

LETTER

Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot

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Abstract

Species' ranges are shifting globally in response to climate warming, with substantial variability among taxa, even within regions. Relationships between range dynamics and intrinsic species traits may be particularly apparent in the ocean, where temperature more directly shapes species' distributions. Here, we test for a role of species traits and climate velocity in driving range extensions in the ocean-warming hotspot of southeast Australia. Climate velocity explained some variation in range shifts, however, including species traits more than doubled the variation explained. Swimming ability, omnivory and latitudinal range size all had positive relationships with range extension rate, supporting hypotheses that increased dispersal capacity and ecological generalism promote extensions. We find independent support for the hypothesis that species with narrow latitudinal ranges are limited by factors other than climate. Our findings suggest that small-ranging species are in double jeopardy, with limited ability to escape warming and greater intrinsic vulnerability to stochastic disturbances.

Keywords

Benthic invertebrates, climate change, climate response, fishes, functional traits, invasion, range expansion, range shifts, range size.

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INTRODUCTION

Changes in the distribution of organisms have been reported globally as a fingerprint of global climate change (Parmesan & Yohe 2003; Poloczanska *et al.* 2013). Species responses have been extremely variable, however, both on land and in the ocean. Even within regions where the rate of warming has been relatively uniform, some species have rapidly extended their geographical distributions, while others have moved to a lesser extent, or have even moved in the opposite direction to that predicted (Parmesan & Yohe 2003; Poloczanska *et al.* 2013). Understanding the pattern of variation and identifying where and when species will respond to climate change through range shifts is critical if we are to manage proactively for changes in resource-based human livelihoods and to meet conservation goals. Such inquiry also represents a key opportunity to test existing ecological hypotheses about the relative role of climate in setting species' geographic distributions.

Given an equal pace of climate change, variation in range shifts among species can be broadly viewed as arising from two potential factors: variation in the relative role of temperature in setting range boundaries (sensitivity), and variation in the pace at which new 'potential' ranges become realised

through occupancy changes (responsiveness). For example, we expect species to vary in the extent to which climate directly limits the geographic range, where biotic interactions or habitat are variably important in restricting or facilitating ranges (Brown *et al.* 1996; Sexton *et al.* 2009), leading to differences in the sensitivity of range limits to temperature change. Independently, where species distributions are currently limited by climate, they are expected to have different intrinsic abilities to respond at the population level as their climatic envelopes move across space – either through the pace of dispersal and population increase at advancing range boundaries, or through the pace of climate adaptation, behavioural change, population decline and local extinction at contracting range boundaries (Bates *et al.* 2014b). Although the amount of ecological information required at the species, community, and landscape scales for reliably predicting such responses is potentially vast, certain intrinsic traits may prove useful as proxies for ecological variables that determine sensitivity and responsiveness among species (Poyry *et al.* 2009; Angert *et al.* 2011; Przeslawski *et al.* 2012; Betzholtz *et al.* 2013; Pinsky *et al.* 2013).

To date, analyses of the relationships between species-level traits (hereafter species traits) and geographic range shifts

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have yielded mixed results among terrestrial-based studies, with some traits found to be important some of the time (Poryry *et al.* 2009; Angert *et al.* 2011; Betzholtz *et al.* 2013). However, there are reasons to expect stronger predictive relationships in the ocean. First, range shifts have been faster in the ocean (Perry *et al.* 2005; Sorte *et al.* 2010; Pinsky *et al.* 2013; Poloczanska *et al.* 2013). This faster rate of change can provide greater capacity for detection and analytical power for understanding variation among species. Second, abundance and occupancy patterns are more temporally conserved in terrestrial compared to marine species, a phenomenon attributed to differences in general life-histories and trophic dynamics between the two realms (Webb *et al.* 2011). Third, recent findings indicate that latitudinal distributions of marine species are more sensitive to temperature change compared to terrestrial species. Specifically, terrestrial species tend to be absent from their predicted equatorward range boundaries and have more extreme poleward distributions than predictions based on their thermal tolerances, whereas marine species have ranges that conform more closely to their physiological thermal limits (Sunday *et al.* 2012). Range dynamics on land may therefore be more complex and driven to a greater extent by factors other than temperature, such as moisture, biotic interactions, or other habitat features (in which there is more capacity to thermoregulate), while range dynamics in the ocean may better reflect intrinsic responsiveness to changing isotherms (Sunday *et al.* 2012).

Range extensions and contractions represent two fundamentally different processes influencing population persistence at local scales - colonization and extinction - which are likely associated with different species traits (Hampe & Petit 2005; Angert *et al.* 2011; Bates *et al.* 2014b). While high propagule production and broad ecological generalism (i.e. broad diet and habitat) may increase invasiveness at range extension fronts (Kolar & Lodge 2001), the same traits likely delay extinctions at contracting range edges by increasing persistence (Purvis *et al.* 2000). Indeed, initial attempts to link range shifts of marine species' ranges that combine extension and contractions have failed to identify intrinsic traits related to range shift responses (Przeslawski *et al.* 2012; Pinsky *et al.* 2013). If intrinsic traits are related to range shift dynamics, these will likely differ at contracting and extending fronts, and will be easier to discern at single rather than combined range edges.

Here, we test how several intrinsic species traits, predicted to affect sensitivity and responsiveness of advancing range boundaries, relate to observed range extensions at poleward range fronts. We focus on the coastal waters off eastern Australia, as this relatively large region of rapid warming coincides with many species-level records of range limits spanning decades, for which there is substantial knowledge of life histories for testing the role of species traits. The increased strength of the East Australian Current has led to warming over the past 60 or so years in this region (Ridgway 2007), resulting in a rate of upper ocean warming 3–4 times greater than the global average over the past half century (Hobday & Pecl 2014). During this period of warming, poleward range extensions in the distribution of many species have been observed (Fig. 1). We took advantage of this 'natural experiment' by collating

all the time series on poleward range limits available in this region to test for relationships between six species traits hypothesised to influence range extension rates based on ecological theory, using 50 fish and 53 invertebrate species. We include climate velocity (Loarie *et al.* 2009) in our analyses to estimate how these species traits interact with the expected rate of range shifts through the study period (Angert *et al.* 2011; Pinsky *et al.* 2013). Our hypotheses were based on direct predictions provided by invasion theory, with the expectation that traits related to dispersal potential, population growth rate and ecological generalism will be important positive predictors of poleward range extensions (Table 1). We also tested the hypothesis that species with smaller ranges are more constrained by factors other than temperature – a hypothesis generated from our first analysis – using an independent data set (Sunday *et al.* 2012). Together our results offer advances in our mechanistic understanding of marine species' distributional responses to climate warming.

MATERIALS AND METHODS

Range shift estimates

We compiled range shift data from several sources: (1) all published studies reporting range shifts within multi-species studies of coastal fish and invertebrates in the Tasman Sea (Pitt *et al.* 2010; Stuart-Smith *et al.* 2010; Last *et al.* 2011; Poloczanska *et al.* 2011), (2) underwater visual census data compiled using a standardised methodology through the Reef Life Survey (RLS; Edgar & Stuart-Smith 2014), (3) long-term temperate reef monitoring programs (LTRMP, Edgar & Barrett 2012) and (4) eight additional observations based on the methods in Last *et al.* (2011; Last, *personal communication*,

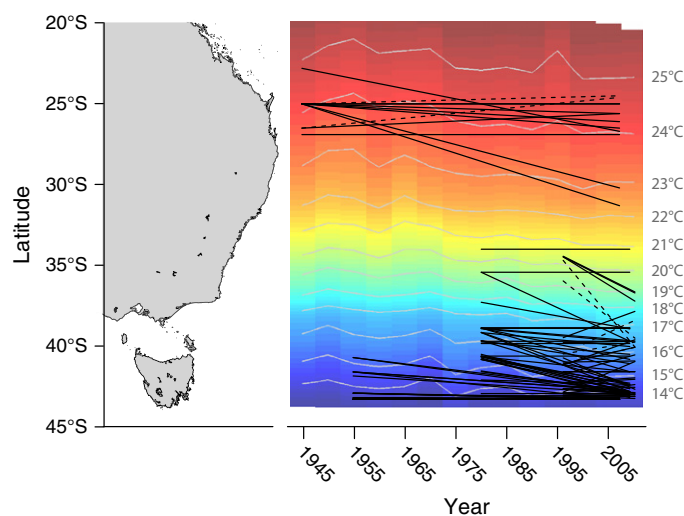


Figure 1 Poleward range boundary shifts of coastal marine fishes and invertebrates in eastern Australia (black lines), and latitudinal changes in mean annual temperature isotherms over study period (colours). Each different colour band represents the mean annual temperature of the coastal zone tracked across latitude through time; light grey lines represent temperature isotherms as labelled at right. Dashed lines represent species not included in analyses because of incomplete trait data.

Table 1 Hypotheses on the influence of species traits on climate-induced range extensions

Trait	Hypotheses
Reproductive mode	<ol style="list-style-type: none"> 1. Species with more dispersive reproductive modes (planktotrophic and lecithotrophic larvae) will have greater extension rates than species that brood offspring or deposit benthic eggs 2. Alternatively, species with less dispersive reproductive modes may better overcome Allee effects, leading to faster colonisation of new regions
Adult motility	<ol style="list-style-type: none"> 1. Species that swim as adults should have faster range extensions than species with low mobility such as crawlers and sessile organisms
Maximum body size	<ol style="list-style-type: none"> 1. Body size correlates positively with fecundity (Roff 1992) and home range size (Kramer & Chapman 1999), so larger-bodied species could more readily populate new regions 2. Alternatively, smaller-bodied species within each taxa (e.g. fishes) have younger ages of first reproduction and faster rates of intrinsic population growth (Denney <i>et al.</i> 2002), and therefore faster range extensions (Perry <i>et al.</i> 2005)
Latitudinal range size	<ol style="list-style-type: none"> 1. Species with broader latitudinal ranges typically experience a broader range of biotic and abiotic conditions, and therefore have greater ecological versatility (Hengeveld 1990). Fewer ecological constraints could lead to greater range extension rates in broad-ranging species 2. Similarly, species with broader latitudinal ranges may have greater local abundance (Lawton 1999) and therefore exert greater propagule production, leading to faster range extensions (Feary <i>et al.</i> 2013)
Trophic level/position	<ol style="list-style-type: none"> 1. Higher trophic levels will have slower range extensions, being more constrained by prey availability (Buckley and Kingsolver, 2012) 2. Alternatively, higher trophic levels may be less sensitive to prey type, being relative generalists (Rooney <i>et al.</i> 2008), and thus have faster range extensions
Diet specificity	<ol style="list-style-type: none"> 1. Species with narrow dietary requirements are less likely to find their specific prey in new regions, and therefore have slower range extensions. In contrast, omnivores may have the greatest diet generalisation and therefore be the least constrained by trophic interactions

Note alternative hypotheses within trait categories can be distinguished by the overall pattern, while the relative importance of each trait can be evaluated by model comparison.

see SOM for details). We only included studies in which range shifts were assessed for multiple species, to avoid the pitfalls of publication bias towards more detectable records of range extensions in single-species studies (see Poloczanska *et al.* 2013 for an exploration of the effect). After filtering for repeated sampling across studies (see Supplementary Methods) we identified estimates of poleward range boundaries across time in 104 species (50 fish, 54 invertebrates; Fig. 1; Dataset 1). For each species and survey time point, the southern-most location in which the species was observed was

taken as the poleward range boundary. Although a simplistic estimate of a range boundary, this was a necessary approach because multiple observations through time and space were not available for most species. Although we expect error-related noise in these estimates of range boundaries, and possibly greater noise for low-detectability species, this should not result in a bias in error related to the magnitude of range shifts or to species detectability if sampling effort is consistent through time (Bates *et al.* 2015). Most range shift estimates were from repeated transect studies or extensive searches for species presence based on species lists – therefore, sampling effort was relatively consistent through time (see Table S1 for details from each study). Furthermore, the species retained within each data source were those detected at multiple sites across time periods, and thus more likely to have high detectability (see Table S1 for details).

For 18 of the 104 species (17%), poleward range boundaries moved towards the equator during the study period, i.e. in the opposite direction as expected. This type of change may represent (1) inherent variability in poleward range edges, (2) indirect ecological responses to warming, (3) responses to other stressors (such as habitat loss or extraction) and/or (4) detection error. Regardless of the underlying mechanism(s), we assumed that the factor(s) leading to these equatorward movements were equally influential across the entire data set, and therefore retained these equatorward-moving species in our analysis as our best means to model the residual error.

Climate expectation

Relating species traits to range shifts observed at different times and places requires accounting for potentially differing rates of temperature change, estimated by the rate of isotherm displacement across space, or ‘climate velocity’, associated with warming (Loarie *et al.* 2009; Pinsky *et al.* 2013). We therefore calculated an expected distance of range boundary shift for each species, based on the displacement of isotherms from the original range boundary during the time period of the study. We analysed displacement of isotherms in the north–south (meridional) direction (Fig. 1), using isotherms of annual mean sea surface temperature based on the HadISST historical reconstruction (Ref. S1 in Supporting Information). We used means for 1-degree latitudinal bands extending from the coast to 156 °E. For each species, we calculated the isotherm at the original poleward range boundary (in latitudinal degrees to 2 decimal places) by interpolating temperatures across each 1° latitudinal band, and determined the north–south displacement of this isotherm from the original poleward range boundary at the end of each study. For species in which the isotherm moved beyond the southern edge of Tasmania during the time period of study ($n = 21$), we cropped the expected distance of southern range extension at the southern latitude of Tasmania’s shallow-water regions (43.64 °S), beyond which coastal species could not exist or could not be observed, as the next suitable coastal habitat is some 1500 km further south at Macquarie Island. However, the final latitudes of isotherms for these species were not far beyond this boundary (all within 0.4° latitude from this imposed limit). Thus, results were similar with or without this cropping.

Changes in abundance

Changes in species' range boundaries may occur as a density-dependant response to changes in abundance within the range through time (Macall 1990). Such abundance changes may be climate related, or may reflect species-level responses to other drivers. To investigate the possible role of abundance change on range limit shifts, we collated available abundance time series for species in our data set from the LTRMP database between 1992 and 2013 (Edgar & Barrett 2012). This yielded abundance time series for 53 species within our data set (51% of species) across multiple sites throughout southern Australia (Fig. S1). We defined abundance change for each of these species as the linear coefficient of year on abundance within sites (see Fig. S1 for details on model fitting to estimate this metric). We included abundance change as a variable in our range shift models (using a subset of data, see Analysis) to investigate the relative role of abundance change on range extensions and their relationships with species traits.

Species traits

We selected six species traits for which we could establish testable hypotheses on range extension rates based on the literature (Table 1), and for which data were generally available (described below; data sources reported in Dataset 1).

For reproductive mode, we categorised species by their life histories into livebearers, egg-layers (with crawl- or swim-away juveniles), and those with lecithotrophic or planktotrophic larval development, respectively. However, there was only sufficient data coverage in our multivariate models when we concatenated reproductive mode into low-dispersive (brooding and egg-laying) and high-dispersive (planktonic) modes. Species that brood or lay eggs and subsequently release planktonic larvae (e.g. the spiny lobster, *Jasus edwardsii*) were considered planktonic. Adult mobility was categorised as high (swimming) or low (crawling or sessile). All fishes were swimmers, and there were two swimming invertebrates (squid), the rest being crawlers ($n = 39$) or sessile (12). Maximum body size estimates were initially based on data in FishBase (Ref. S2 in Supporting Information), and validated or updated where possible with more recent values from the primary literature, from the CSIRO life history database (Ref. S3 in Supporting Information), and from the RLS database used by Stuart-Smith *et al.* (2013). Total length was used as the estimate of body size for fishes, anterior-to-posterior length for most invertebrates, diameter for sea urchins and anemones, dorsal mantle length for cephalopods, and ray-length for sea stars. Trophic position was categorised based on diet descriptions as herbivores, omnivores or predators. In our fish-only analyses, we used trophic level scored from data provided through FishBase as a continuous numeric variable.

Latitudinal range size estimates were based on information from the Global Biodiversity Information Facility (Ref. S4 in Supporting Information), from FishBase, or from values in the primary literature. Latitudinal range size was correlated with the equatorward (usually tropical) extent of species' ranges ($r^2 = 0.93$) but not the poleward range

boundary in southeast Australia ($r^2 = 0.16$). For diet specificity, we used expert knowledge (authors SF and GE) to identify species known to be dietary specialists. However, only three specialist species (all herbivores) were identified: *Aplodactylus lophodon*, *Kyphosus sydneyanus* and *Olisthops cyanomelas*. We had complete species trait coverage for 89 species (46 invertebrates; 43 fishes; Dataset 1), and near-complete coverage (lacking reproductive mode) for 104 species (54 invertebrates and 50 fishes). This represents *c.* 15% of shallow reef fishes from this region and 8% of the mobile invertebrates (based on all records in the RLS database for this region).

Analysis

We used multi-model averaging of mixed-effects linear models with maximum likelihood estimation to test the effect of species traits on shifts in poleward range boundaries. We tested for relationships in all data together and in fishes alone, expecting some traits (e.g. body size and trophic level) to be a better proxy for ecological processes within fishes. Climate expectation, abundance change, and all species traits were initially included as explanatory variables in our global models. We subset the data to include only species for which we had information on every variable and normalised all continuous variables around zero with a standard deviation of one. All variables were examined for multi-collinearity and we found mobility and body size to be highly collinear in the all-species models (see Table S2). We therefore included only mobility, expecting a more direct mechanistic effect of mobility on range shifts. In the fish-only model, body size was not strongly collinear with other traits and so was included. All other traits had variance inflation factors < 2.5 (Table S2).

Interactions between each trait and the climate expectation were included to allow for trait-based differences in the rate of responses to locally changing isotherms. We also explored the interaction between mobility and life history mode, with the explicit expectation that life history mode would have a stronger effect on range extensions in species with low adult mobility. Although phylogenetic relationships were not available for the wide sample of taxa within our analysis, we accounted for non-random sampling across taxonomic groups by including taxonomic position as a hierarchical random effect on the intercept from Phylum to Family. We explored the inclusion of source 'study' as a second (crossed) random effect to test for systematic differences in the relationship between range shift and traits among studies, but found that the global models were not better fit when study was included (using the Akaike information criterion; AIC; Table S3), and relationships between traits and range shifts were similar with or without its inclusion (Table S4), and therefore dropped it from global models. In the fish-only model, we found that study duration had a positive effect on residual variance (lower AICs in Table S3) and assumptions of heteroscedasticity were better met with its inclusion, so we included duration as a factor affecting variance structure in our global models. We fit these models using the *nlme* package in *R* (Ref. S5 in Supporting Information).

From each of our global models, we ran all possible candidate models that included climate expectation, setting the maximum number of variables as less than one-tenth of the sample size to avoid over-parameterisation (model results were similar if the number of variables was 1/15 the sample size, see Table S5). From these model sets, we identified the confidence set of models as those comprising the top 95% of model weights using AIC adjusted for small sample sizes (AICc). For each variable we calculated the model-averaged parameter estimates and relative variable importance values (w_i) as the sum of Akaike weights from the confidence set of models which included the trait, using the MuMIn package in R (Ref. S6 in Supporting Information). We calculated a likelihood-ratio-based pseudo-R-squared for each model as implemented in the MuMIn package. In addition, we extracted the results of the single best model that included species traits, and the climate-only model, which used only climate expectation as a predictor for range shifts (Pinsky *et al.* 2013).

Preliminary results showed that range shifts were not related to abundance change (Tables S6 and S7; Fig. S1), and the basic relationships with other traits were similar when this variable was excluded from the analysis to yield a much larger complete data set (Table 2). Likewise, in the fish-only model, reproductive mode had low variable importance with uncertain effects (Tables S6 and S8), and removing it further increased sample size without changing relationships between range extensions and other traits (Table 2). We therefore re-ran the models using the larger complete data set without abundance change and (for fish) reproductive mode in order to increase sample size.

Relationship between latitudinal range size and climate equilibrium

We used an independent data set to further test the hypothesis that marine species with smaller ranges are in greater disequilibrium with climate (Early and Sax, 2014). We used previously published data on thermal tolerance limits and latitudinal range size from a global sample of marine species (Sunday *et al.* 2012). For 33 marine fishes and one invertebrate (Dataset 2), we extracted the *underfilling* metric described in Sunday *et al.* (2012), representing the extent to which species occupy a smaller latitudinal range than would be predicted given their thermal tolerance. For these species, we regressed underfilling as a function of latitudinal range size, considering poleward and equatorward range boundaries separately, by fitting a generalised linear model with a Poisson error distribution for zero-bound data using the *lme4* package in R (Ref. S7 in Supporting Information). We cropped range overfilling at zero (i.e. ranges that extended to more latitudes than predicted from species' thermal tolerance), for illustrative purposes, although this did not impact results.

RESULTS

Species' poleward range boundaries moved towards the poles on average, with high variation in shift rates (mean \pm SD, all species: 24 ± 87 km dec⁻¹; just fishes: 38 ± 70 km dec⁻¹). Although highly variable, the means of these rates were similar to the mean rate of isotherm displacement from the original range boundaries (all species: 21 ± 13 km dec⁻¹; just

fishes: 27 ± 6 km dec⁻¹). Climate expectation alone thus explained some of the variation (23.1% in the full data set and 17.3% in fishes; see pseudo-R-squared of climate expectation only models in Table 2). However, including species traits more than doubled our ability to explain variation in range extensions. The best model with species traits explained 57.8% of the variation in all species (a 2.5 times increase), and 46.2% of variation in fishes (a 2.7 times increase; see pseudo-R-squared values in Table 2).

In the all-species model ($n = 89$), trophic position was the most important trait, and there was a positive interaction between omnivory and climate expectation on distance of range extensions (Table 2, Fig. 2). This suggests omnivores tracked climate expectations better than predators and herbivores. However, this finding was highly influenced by two omnivorous barnacles with large range shifts (*Chthamalus malayensis* and *C. withersii*), in contrast to seven herbivorous snails with little movement despite high expectations (Fig. 2), and the effect of trophic position was lost if these two barnacle species were removed (Table S9).

In addition to trophic position, mobility had a positive interaction with climate expectation, and latitudinal range size had a direct positive effect on range extensions. These effects were even stronger (with higher certainty and variable importance) when the two high-leverage barnacle species were removed (Table S9). Hence, species with high mobility (swimmers) tracked climate velocity faster than those with low mobility, and wide-ranging species moved faster regardless of climate velocity.

In the fish-only model ($n = 50$), latitudinal range size was the most important single trait explaining variation in range extensions (Table 2, Fig. 3). There was a strong positive interaction between latitudinal range size and climate expectation; species with larger latitudinal ranges had the greatest range shifts and were best able to track mean isotherms (Fig. 3). The species with the largest latitudinal range sizes were the giant grouper (*Epinephelus lanceolatus*), yellowtail kingfish (*Seriola lalandi*), tiger shark (*Galeocerdo cuvier*), short-tail stingray (*Dasyatis brevicaudata*), and the Maori wrasse (*Ophthalmolepis lineolata*), which were all above the 85% quantile of range shift velocities for fishes (> 92 km dec⁻¹).

There was also evidence for a weak negative relationship between trophic level and range extensions in fishes, with low-trophic level fishes responding faster than higher trophic level fishes for a given range size (although the 95% confidence interval did cross zero; Fig. 3a and c). This was driven mainly by greater range extensions in herbivores with medium-sized ranges, such as the black drummer (*Girella elevata*), silver drummer (*Kyphosus sydneyanus*), zebrafish (*Girella zebra*) and rock cale (*Aplodactylus lophodon*), compared to higher level consumers (Fig. 3c).

Other traits had more uncertain effects, with 95% confidence intervals of model coefficients crossing zero (Figs. 2 and 3). Notably, reproductive mode was not strongly related to the rate of range shifts in either fishes or invertebrates, and there was high variation in responses within each reproductive mode (Fig. S2). Indeed, some species without a larval dispersal phase extended their ranges as quickly as those with planktonic larvae (Fig. S2).

Table 2 Models explaining the distance (km) of latitudinal shifts in all marine species and fishes only

Explanatory variable(s)	Multi-modal average				Best model	Climate-only model
	w_i	coef.	Lower CL	Upper CL		
All taxa ($n = 89$)						
Climate expectation	1	0.06	-0.32	0.43	+	+
Trophic position (omnivore)	1	0.78	0.24	1.31	+	
Trophic position (predator)	1	-0.28	-0.86	0.31	+	
Trophic position (omni.) × climate expectation	1	1.07	0.67	1.48	+	
Trophic position (pred.) × climate expectation	1	-0.61	-1.75	0.53	+	
Adult mobility (high)	1	0.59	-0.37	1.55	+	
Adult mobility (high) × climate expectation	1	2.05	0.91	3.20	+	
Log lat. range size	0.52	0.25	0.03	0.47	+	
Specialisation	0.4	0.54	-0.40	1.48		
Specialisation × climate expectation	0.2	0.61	-1.82	3.04		
Life history mode (pelagic)	0.16	0.22	-0.43	0.87		
Life history mode (pel.) × climate expectation	0.03	-0.39	-1.60	0.81		
Life history mode (pel.) × adult mobility (high)	0.03	-0.14	-1.37	1.10		
Lat. range size × climate expectation	0.01	-0.06	-0.26	0.15		
pseudo-R-squared					0.578	0.231
AICc					226.0	250.1
Akaike weight					0.228	< 0.001
Fishes ($n = 50$)						
Climate expectation	1	0.40	0.11	0.69	+	+
Log lat. range size	1	0.21	-0.19	0.60	+	
Log lat. range size × climate expectation	0.8	0.44	0.11	0.77	+	
Trophic level	0.32	0.64	-0.31	1.59		
Specialisation	0.3	-0.23	-0.48	0.02		
Log body size	0.05	-0.11	-0.42	0.20		
Trophic level × climate expectation	0.02	-0.14	-0.46	0.18		
pseudo-R-squared					0.462	0.173
AICc					142.1	152.4
Akaike weight					0.256	0.001

The relative variable importance (w_i), variable coefficients (*coef*) and their 95% confidence limits (*CL*) are shown for each variable from the multi-model average, showing contrasts from base levels (climate expectation = 0, log latitudinal range size = 0, trophic position = herbivores, trophic level = 1, specialisation = not specialised, life history mode = benthic, adult mobility = low). Model diagnostics (r^2 , AICc, Akaike weight) of the most parsimonious single model (*best model*) and the model in which only climate expectation was included (*climate-only model*) indicates the greater variation explained when species traits were included, identified as explanatory variables. Plus sign (+) denotes traits included in the best model.

Analysis of range-filling from the data set of Sunday *et al.* (2012) showed that marine species with smaller ranges have greater range underfilling. In other words, there was a greater distance between their current range boundary and the predicted boundary based on their thermal tolerance (Fig. 4). Although this relationship was only significant at species' equatorward range boundaries (equatorward range boundary, $p < 0.001$; poleward range boundary, $p = 0.17$), the overall pattern was similar in both cases, indicating that smaller ranges are restricted by factors other than temperature.

DISCUSSION

We have identified traits related to range extension that support several ecological hypotheses based on invasion ecology: omnivores, species with high adult mobility, and species with large latitudinal ranges have shown faster range extensions. Including species traits more than doubled our ability to

explain range shift variation in the marine fauna of eastern Australia. Our analysis was facilitated by explicitly considering the climate velocity at each species' range edge, and by considering only one range boundary type for which a specific suite of ecological processes are expected to drive change (extending range edges; Bates *et al.* 2014b). This is a critical advance over findings from previous marine studies in which species traits were found to be unimportant (Przeslawski *et al.* 2012; Pinsky *et al.* 2013). Our findings are consistent with previous work on butterflies, in which mobility and range size were also strong predictors of range extensions (Poyry *et al.* 2009), but contrast with other terrestrial studies in which no consistent traits were identified across studies (Angert *et al.* 2011). Our independent analysis of range filling as a function of range size provides a possible mechanism for why range size predicts range shifts so robustly. We explore the ecological underpinnings of our findings and implications for future distributions.

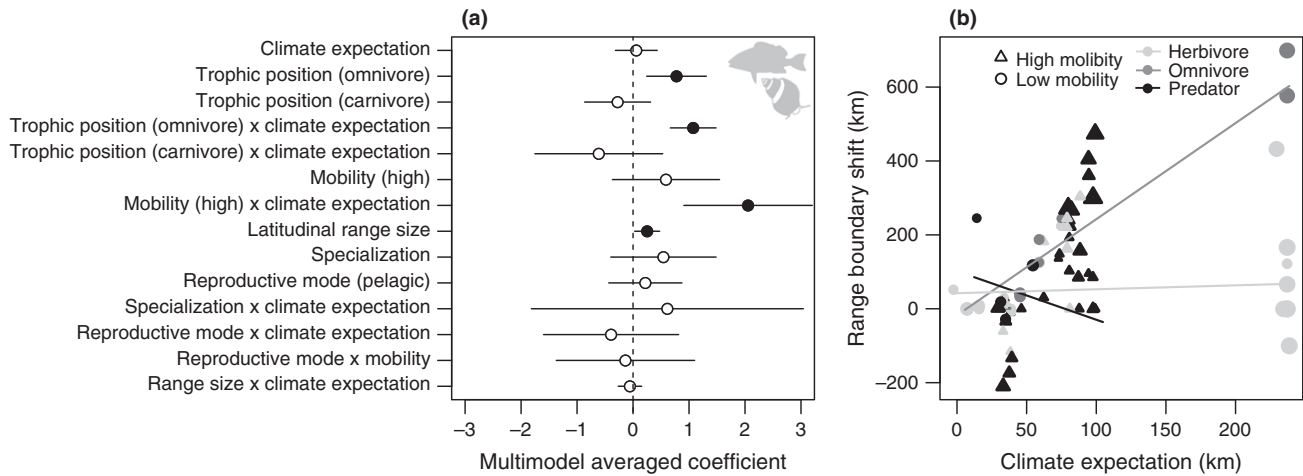


Figure 2 Traits explaining variation in range shifts of all species. (a) Multimodel average coefficient estimates; lines indicate 95% confidence intervals; units are in standard deviations of each trait upon range shifts (in km). Positive values represent a positive effect of the variable on the distance of range extensions, while negative values represent a negative effect. Black points indicate factors in which 95% confidence interval does not cross zero. (b) Range shifts as a function of climate expectation, grey scale and point shape represent trophic position and adult mobility as indicated, point size indicates relative latitudinal range size. Lines represent multi-model average coefficients.

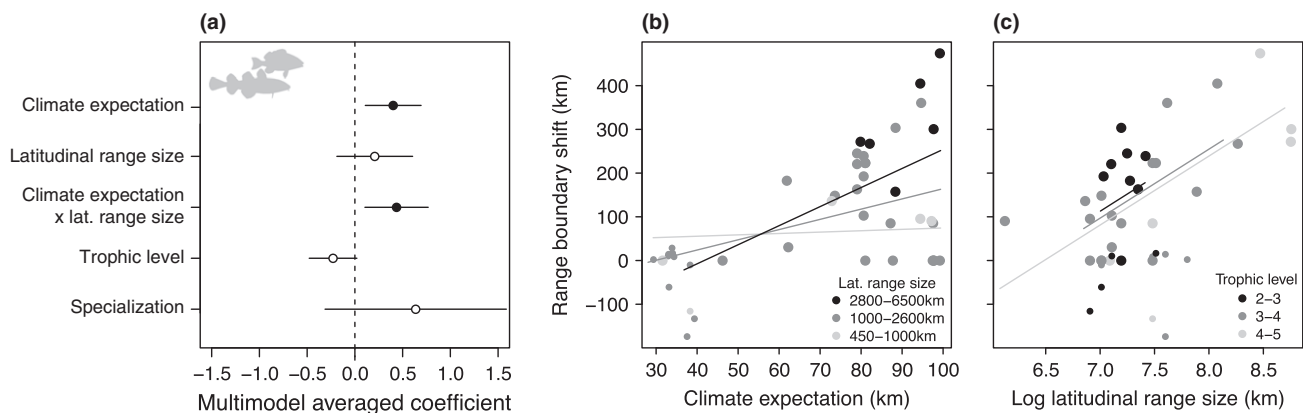


Figure 3 Traits explaining variation in range shifts of marine fishes only. (a) Multi-model average parameter estimates for each species trait; lines indicate 95% confidence intervals; units are in standard deviations of each trait upon range shifts (in km). Black points indicate factors in which 95% confidence interval did not cross zero. (b) Range shifts as a function of climate expectation, grey scale represents latitudinal range size. (c) Range shifts in fishes as a function of log latitudinal range size, grey scale represents trophic level. (b and c) Lines represent multi-model average coefficients and point size represents duration of study from 14 (smallest point) to 29 years.

The importance of omnivory suggests resource generalism promotes range extensions among marine species, increasing the chance of finding suitable food resources in new locations. However, because the importance of this trait was driven mainly by two filter-feeding barnacles with large range extensions (Fig. 3; data from Poloczanska *et al.* 2011), we heed caution in the robustness of this finding. Nevertheless, benthic filter-feeders represent the greatest fraction (nearly 50%) of all marine species invasions, which may in part be facilitated by their broad resource generalism (Byrnes *et al.* 2007). Barnacles in particular may have rapid demographic responses to temperature fluctuations (Mieszowska *et al.* 2014).

Our finding that high mobility (swimming) species have extended their ranges faster than non-swimming species sup-

ports the ecological prediction that adult dispersal ability promotes range extensions under climate warming (Brooker *et al.* 2007). Indeed, swimming taxa can move vast distances within their lifetimes while non-swimming species are more dependent on multi-generational changes in range limits through reproduction and dispersal. Despite this, life history mode of low mobility species was not related to range extensions, and there was no identifiable interaction between life history mode and adult mobility, suggesting that directed movement (i.e. swimming) rather than diffuse dispersal (through larval advection) leads to more predictable gains on poleward ranges. This is congruent with another analysis of marine species' ranges, in which adult traits were more closely related to establishment across barriers than larval traits (Luiz *et al.* 2012). It is also consistent with our understanding of range expansions in

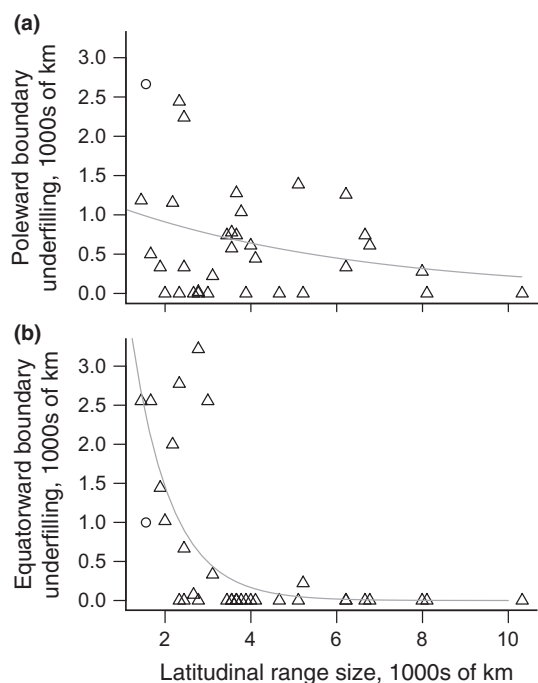


Figure 4 Underfilling of the potential thermal latitudinal range as a function of latitudinal range size in marine organisms from Sunday *et al.* (2012). Lines represent best-fit model coefficients for zero-bound data indicating the trend at (a) poleward and (b) equatorward range limits: species with larger latitudinal ranges better fill their full range potential based on thermal tolerance. A single invertebrate was included in the analysis, denoted by a circle. Grey lines represent best-fit linear model regressions using a Poisson error distribution.

introduced marine species, where spread rates have been unrelated to planktonic larval duration (Kinlan & Hastings 2005), and with theoretical work that suggests rare long-distance dispersal is decoupled from mean dispersal ability, as captured by reproductive mode (Clark *et al.* 2003).

Species with larger latitudinal ranges extended their poleward range boundaries fastest, and among fishes the effect increased as a function of climate expectation. This result matched our predictions (Table 1), based on wide-ranging species having either (i) broader ecological niches and/or fewer ecological interactions limiting their ranges (Hengeveld 1990; Brown *et al.* 1996, Early and Sax, 2014), or (ii) having greater local abundance and therefore greater propagule production (Lawton 1999). Our re-analysis of marine thermal tolerance and distributional data provides evidence consistent with the first hypothesis: marine species with larger latitudinal ranges occupy a greater proportion of their potential thermal niche, hence their latitudinal ranges are more feasibly limited directly by temperature. In accordance, marine species with smaller latitudinal ranges underfill their thermal ranges, and so are limited by factors other than temperature. These findings are consistent with patterns in terrestrial invasive plants, in which smaller native ranges were found to be in greater disequilibrium with climate (Early and Sax, 2014).

The link between latitudinal range size and marine range dynamics is also consistent with the findings of several previous studies. First, latitudinal range size was positively related

to fishes' ability to establish populations on both sides of two oceanic barriers (Luiz *et al.* 2012). Second, in a multi-factorial analysis, latitudinal range size was the most important trait explaining observations of tropical fish found outside of tropical waters (Feary *et al.* 2013). Third, although weak in effect size, range size was positively related to poleward shifts of range centroids in North American fishes (Pinsky *et al.* 2013). Finally, in terrestrial plants, range size has consistently emerged as a predictor of species invasion success (Williamson & Fitter 1996; Goodwin *et al.* 1999). Each of these studies is consistent with the hypothesis that broad ecological tolerances are important for range extensions.

The weak negative trend between trophic level and range extension in fishes is consistent with some previous findings and hypotheses. Herbivorous fishes have shown faster abundance increases associated with tropicalisation of fish assemblages compared to higher level consumers in the same region (Bates *et al.* 2014a), and globally (Vergés *et al.* 2014), and a negative (but weak) effect of trophic level was found on range centroid shifts in North American fishes (Pinsky *et al.* 2013). These relationships provide some support for the hypothesis that poleward limits of herbivorous fishes are more sensitive to temperature change than carnivorous fishes due to temperature dependency of plant digestion, but requires further testing (Floeter *et al.* 2005; Clements *et al.* 2009). Our results did not corroborate a negative relationship between body size and range extensions, as found in North Atlantic fishes (Perry *et al.* 2005; Dulvy *et al.* 2008). Hence characterising the global generality of the relationship between species traits and range extensions, using multiple traits, range limits and climate velocities, will be of key importance in future work.

Although climate expectation explained substantial variation in species range extension rates, approximately half of the species shifted their ranges faster than this expectation (Figs 2b and 3b), a result found in other studies of range shifts and climate velocity (Pinsky *et al.* 2013; Poloczanska *et al.* 2013). This may be due to a decoupling between the metrics used to define climate velocity and the fine-scale temporal and spatial aspects of climate (e.g. duration of summer season, local minimum temperature in winters), including possible indirect effects through species interactions, which may each more directly limit species distributions and differ across taxa (Poloczanska *et al.* 2013). We caution that our metric of climate expectation provides a useful index of mean range shifts of an assemblage, but a poor predictor of maximum range shifts in the most responsive species.

CONCLUSION

The mean variation in range extensions explained by changes in temperature isotherms in our models provides support for the use of climate trajectories in predicting species shifts and identifying spatial patterns of species loss and movement (Burrows *et al.* 2014). However, as in previous analyses incorporating climate, there was substantial variability around the climate velocity prediction (Pinsky *et al.* 2013; Poloczanska *et al.* 2013), which was greatly reduced when we included species traits. Our most important findings were the positive relationships between adult mobility and latitudinal range size on

range extension rate: i.e. species with the ability to swim as adults, and which are already broadly distributed, have moved more rapidly into newly available thermal habitats. Our analysis of potential and realised latitudinal ranges provides a mechanism for the range size finding, indicating that marine species with smaller latitudinal ranges tend to be out of equilibrium with climate (Early and Sax, 2014). Species with narrow ranges also face a greater risk of extinction due to metapopulation dynamics and localised extinction from stochastic threats (Roberts & Hawkins 1999; Purvis *et al.* 2000). Therefore, narrow-range species may face double jeopardy in a warming ocean, being intrinsically more vulnerable to extinction and less able to track their thermal preferences.

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AUTHORSHIP

All authors contributed substantially to initial study design; JS, GP, AH, SF, NH, NJH and AB reworked design to overcome obstacles; GE, NB, RSS, SF, AH and AB contributed data; JS did analyses and wrote the manuscript; all contributed substantially to revisions.

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