckley, Lauren B.; Burrows, Michael; Duarte, Carlos M.; Halpern, Benjamin S.; Pandolfi, John M.; Parmesan, Camille; Richardson, Anthony J.

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Causes of variation in estimates of species’ distribution and phenology responses to climate change

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Title: Causes of variation in estimates of species’ distribution and phenology responses to climate change

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Abstract

Climate change is driving shifts in species’ distribution and phenology. Studies have evaluated how well ecological traits, such as mobility or reproductive mode, explain variation in observed rates of shift. However, these estimates could also be influenced by methodological attributes. We compiled a global dataset of marine species’ distribution (n=359) and phenology (n=125) responses to climate change to assess the relative importance of ecological traits and methods in measurements of change. We found methodological attributes explained 42% of the variation in range shifts compared to 53% that could be attributed to ecological traits. For ecological traits, we found strong variation in the magnitude of distribution change among taxa, that changes were greater for pelagic and demersal (vs coastal) species, and greater for studies measuring populations at range centres and leading (rather than trailing) edges. For methodological traits, greater range shifts were observed when single occurrences were used to define range shifts (rather than abundances or multiple occurrences over a large portion of a range boundary), and for time series with lower than annual frequency. For phenology, different taxa clearly had different rates, but no ecological traits were important for explaining this variation, whereas methodological attributes were significant although they accounted for only 13% of observed variation. Studies in which other potential drivers of phenology were considered, such as fishing pressure, documented faster changes in timing. Finally, we found indications of publication bias in phenology studies, with those having fewer species more likely to report stronger advancement. Our analyses indicate that methodological attributes should be explicitly considered when designing, analysing and comparing results among studies. We provide recommendations for the most appropriate metrics and analyses for measuring the response of organisms to climate change.
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 global climate change has been matched by a global biological response. At local scales, measurements and forecasts of distribution and phenology change driven by climate change can inform conservation and our understanding of basic ecological processes. For instance, recent climate change has driven the invasion of pest species (Ling et al., 2008), contributed to declines in commercial important fish species (Beaugrand & Kirby, 2010) and appears to be increasing mismatch in seasonal timings between predators and their prey (Barbraud & Weimerskirch, 2006, Edwards & Richardson, 2004).

Despite an overall broad consistency in species’ responses to climate change, there is a large amount of variability in magnitudes and patterns of responses (Parmesan, 2007, Poloczanska et al., 2013). 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, biological traits and local environmental variables may explain variability in responses (Perry et al., 2005, Pinsky et al., 2013, Poloczanska et al., 2013, Wolkovich et al., 2012). All of these approaches base their inferences on robust measures of distribution and phenology.

Measures of distribution and phenology change are influenced by a suite of decisions that are made in two stages of all studies: their design and data analysis (Bates et al., 2014a, Brown et al., 2011). In the study design phase, for example, it is decided how a species’ distribution is measured. It could be by censuses of populations across latitude, with distribution change quantified as shifts in the mean latitude (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 seasonal events can be measured by censusing a population throughout a
season, or as the first and last individuals to breed (e.g. Barbraud & Weimerskirch, 2006, Fitter & Fitter, 2002). Measures of distribution and phenology based on single individuals rather than population averages may lead to inaccurate estimates of population response to climate change. For instance, single individuals may by chance have extreme responses (Brown et al., 2011) and measurements using single individuals are susceptible to detection biases (Bates et al., 2015, Cook et al., 2012).

In the analysis phase, most climate change studies include only a single predictor – temperature – to explain changes in distribution or phenology (Brown et al., 2011). Other anthropogenic variables (e.g. fishing, eutrophication, habitat loss) and not climate change could potentially be responsible for the observed biological changes (Engelhard et al., 2014). Some studies use more sophisticated approaches. For example, the distribution of marine fish has been separated into drivers related to climate change and those related to changes in fishing pressure (Engelhard et al., 2011). It is unknown whether studies that do not account for other potential anthropogenic drivers lead to higher estimates of impacts of climate change.

Measurement type can affect the estimates of a species’ response to climate change. A greater understanding of how measurement type affects observed responses to climate change will benefit distribution and phenology studies in four main ways. First, studies that analyse existing data sets need to know if historical choices made about field data collection limit the questions that can be asked about responses to climate change. For instance, museum records of species occurrences can be an unreliable source of information for historical range boundaries, because sampling effort is often unknown (Przeslawski et al., 2012, Shoo et al., 2006). Second, many regional studies draw comparisons of rates of change with other studies, to identify how biological differences and similarities may influence a species’ response (e.g. Richardson, 2008). Comparisons of change may also need to consider
differences in measurement methods across studies. Third, new time-series are being designed
with the aim of quantifying future distribution and phenology change. The design of new
time-series should consider how data collection methods, like consistency of sampling effort
through time (Bates \textit{et al.}, 2015), affects the estimated magnitude of responses to climate
change. Finally, meta-analyses of existing studies must standardise for study differences, or
constrain comparisons to be among studies with similar methods (Parmesan, 2007,
Przeslawski \textit{et al.}, 2012). For instance, differences in rates of range shifts among European
butterflies, birds and plants could be a consequence of taxonomic identity, geographic biases
or differences in the metrics used (Parmesan and Yohe 2003).

Here we examine potential causes of variability in marine species distribution and phenology
responses to climate change using a meta-analysis. We control for biological traits of the
study organism, the study design and measurement types in analysis. This enables us to
examine how study differences may bias measured rates of change and affect inferences about
the biological drivers of change. After identifying key variables that modify rates of change,
we then investigate the variation in what different studies are measuring.

\textbf{Methods}

\textit{Database}

We analysed the database of peer-reviewed studies of observed impacts of climate change on
marine organisms compiled by Poloczanska \textit{et al.} (2013). Analyses were restricted to a subset
of studies where rates of range change in phenology or distribution were reported or could be
calculated.

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 biological 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 experiments were excluded. Data spanning at least twenty years 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, since 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 pseudo-replication of observations. Multiple studies may analyse the same dataset, or multiple metrics of change can be 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. Pseudo-replicated observations were removed from the database, using a decision tree based on data and analysis quality (Poloczanska et al., 2013). A resulting 35 distribution studies with 359 observations of change and 26 phenology studies with 125 observations of change were included in our analyses.

**Analysis of rates of change**

First, we summarize measurements of distribution and phenology change by type of metric, taxon, and how they were measured. We then conducted analyses to examine how rates of change were influenced by ecological and measurement predictor variables. Rates of change, in kilometres 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. Rates were recorded as positive where they were consistent with a response to climate change (generally polewards for distribution or earlier timing for phenology, but see Burrows et al., 2011) and negative if they were not consistent with climate change.

Analysis of rates of change tested predictor variables that were selected based on available data. Predictors were divided into two categories: measurement types and biological traits.
For measurement types 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 an 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 with 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 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.

For biological traits we considered whether life-history development type (direct, meroplanktonic, planktonic), the depth range of the organism, exploitation status, and the mean latitude of the observations for a species could influence the rates of change measured. Additionally, for distribution we considered whether the measurement was made for a leading or trailing edge, or for the population centre. For phenology we considered the season of the measurement. We included the velocity of climate change for distribution and phenology as a measure of physical variation among sites (Burrows et al., 2011). For distribution, velocities were calculated as the spatial gradient in temperature divided by the temporal change, following the methods in Burrows et al. (2011). For phenology, velocities were calculated as
the seasonal gradient in temperature divided by the inter-annual trend (Burrows et al., 2011).

For each study, we used the velocity at the observation’s centroid and velocities were calculated over the time-period for each specific observation.

Analyses for how predictor variables influenced rates of change were conducted with linear mixed-effects models using the ‘lme4’ package in the R programming language (Bates et al., 2014b). Taxon was treated as a random effect because our main interest was to characterise rates of change by biological traits and measurement type, which are correlated with taxa. We developed full models including all physical, ecological and measurement predictor variables for each of distribution and phenology. Models were simplified using a step-wise 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 Aikake Information Criteria because the BIC is less likely to include spurious predictors and it controls for sample size (Burnham & Anderson, 2002). Thus, our final model is conservative in only including the strongest predictors of responses to climate change.

We plotted the effects of the predictors included in the final model with confidence intervals on a term plot. Confidence intervals were estimated using bootstrapping (using the ‘boot’ package in R, see Canty and Ripley (2014)). Term plots illustrate the mean effects for a predictor relative to the mean across all values or levels that a predictor can take. Term plots are an appropriate way to present modelled effect sizes when there is no clear control treatment. Note that a negative effect size on the term plot does not necessarily mean an inconsistent response to climate change, because it may simply mean a slower response than other effects. We estimate the relative importance of measurement predictors when compared to ecological predictors by comparing the variance explained by each set of predictors. We estimate variance explained by either measurement of ecological predictors 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 examine in more detail how the inferences drawn from 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**

**Gaps in observations of distribution and phenology**

Published studies had some biases in their attributes (Fig. 1). Most studies had more than one species, although very few studies analysed >10 species (Fig. 1a). Occurrence-based measures of distribution were slightly more common than abundance-based measures (Fig. 1b). For phenology, abundance-based measures were more common than measurements of extreme individuals (Fig 1b). A large number of distribution records compared two points in time, whereas most phenology records used continuous time series (Fig. 1c). Both distribution and phenology records tended to be at mid-to-high latitudes, with phenology records, in particular, biased towards the northern hemisphere and a remarkable paucity of observation for tropical species (Fig. 1d). There was considerable bias in taxon representation. There were a large number of distribution records for bony fish and benthic algae (Fig. 1e), whereas most phenology records were for seabirds and plankton, which were poorly represented in distribution records. 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 rate of distribution change was affected significantly by two biological factors and two measurement biases (Table 1, Fig 2). Measurements made using irregular time-series or those that were calculated by comparing two points in time tended to be faster than continuous time-series. Occurrence-based measures of distribution change were also faster than abundance-based measures. Leading edges and range centres moved faster than trailing edges, and demersal and pelagic species moved faster than coastal species (intertidal species and seabirds). When these effects were accounted for, the model indicated that phytoplankton had the fastest rate of change, whereas benthic cnidarians and benthic molluscs had the slowest rates of change (Fig. 2). Overall, methodological variables accounted for 42% of the variation in rates of change, whereas ecological variables accounted for 53%.

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

The rate of phenology change was affected significantly by two factors (Table 1, Fig 3). Studies that included fewer species 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. Overall the effects of the fixed effects were small compared to the effect of taxa on rates of change. Larval bony fish were most likely to be moving to earlier timings, whereas, seabirds had slow timings or were likely to be moving later. Overall, the two methodological variables accounted for 13% of the variation in rates of change.

Differences in how responses are measured across taxa

For the factors that were significant in the analyses of rates of change, we now examine how observations are distributed across taxa to explore biases in global research. Numerous taxa did not have measurements at some levels of each factor (Figs 4 & 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 abundance-based measures came from fish studies, which typically use nets to sample species in fisheries surveys (Fig. 4). Occurrence-based measures were predominant in other taxa. Fishery surveys also had many more continuous time-series (that tended to underestimate range change), rather than comparisons of two points in time. In particular, benthic molluscs, cnidarians, algae and other invertebrates had no continuous time-series. Fish studies also tended to focus the centres of distribution, rather than the edges.

For phenology, a few taxa tended to have multi-species studies, whereas studies of other taxa focussed on single or just a few species (that tended to show greater change, Fig. 5). Studies with numerous species came from phytoplankton and zooplankton studies, predominantly the Continuous Plankton Recorder survey in the North Atlantic. Studies for seabirds and bony fish had fewer species than for plankton, although most observation came from studies of more than one species.

Very few observations came from studies that considered non-climatic factors in their analyses (Fig. 5). Observations that come from studies that considered multiple factors were mostly for seabirds, but there was also a small proportion for phytoplankton and benthic crustaceans.

**Discussion and recommendations**

We found that variation in methodological approaches explained 42% of the variation in range shifts compared to 53% attributed to ecological traits. For phenology, variation in methodological explained only 13% of observed variation, but there no important ecological traits.

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.,
Typically, meta-analysis exclude some studies to achieve consistency, such as excluding studies of single species to avoid publication bias (Parmesan, 2007, Parmesan & Yohe, 2003). Rather than excluding studies, we used linear models to standardise 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. 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 (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 are an important way to fill data gaps, where there has not been funding to support long-term sampling (e.g. Przeslawski et al., 2012, Robinson et al., 2015, Southward et al., 2005). In particular, 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. 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 changes in single individuals or
detectability of a species, so we expect the observed rate of change to be greater (Bates et al.,
2015, Brown et al., 2011). 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 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 about an
60km/decade lag, which of similar magnitude to rates of change in individual species’ range
centres. Further, this result indicates that caution should be taken when extrapolating rates of
change across different places. 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 are often excluded from meta-analyses because of perceived
publication bias toward publishing results consistent with climate change (Parmesan, 2007,
Parmesan & Yohe, 2003). We did not find this publication bias effect in distribution studies,
but we did find that multi-species studies of phenology tended to have slightly slower rates of
change. Publication bias may be less prevalent in marine than terrestrial studies because
overall there are more multi-species 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. 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. However, it is not clear if the faster phenology
change in studies that considered multiple factors is an interactive response to climate change
and other human impacts. Further work is required to assess the interaction between climate
change and other variables (Parmesan *et al.*, 2013). Including non-climate factors also helps
to test competing hypotheses (Brown *et al.*, 2011). For example, fishing can influence
distribution and estimates of the magnitude of climate change response (Engelhard *et al.*, 2011). Few studies included non-climatic factors, so further investigation of how climate
impacts interact with factors like fishing pressure and eutrophication is important.

*Biological traits*

We found that pelagic and demersal species tended to move faster than coastal 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 biogeographic
barriers to simple latitudinal shifts, and their habitat requirements largely rule out depth shifts
(Broitman *et al.*, 2008). Thus, the taxa effects in our mixed model were similar to previous
analyses which did not account for multiple factors (Poloczanska *et al.*, 2013).

We found that leading edges and centres of ranges moved at similar rates, and both were
faster than trailing edges. This result is similar to that found for European butterflies, in which
leading edges were more than three times as likely to have responded to regional climate
warming than were trailing edges (Parmesan *et al* 1999). However, it contrasts with previous
studies that found range centres moved at rates intermediate to leading and trailing edges
In the analysis here, the type of measure was included as a covariate. Occurrence based measurements were generally faster than abundance based measurements, and there was a bias towards occurrence based measurements at range edges and abundance based measurements at range centres. Therefore, if measurement type is not accounted for, range edges appear to move significantly faster than range centres.

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 of how different taxa are studied. In particular a strong geographic bias exists towards temperate regions, where data collection efforts have historically been the greatest. Tropical regions, grossly underrepresented 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, Molinos et al., accepted) and the distributions of tropical taxa may be particularly susceptible to warming (Sunday et al., 2012). 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, warming can still drive temporal changes in species abundance, for instance blooms of dangerous jellyfish (Jacups, 2010). In addition to warming, tropical seasonality is also driven by precipitation (Chambers et al., 2013, van Schaik et al., 1993). For instance, 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). The impacts of climate change on tropical seasonality warrant further studies.

There was systematic variation 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 no 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 programs (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 uncommon. Fish studies in the database often used fisheries data-sets for analyzing climate patterns. Fisheries surveys are large-scale, regular (usually annual) surveys of abundance indices. They do not have precise information on phenology, but commonly examine distribution change using abundance based measures.

Few observations of marine phenology were available from autumn or winter, a temporal bias that also occurs in terrestrial studies of phenology (Gallinat et al., 2015). 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 year, (Menzel, 2005)), and charismatic (e.g. fall color indexes in New England, USA (Gallinat et al., 2015)) autumn measurements. 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.

(1) Re-analysis 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 colonisation 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.

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).

(2) Qualitative comparisons with other studies

Qualitative comparisons among rates of change are common in regional or taxa 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.

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

Meta-analyses of species responses across many studies should consider the influence of
different variables explicitly in a statistical model. Important covariates include measurement
and biological variables. Past studies have either ignored these differences (Poloczanska et
al., 2013) or removed non-similar studies (Parmesan, 2007, Parmesan & Yohe, 2003,
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 analysis to standardise measurement differences also reduces the
power to detect real biological effects, and should be avoided where possible.

(4) 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 ecological states the time-series aim to monitor should be explicitly
defined and a protocol designed to address these processes. A study that seeks to monitor
invasion of pest species may focus on monitoring for occurrences, to obtain early warnings of
ranges shifts. In contrast, a study that aims to detect ecologically significant change should
focus on abundance monitoring.
When designing a study, abundance-based measures therefore offer more explanatory power because they can be used to measure both colonisation 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, so occurrence surveys may often cover larger areas than abundance-based surveys. Further, occurrence-based measures are easier to obtain from non-experts, such as through citizen science programs 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 sights 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 amongst these is that there is 3 times as much information on changes in distribution than phenology in the ocean, whereas on land there is 100 times more information on phenology than on distribution change (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.

Conclusion
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 impacts studies will improve our understanding for how measurement methods affect observations and ultimately contribute to a less biased view of the impacts of climate change on organisms.

**Acknowledgements**

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### Table 1

Analysis of rates of distribution and phenology change, with the ΔBIC for removing each factor from the reduced model. N.A. Not applicable

<table>
<thead>
<tr>
<th>Factor</th>
<th>Distribution data-set ΔBIC</th>
<th>Phenology data-set ΔBIC</th>
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<tr>
<td>Planktonic larval dispersal type</td>
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<td>Latitude</td>
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**Figure legends**

**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 studies only.

**Fig 2** Term plot for distribution mixed effects model (taxa was random), showing final effects only (selected using BIC, Full model BIC = 3859, reduced model BIC = 3823). Points indicate mean predicted effects and bars are 95% confidence intervals. 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. Note the varying scales for the y-axes.

**Fig 3** Term plot for phenology mixed effects model (taxa was random), showing final effects only (selected using BIC, Full model BIC = 866, reduced model BIC = 851). Points indicate mean predicted effects and bars the 95% confidence intervals. Effects are standardised to the overall mean, so negative effects indicate a tendency toward phenology change that is earlier and consistent with climate change, whereas positive effects indicate a tendency toward 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 0.35.

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.
<table>
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<td>Coastal</td>
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<td>Leading edge</td>
<td>Occurrence</td>
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<td>Two periods</td>
<td>Trailing edge</td>
<td>Abundance</td>
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### Legend

- 0.35
- 0.3
- 0.25
- 0.2
- 0.15
- 0.1
- 0.05
- 0.0

- Zooplankton
- Phytoplankton
- Non-bony fish
- Larval bony fish
- Bony fish
- Benthic molluscs
- Benthic invert.
- Benthic crustacea
- Benthic cnidarians
- Benthic algae
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<td>Benthic molluscs</td>
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Legend:
- 0
- 0.05
- 0.1
- 0.15
- 0.2
- 0.25
- 0.3
- 0.35
- 0.4

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