1   **Species traits and climate velocity explain geographic range shifts in an ocean**

2   **warming hotspot**

3

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38

43 **Abstract**

44 Species' ranges are shifting globally in response to climate warming, with substantial

45 variability among taxa, even within regions. Relationships between range dynamics and

46 intrinsic species traits may be particularly apparent in the ocean, where temperature more

47 directly shapes species distributions. Here we test for a role of species traits and climate

48 velocity in driving range extensions in the ocean-warming hotspot of Southeast Australia.

49 Climate velocity explained some variation in range shifts, however, including species

50 traits more than doubled the variation explained. Swimming ability, omnivory, and

51 latitudinal range size all had positive relationships with range extension rate, supporting

52 hypotheses that increased dispersal capacity and ecological generalism promote

53 extensions. We find independent support for the hypothesis that species with narrow

54 latitudinal ranges are limited by factors other than climate. Our findings suggest that

55 small-ranging species are in double jeopardy, with limited ability to escape warming and

56 greater intrinsic vulnerability to stochastic disturbances.

57

58 **Introduction**

59 Changes in the distribution of organisms have been reported globally as a fingerprint of

60 global climate change (Parmesan & Yohe 2003; Poloczanska *et al.* 2013). Species

61 responses have been extremely variable, however, both on land and in the ocean. Even

62 within regions where the rate of warming has been relatively uniform, some species have

63 rapidly extended their geographical distributions, while others have moved to a lesser

64 extent, or have even moved in the opposite direction to that predicted (Parmesan & Yohe

65 2003; Poloczanska *et al.* 2013). Understanding the pattern of variation and identifying

66 where and when species will respond to climate change through range shifts is critical if

67 we are to manage proactively for changes in resource-based human livelihoods and to

68 meet conservation goals. Such inquiry also represents a key opportunity to test existing

69 ecological hypotheses about the relative role of climate in setting species' geographic

70 distributions.

71

72 Given an equal pace of climate change, variation in range shifts among species can be

73 broadly viewed as arising from two potential factors: variation in the relative role of

74 temperature in setting range boundaries (sensitivity), and variation in the pace at which

75 new 'potential' ranges become realized through occupancy changes (responsiveness). For

76 example, we expect species to vary in the extent to which climate directly limits the

77 geographic range, where biotic interactions or habitat are variably important in restricting

78 or facilitating ranges (Brown *et al.* 1996; Sexton *et al.* 2009), leading to differences in

79 sensitivity of range limits to temperature change. Independently, where species

80 distributions are currently limited by climate, they are expected to have different intrinsic

81   abilities to respond at the population level as their climatic envelopes move across space

82   – either through the pace of dispersal and population increase at advancing range

83   boundaries, or through the pace of climate adaptation, behavioural change, population

84   decline, and local extinction at contracting range boundaries (Bates *et al.* 2014c).

85   Although the amount of ecological information required at the species, community, and

86   landscape scales for reliably predicting such responses is potentially vast, certain intrinsic

87   traits may prove useful as proxies for ecological variables that determine sensitivity and

88   responsiveness among species (Poyry *et al.* 2009; Angert *et al.* 2011; Przeslawski *et al.*

89   2012; Betzholtz *et al.* 2013; Pinsky *et al.* 2013).

90

91   To date, analyses of the relationships between species' traits and geographic range shifts

92   have yielded mixed results among terrestrial-based studies, with some traits found to be

93   important some of the time (Poyry *et al.* 2009; Angert *et al.* 2011; Betzholtz *et al.* 2013).

94   However, there are reasons to expect stronger predictive relationships in the ocean. First,

95   range shifts have been faster in the ocean (Perry *et al.* 2005; Sorte *et al.* 2010; Pinsky *et*

96   *al.* 2013; Poloczanska *et al.* 2013). This faster rate of change can provide greater capacity

97   for detection and analytical power for understanding variation among species. Second,

98   abundance and occupancy patterns are more temporally conserved in terrestrial compared

99   to marine species, a phenomenon attributed to differences in general life-histories and

100   trophic dynamics between the two realms (Webb *et al.* 2011). Third, recent findings

101   indicate that latitudinal distributions of marine species are more sensitive to temperature

102   change compared to terrestrial species. Specifically, terrestrial species tend to be absent

103   from their predicted equatorward range boundaries and have more extreme poleward

104 distributions than predictions based on their thermal tolerances, whereas marine species

105 have ranges that conform more closely to their physiological thermal limits (Sunday *et al.*

106 2012). Range dynamics on land may therefore be more complex and driven to a greater

107 extent by factors other than temperature, such as moisture, biotic interactions, or other

108 habitat features (in which there is more capacity to thermoregulate), while range

109 dynamics in the ocean may better reflect intrinsic responsiveness to changing isotherms

110 (Sunday *et al.* 2012).

111

112 Range extensions and contractions represent two fundamentally different processes

113 influencing population persistence at local scales that are likely associated with different

114 species traits: colonization and extinction (Hampe & Petit 2005; Angert *et al.* 2011; Bates

115 *et al.* 2014c). While high propagule production and broad ecological generalism (i.e.

116 broad diet and habitat) may increase invasiveness at range extension fronts (Kolar &

117 Lodge 2001), the same traits likely delay extinctions at contracting range edges by

118 increasing persistence (Purvis *et al.* 2000). Indeed, initial attempts to link range shifts of

119 whole species' ranges that combine extension and contractions have failed to identify

120 intrinsic traits related to range shift responses (Przeslawski *et al.* 2012; Pinsky *et al.*

121 2013). If intrinsic traits are related to range shift dynamics, these will likely differ at

122 contracting and extending fronts, and will be easier to discern at single rather than

123 combined range edges.

124

125 Here we test how several intrinsic species traits predicted to affect sensitivity and

126 responsiveness of advancing range boundaries, relate to observed range extensions at

127   poleward range fronts. We focus on the coastal waters off Eastern Australia, as this

128   relatively large region of rapid warming coincides with many species-level records of

129   range limits spanning decades, for which there is substantial knowledge of life histories

130   for testing the role of species traits. The increased strength of the East Australian Current

131   has lead to warming over the past 60 or so years in this region (Ridgway 2007), resulting

132   in a rate of upper ocean warming 3-4 times greater than the global average over the past

133   half century (Hobday & Pecl 2014). During this period of warming, poleward range

134   extensions in the distribution of many species have been observed (Fig. 1). We took

135   advantage of this 'natural experiment' by collating all the time series on poleward range

136   limits available in this region to test for relationships between six species traits

137   hypothesized to influence range extension rates based on ecological theory, using 50 fish

138   and 53 invertebrate species. We include climate velocity (Loarie *et al.* 2009) in our

139   analyses to estimate how these species traits interact with the expected rate of range shifts

140   through the study period (Angert *et al.* 2011; Pinsky *et al.* 2013). Our hypotheses were

141   based on direct predictions provided by invasion theory, with the expectation that traits

142   related to dispersal potential, population growth rate, and ecological generalism will be

143   important positive predictors of poleward range extensions (Table 1). We also tested the

144   hypothesis that species with smaller ranges are more constrained by factors other than

145   temperature - a hypothesis generated from our first analysis - using an independent

146   dataset (Sunday *et al.* 2012). Together our results offer advances in our mechanistic

147   understanding of marine species' distributional responses to climate warming.

148

149   **Materials and Methods**

150 ***Range shift estimates***

151 We compiled range shift data from several sources: (1) all published studies reporting

152 range shifts within multi-species studies of coastal fish and invertebrates in the Tasman

153 Sea (Pitt *et al.* 2010; Stuart-Smith *et al.* 2010; Last *et al.* 2011; Poloczanska *et al.* 2011),

154 (2) underwater visual census data compiled using a standardized methodology through

155 the Reef Life Survey (RLS; Edgar & Stuart-Smith 2014), (3) long-term temperate reef

156 monitoring programs (LTRMP, Edgar & Barrett 2012), and (4) eight additional

157 observations based on the methods in Last *et al.* (2011; Last, *personal communication*,

158 see SOM for details). We only included studies in which range shifts were assessed for

159 multiple species, to avoid the pitfalls of publication bias towards more detectable records

160 of range extensions in single-species studies (see Poloczanska *et al.* 2013). After filtering

161 for repeated sampling across studies (see Supplementary Methods) we identified range

162 shifts of poleward range boundaries in 104 species (50 fish, 54 invertebrates; Fig. 1;

163 Dataset 1). For each species and survey time point, the southern-most location in which

164 species were observed was taken as the poleward range boundary. Although a simplistic

165 estimate of a range boundary, this was a necessary approach because multiple

166 observations through time and space were not available for most species. Although we

167 expect error-related noise in these estimates of range boundaries, and possibly greater

168 noise for low-detectability species, this should not result in a bias in error related to the

169 magnitude of range shifts or to species detectability if sampling effort is consistent

170 through time (Bates *et al.* 2014b). Most range shift estimates were from repeated transect

171 studies or extensive searches for species presence based on species lists – therefore,

172 sampling effort was relatively consistent through time (see Table S1 for details from each

173   study). Furthermore, the species retained within each dataset were those detected at

174   multiple sites across time periods, and thus more likely to have high detectability (see

175   Table S1 for details).

176

177   For 18 of the 104 species (17%), poleward range boundaries moved towards the equator

178   during the study period. This type of change may represent (i) inherent variability in

179   poleward range edges, (ii) indirect ecological responses to warming, (iii) responses to

180   other stressors (such as habitat loss or extraction), and/or (iv) detection error. Regardless

181   of the underlying mechanism(s), we assumed that the factor(s) leading to these

182   equatorward movements were equally influential across the entire dataset, and therefore

183   retained these equatorward-moving species in our analysis as our best means to model the

184   residual error.

185

186   ***Climate expectation***

187   Relating species traits to range shifts observed at different times and places requires

188   accounting for potentially differing rates of temperature change, estimated by the rate of

189   isotherm displacement across space, or 'climate velocity', associated with warming

190   (Loarie *et al.* 2009; Pinsky *et al.* 2013). We therefore calculated an expected distance of

191   range boundary shift for each species, based on the displacement of isotherms from the

192   original range boundary during the time period of the study. We analysed displacement of

193   isotherms in the north-south (meridional) direction (Fig. 1), using isotherms of annual

194   mean sea surface temperature based on the HadISST historical reconstruction (Ref. S1 in

195   Supporting Information). We used means for 1-degree latitudinal bands extending from

196 the coast to 156°E. For each species, we calculated the isotherm at the original poleward

197 range boundary (in latitudinal degrees to 2 decimal places) by interpolating temperatures

198 across each 1° latitudinal band, and determined the north-south displacement of this

199 isotherm from the original poleward range boundary by the end of each study. For

200 species in which the isotherm moved beyond the southern edge of Tasmania during the

201 time period of study (n=21), we cropped the expected distance of southern range

202 extension at the southern latitude of Tasmania's shallow-water regions (43.64°S), beyond

203 which coastal species could not exist or could not be observed, as the next suitable

204 coastal habitat is some 1500 km further south at Macquarie Island. However, the final

205 latitudes of isotherms for these species were not far beyond this boundary (all within 0.4°

206 latitude from this imposed limit). Thus, results were similar with or without this cropping.

207

208 ***Changes in Abundance***

209 Changes in species' range boundaries may occur as a density-dependant response to

210 changes in abundance within the range through time (Macall 1990). Such abundance

211 changes may be climate-related, or may reflect species-level responses to other drivers.

212 To investigate the possible role of abundance change on range limit shifts, we collated

213 available abundance time series for species in our dataset from the *LTRMP* database

214 between 1992 and 2013 (Edgar & Barrett, 2012). This yeilded abundance time-series for

215 53 species within our dataset (51% of species) across multiple sites throughout Southern

216 Australia (Fig. S1). We defined abundance change for each of these species as the linear

217 coefficient of year on abundance within sites (see Fig. S1 for details on model fitting to

218 estimate this metric). We included abundance change as a variable in our species traits

219   models (using a subset of data, see *Analysis*) to investigate the relative role of abundance

220   change on range extensions and their relationships with species traits.

221

222   ***Species traits***

223   We selected six species traits for which we could establish testable hypotheses on range

224   extension rates based on the literature (Table 1), and for which data were generally

225   available (described below; data sources reported in Dataset 1).

226

227   For reproductive mode, we categorized species by their life histories into livebearers,

228   egg-layers (with crawl- or swim-away juveniles), and those with lecithotrophic or

229   planktotrophic larval development, respectively. However, there was only sufficient data

230   coverage in our multivariate models when we concatenated reproductive mode into low-

231   dispersive (brooding and egg-laying) and high-dispersive (planktonic) modes. Species

232   that brood or lay eggs and subsequently release planktonic larvae (e.g. the spiny lobster,

233   *Jasus edwardsii*) were considered planktonic. Adult mobility was categorized as high

234   (swimming) or low (crawling or sessile). All fishes were swimmers, and there were two

235   swimming invertebrates (squid), the rest being crawlers (n=39) or sessile (12). Maximum

236   body size estimates were initially based on data in FishBase (Ref. S2 in Supporting

237   Information), and validated or updated where possible with more recent values from the

238   primary literature, from the CSIRO life history database (Ref. S3 in Supporting

239   Information), and from the RLS database used by Stuart-Smith *et al.* (2013). Total length

240   was used as the estimate of body size for fishes, anterior-to-posterior length for most

241   invertebrates, diameter for sea urchins and anemones, dorsal mantle length for

242 cephalopods, and ray-length for sea stars. Trophic position was categorized based on diet

243 descriptions as herbivores, omnivores, or predators. In our fish-only analyses, we used

244 trophic level scored from data provided through FishBase as a continuous numeric

245 variable.

246

247 Latitudinal range size estimates were based on information from the Global Biodiversity

248 Information System (Ref. S4 in Supporting Information), from FishBase, or from values

249 in the primary literature. Latitudinal range size was correlated with the equatorward

250 (usually tropical) extent of species' ranges ($r^2 = 0.93$) but not the poleward range

251 boundary in southeast Australia ($r^2 = 0.16$). For diet specificity, we used expert

252 knowledge (authors SF and GE) to identify species known to be dietary specialists.

253 However, only 3 specialist species (all herbivores) were identified: *Aplodactylus*

254 *lophodon*, *Kyphosus sydneyanus*, and *Olisthops cyanomelas*. We had complete species

255 trait coverage for 89 species (46 invertebrates; 43 fishes; Dataset 1), and near-complete

256 coverage (lacking reproductive mode) for 104 species (54 invertebrates and 50 fishes).

257 This represents approximately 15% of shallow reef fishes from this region and 8% of the

258 mobile invertebrates (based on all records in the Reef Life Survey database for this

259 region).

260

261 ***Analysis***

262 We used multi-model averaging of mixed-effects linear models with maximum likelihood

263 estimation to test the effect of species traits on shifts in poleward range boundaries. We

264 tested for relationships in all data together and in fishes alone, expecting some traits (e.g.

265   body size and trophic level) to be a better proxy for ecological processes within fishes.

266   Climate expectation, abundance change, and all species traits were initially included as

267   explanatory variables in our global models. We subset the data to include only species for

268   which we had information on every variable and normalized all continuous variables

269   around zero with a standard deviation of one. All variables were examined for multi-

270   collinearity and we found mobility and body size to be highly collinear in the all-species

271   models (see Table S2). We therefore included only mobility, expecting a more direct

272   mechanistic effect of mobility on range shifts. In the fish-only model, body size was not

273   collinear with other traits and so was included. All other traits had variance inflation

274   factors less than 2.5 (Table S2).

275

276   Interactions between each trait and the climate expectation were included to allow for

277   trait-based differences in the rate of responses to locally changing isotherms. We also

278   explored the interaction between mobility and life history mode, with the explicit

279   expectation that life history mode would have a stronger effect on range extensions in

280   species with low adult mobility. Although phylogenetic relationships were not available

281   for the wide sample of taxa within these datasets, we accounted for non-random sampling

282   across taxonomic groups by including taxonomic position as a hierarchical random effect

283   on the intercept from Phylum to Family. We explored the inclusion of source 'study' as a

284   second (crossed) random effect to test for systematic differences in the relationship

285   between range shift and traits among studies, but found that the global models were not

286   better fit when study was included (using the Akaike information criterion; AIC; Table

287   S3), and relationships between traits and range shifts were similar with its inclusion

288   (Table S4), and therefore dropped it from global models. In the fish-only model, we

289   found that study duration had a positive effect on residual variance (lower AICs in Table

290   S3) and assumptions of heteroscedasticity were better met with its inclusion, so we

291   included duration as a factor affecting variance structure in our global models. We fit

292   these models using the *nlme* package in *R* (Ref. S5 in Supporting Information).

293

294   From each of our global models, we ran all possible candidate models that included

295   climate expectation, setting the maximum number of variables as less than one-tenth of

296   the sample size to avoid over-parameterization (and model results were similar if the

297   number of variables was 1/15 the sample size, see Table S5). From these model sets, we

298   identified the confidence set of models as those comprising the top 95% of model weights

299   using AIC adjusted for small sample sizes (AICc). For each variable we calculated the

300   model-averaged parameter estimates and relative variable importance values (w_i) as the

301   sum of Akaike weights from the confidence set of models which included the trait, using

302   the MuMIn package in R (Ref. S6 in Supporting Information). We calculated a

303   likelihood-ratio based pseudo-R-squared for each model as implemented in the MuMIn

304   package. In addition, we extracted the results of the single best model that included

305   species traits, and the climate-only model, which used only climate expectation as a

306   predictor for range shifts (Pinsky *et al.* 2013).

307

308   Preliminary results showed that range shifts were not related to abundance change

309   (Tables S6 and S7; Fig. S1), and the basic relationships with other traits were similar

310   when this variable was excluded from the analysis to yield a much larger complete

311 dataset (Table 2). Likewise, in the fish-only model, reproductive mode had low variable

312 importance with uncertain effects (Tables S6 and S8), and removing it further increased

313 sample size without changing relationships between range extensions and other traits

314 (Table 2). We therefore reran the models using the larger complete dataset without

315 abundance change and (for fish) reproductive mode in order to increase sample size.

316

317 ***Relationship between latitudinal range size and climate equilibrium***

318 We used an independent dataset to further test the hypothesis that latitudinal range size is

319 related to the extent to which species fill their potential thermal niche, or are in

320 disequilibrium with climate. We used a previously-published dataset on thermal tolerance

321 limits and latitudinal range size from a global sample of marine species (Sunday *et al*,

322 2012). For 33 marine fishes and one invertebrate (Dataset 2), we extracted the

323 *underfilling* metric described in Sunday *et al.* (2012), representing the extent to which

324 species occupy a smaller latitudinal range than would be predicted given their thermal

325 tolerance. For these species, we regressed underfilling as a function of latitudinal range

326 size, considering poleward and equatorward range boundaries separately, by fitting a

327 generalized linear model with a Poisson error distribution for zero-bound data using the

328 *lme4* package in R (Ref. S7 in Supporting Information). We cropped range overfilling at

329 zero (i.e., ranges that extended to more latitudes than predicted from species' thermal

330 tolerance), for illustrative purposes, although this did not impact results.

331

332 **Results**

333 Species' poleward range boundaries moved towards the poles on average, with high

334   variation in shift rates (mean ± s.d. all species: 24 ± 87 km dec^{-1}; for fishes: 38 ± 70 km

335   dec^{-1}). Although highly variable, the means of these rates were similar to the mean rate of

336   isotherm displacement from the original range boundaries (all species: 21 ± 13 km dec^{-1};

337   for fishes: 27 ± 6 km dec^{-1}). Climate expectation alone thus explained some of the

338   variation (25.5% in the full dataset and 17.8% in fishes; see pseudo-R-squared of climate

339   expectation only models in Table 2). However, including species traits more than doubled

340   our ability to explain variation in range extensions. The best model with species traits

341   explained 60% of the variation in all species (an additional 35.4%, or 3.4 times increase),

342   and 45.2% of variation in fishes (an additional 27.4%, or 2.5 times increase; see pseudo-

343   R-squared values in Table 2).

344

345   In the all-species model (n = 89), trophic position was the most important trait, and there

346   was a positive interaction between omnivory and climate expectation on distance of range

347   extensions (Table 2, Fig. 2). This suggests omnivores tracked climate expectations better

348   than predators and herbivores. However, this finding was highly influenced by two

349   omnivorous barnacles with large range shifts (*Chthamalus malayensis* and *C. withersii*),

350   in contrast to seven herbivorous snails with little movement despite high expectations

351   (Fig. 2), and the effect of trophic position was lost if the two barnacle species were

352   removed (Table S9).

353

354   In addition to trophic position, mobility had a positive interaction with climate

355   expectation, and latitudinal range size had a direct positive effect on range extensions.

356   These effects were even stronger (with higher certainty and variable importance) when

357   the two high-leverage barnacle species were removed (Table S9). Hence, species with

358   high mobility (swimmers) tracked climate velocity faster than those with low mobility,

359   and wide-ranging species moved faster regardless of climate velocity.

360

361   In the fish-only model (n=50), latitudinal range size was the most important single trait

362   explaining variation in range extensions (Table 2, Fig. 3). There was a strong positive

363   interaction between latitudinal range size and climate expectation; species with larger

364   latitudinal ranges had the greatest range shifts and were best able to track mean isotherms

365   (Fig. 3). The species with the largest latitudinal range sizes were the giant grouper

366   (*Epinephelus lanceolatus*), yellowtail kingfish (*Seriola lalandi*), tiger shark (*Galeocerdo*

367   *cuvier*), short-tail stingray (*Dasyatis brevicaudata*), and the Maori wrasse

368   (*Ophthalmolepis lineolata*), which were all within the 85% quantile of range shift

369   velocities for fishes (> 92 km dec^{-1}).

370

371   There was also evidence for a weak negative relationship between trophic level and range

372   extensions in fishes, with low-trophic level fishes responding faster than higher-trophic

373   level fishes for a given range size (Fig. 3a,c). This was driven mainly by greater range

374   extensions in herbivores with medium-sized ranges, such as the black drummer (*Girella*

375   *elevata*), silver drummer (*Kyphosus sydneyanus*), zebrafish (*Girella zebra*), and rock cale

376   (*Aplodactylus lophodon*), compared to higher-level consumers (Fig. 3c).

377

378   Other traits had more uncertain effects, with 95% confidence intervals of model

379   coefficients crossing zero (Fig. 2). Notably, reproductive mode was not strongly related

380   to the rate of range shifts in either fishes or invertebrates, and there was high variation in

381   responses within each reproductive mode (Fig. S2). Indeed, some species without a larval

382   dispersal phase extended their ranges as quickly as those with planktonic larvae (Fig. S2).

383

384   Analysis of range filling from the dataset of Sunday *et al.* (2012) showed that marine

385   species with smaller ranges have a greater range underfilling. In other words, there was a

386   greater distance between their current range boundary and the predicted boundary based

387   on their thermal tolerance (Fig. 4). Although this relationship was only significant at

388   species' equatorward range boundaries (equatorward range boundary, $p<0.001$; poleward

389   range boundary, $p=0.17$), the overall pattern was similar in both cases, indicating that

390   smaller ranges are restricted by factors other than temperature.

391

392   **Discussion**

393   We have identified traits related to range extension that support several ecological

394   hypotheses based on invasion ecology: omnivores, species with high adult mobility, and

395   species with large latitudinal ranges have shown faster range extensions. Including

396   species traits more than doubled our ability to explain range shift variation in the marine

397   fauna of Eastern Australia. Our analysis was facilitated by explicitly considering the

398   climate velocity at each species' range edge, and by considering only one range boundary

399   type for which a specific suite of ecological processes are expected to drive change

400   (extending range edges; Bates *et al.* 2014c). This is a critical advance over findings from

401   previous marine studies in which species traits were found to be unimportant

402   (Przeslawski *et al.* 2012; Pinsky *et al.* 2013). Our findings are consistent with previous

403   work on butterflies, in which mobility and range size were also strong predictors of range

404   extensions (Poyry *et al.* 2009), but contrast with other terrestrial studies in which no

405   consistent traits were identified across studies (Angert *et al.* 2011). Our independent

406   analysis of range filling as a function of range size provides a possible mechanism for

407   why range size predicts range shifts so robustly. We explore the ecological underpinnings

408   of our findings and implications for future distributions.

409

410   The importance of omnivory suggests resource generalism promotes range extensions

411   among marine species, increasing the chance of finding suitable food resources in new

412   locations. However, because the importance of this trait was driven mainly by two filter-

413   feeding barnacles with large range extensions (Fig. 3; data from Poloczanska *et al.* 2011),

414   we heed caution in the robustness of this finding. Nevertheless, benthic filter-feeders

415   represent the greatest fraction (nearly 50%) of all marine species invasions, which may in

416   part be facilitated by their broad resource generalism (Byrnes *et al.* 2007). Barnacles in

417   particular may have rapid demographic responses to temperature fluctuations

418   (Mieszkowska *et al.* 2014).

419

420   Our finding that high mobility (swimming) species have extended their ranges faster than

421   non-swimming species supports the ecological prediction that adult dispersal ability

422   promotes range extensions under climate warming (Brooker *et al.* 2007). Indeed,

423   swimming taxa can move vast distances within their lifetimes while non-swimming

424   species are more dependent on multi-generational changes in range limits through

425   reproduction and dispersal. Despite this, life-history mode of low-mobility species was

426   not related to range extensions, and there was no identifiable interaction between life-

427   history mode and adult mobility, suggesting that directed movement (i.e., swimming)

428   rather than diffuse dispersal (through larval dispersal) leads to more predictable gains on

429   poleward ranges. This is congruent with another analysis of marine species' ranges, in

430   which adult traits were more closely related to establishment across barriers than larval

431   traits (Luiz *et al.* 2012). It is also consistent with our understanding of range expansions

432   in introduced marine species, where spread rates have been unrelated to planktonic larval

433   duration (Kinlan & Hastings 2005), and theoretical work that suggests rare long-distance

434   dispersal may be decoupled from mean dispersal ability, as captured by reproductive

435   mode (Clark *et al.* 2003).

436

437   Species with larger latitudinal ranges extended their poleward range boundaries fastest,

438   and among fishes the effect increased as a function of climate expectation. This result

439   matched our predictions (Table 1), based on wide-ranging species having either (i)

440   broader ecological niches and/or fewer ecological interactions limiting their ranges

441   (Hengeveld 1990; Brown *et al.* 1996), or (ii) having greater local abundance and

442   therefore greater propagule production (Lawton 1999). Our re-analysis of marine thermal

443   tolerance and distributional data provides evidence consistent with the first hypothesis:

444   marine species with larger latitudinal ranges occupy a greater proportion of their potential

445   thermal niche, hence their latitudinal ranges are more feasibly limited directly by

446   temperature. In accordance, species with smaller latitudinal ranges underfill their thermal

447   ranges, and so are limited by factors other than temperature.

448

449   This link between latitudinal range size and marine range dynamics is consistent with the

450   findings of several previous studies. First, latitudinal range size was positively related to

451   fishes' ability to establish populations on both sides of two oceanic barriers (Luiz *et al.*

452   2012). Second, in a multi-factorial analysis, latitudinal range size was the most important

453   trait explaining observations of tropical fish found outside of tropical waters (Feary *et al.*

454   2013). Third, although weak in effect size, range size was positively related to poleward

455   shifts of range centroids in North American fishes (Pinsky *et al.* 2013). Finally, in

456   terrestrial plants, range size has consistently emerged as a predictor of species invasion

457   success (Williamson & Fitter 1996; Goodwin *et al.* 1999). Each of these studies is

458   consistent with the hypothesis that broad ecological tolerances are important for range

459   extensions.

460

461   The weak negative trend between trophic level and range extension in fishes is consistent

462   with some previous findings and hypotheses. Herbivorous fishes have shown faster

463   abundance increases associated with tropicalization of fish assemblages compared to

464   higher-level consumers in the same region (Bates *et al.* 2014a), and globally (Vergés *et*

465   *al.* 2014), and a negative (but weak) effect of trophic level was found on range centroid

466   shifts in North American fishes (Pinsky *et al.* 2013). These relationships provide some

467   support for the hypothesis that poleward limits of herbivorous fishes are more sensitive to

468   temperature change than carnivorous fishes due to temperature dependency of plant

469   digestion, but requires further testing (Floeter *et al.* 2005; Clements *et al.* 2009). Our

470   results did not corroborate a negative relationship between body size and range

471   extensions, as found in North Atlantic fishes (Perry *et al.* 2005; Dulvy *et al.* 2008). Hence

472   characterizing the global generality of the relationship between species traits and range

473   extensions, using multiple traits, range limits, and climate velocities, will be of key

474   importance in future work.

475

476   Although climate expectation explained substantial variation in species range extension

477   rates, approximately half of the species shifted their ranges faster than this expectation

478   (Figs. 2b and 3b), a result found in other studies of range shifts and climate velocity

479   (Pinsky *et al*. 2013; Poloczanska *et al*. 2013). This may be due to a decoupling between

480   the metrics used to define climate velocity and the fine-scale temporal and spatial aspects

481   of climate (e.g., duration of summer season, local minimum temperature in winters),

482   including possible indirect effects through species interactions, which may more directly

483   limit species distributions and differ across taxa (Poloczanska *et al*. 2013). We caution

484   that our metric of climate expectation provides a useful index of mean range shifts, but a

485   poor predictor of maximum potential range shifts of the most responsive species.

486

487   **Conclusion**

488   The variation in range extensions explained using climate velocity to generate expected

489   range shifts in our models provides support for the use of climate trajectories in

490   predicting species shifts and identifying spatial patterns of species loss and movement

491   (Burrows *et al.* 2014). However, as in previous analyses incorporating climate velocity,

492   there was substantial variability around the climate velocity prediction (Pinsky *et al.*

493   2013; Poloczanska *et al.* 2013), which was greatly reduced when we included species

494   traits. Our most important findings were the positive relationships between adult mobility

495 and latitudinal range size on range extension rate: i.e. species with the ability to swim as

496 adults, and which are already broadly distributed, have moved more rapidly into newly

497 available thermal habitats. Our analysis of potential and realized latitudinal ranges

498 provides a mechanism for the range size finding, indicating that marine species with

499 smaller latitudinal ranges tend to be out of equilibrium with climate. Narrow-range

500 species also face a greater risk of extinction due to metapopulation dynamics and

501 localised extinction from stochastic threats (Roberts & Hawkins 1999; Purvis *et al.*

502 2000). Therefore narrow-range species may face double jeopardy in a warming ocean,

503 being intrinsically more vulnerable to extinction and less able to track their thermal

504 preferences.

505

520

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702 **Tables**
703
704 Table 1. Hypotheses on the influence of species traits on climate-induced range
705 extensions. Note alternative hypotheses within trait categories can be distinguished by the
706 overall pattern, while the relative importance of each trait can be evaluated by model
707 comparison.
708

Trait	Hypotheses
Reproductive mode	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 colonization of new regions.
Adult motility	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	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 *et al*. 2002), and therefore faster range extensions (Perry *et al*. 2005).
Latitudinal range size	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 *et al*. 2013).
Trophic level / position	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 *et al*. 2008), and thus have faster range extensions.
Diet Specificity	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 generalization and therefore be the least constrained by trophic interactions.

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712

713 Table 2. Models explaining the distance (km) of latitudinal shifts in all marine species

714 and fish only. The relative variable importance (w_i), variable coefficients (*coef*) and their

715 95% confidence limits (*CL*) are shown for each variable from the multimodel average,

716 showing contrasts from base levels (climate expectation = 0, latitudinal range size = 0,

717 trophic position = herbivores, trophic level = 1, specialization = not specialized, life

718 history mode = benthic, adult mobility=low). Model diagnostics (r^2, AICc, Akaike

719 weight) of the most parsimonious single model (*best model*) and the model in which only

720 climate expectation was included (*climate only model*) indicates the greater variation

721 explained when species traits were included, identified as explanatory variables. Plus sign

722 (+) denotes traits included in the best model.

723

Explanatory variable(s)	multimodel average				best model	climate only model
	w_i	coef.	Lower CL	Upper CL	coef.	coef.
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.) x climate expectation	1	1.07	0.67	1.48	+	
Trophic position (pred.) x climate expectation	1	-0.61	-1.75	0.53	+	
Adult mobility (high)	1	0.59	-0.37	1.55	+	
Adult mobility (high) x climate expectation	1	2.05	0.91	3.20	+	
Log lat. range size	0.52	0.25	0.03	0.47	+	
Specialization	0.4	0.54	-0.40	1.48		
Specialization x 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.) x climate expectation	0.03	-0.39	-1.60	0.81		
Life history mode (pel.) x adult mobility (high)	0.03	-0.14	-1.37	1.10		
Lat. range size x 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 x climate expectation	0.8	0.44	0.11	0.77	+	
Trophic level	0.32	0.64	-0.31	1.59		
Specialization	0.3	-0.23	-0.48	0.02		
Log body size	0.05	-0.11	-0.42	0.20		

|						
Trophic level x 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

724

Figures
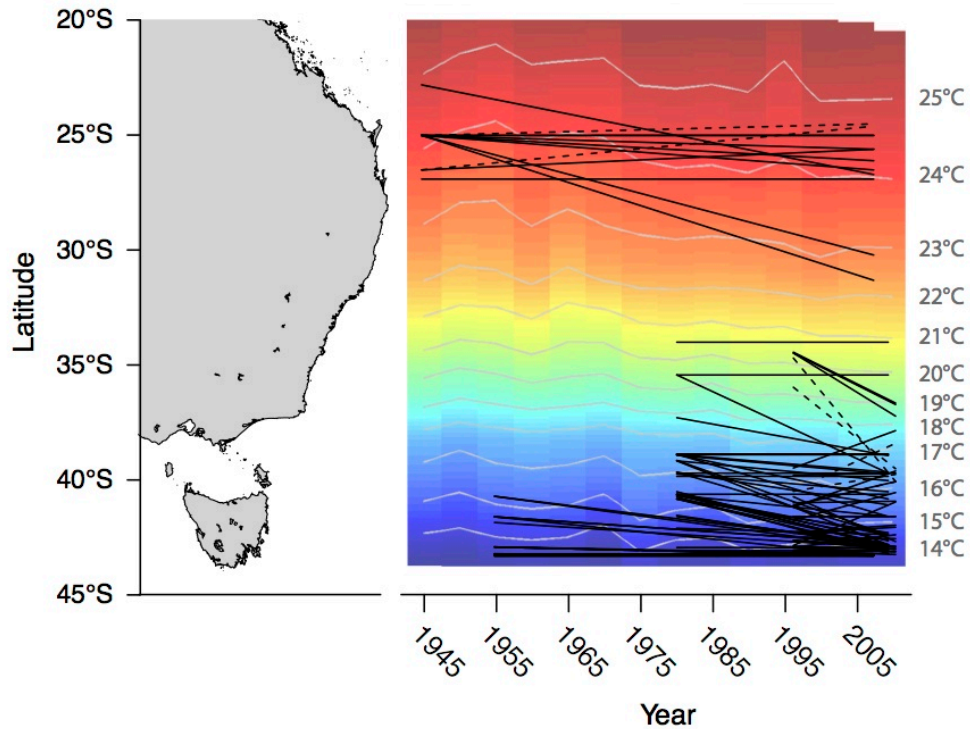
Fig. 1. Poleward range boundary shifts of coastal marine fish and invertebrates in eastern
Australia (black lines), and latitudinal changes in mean annual temperature isotherms
over study period (colours). Each different colour band represents the mean annual
temperature of the coastal zone tracked across 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.

733
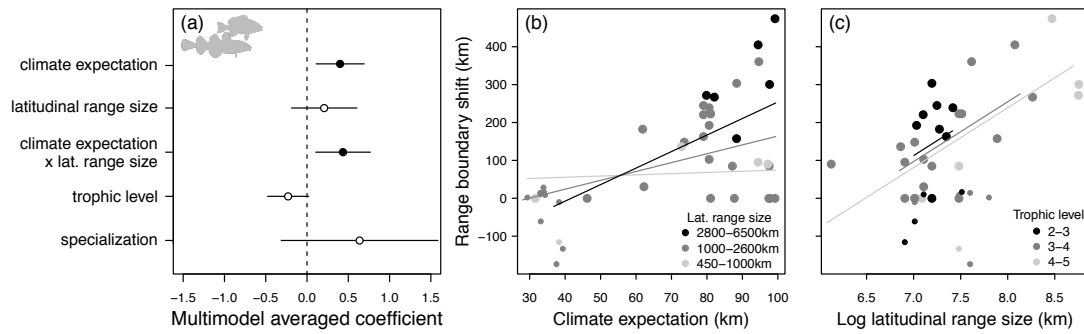
Fig. 2. Traits explaining variation in range shifts of all species. (a) Multi-model average

coefficient estimates; lines indicate 95% confidence intervals; units are in standard

deviations of each trait upon standard deviation of range shifts. 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 do 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.

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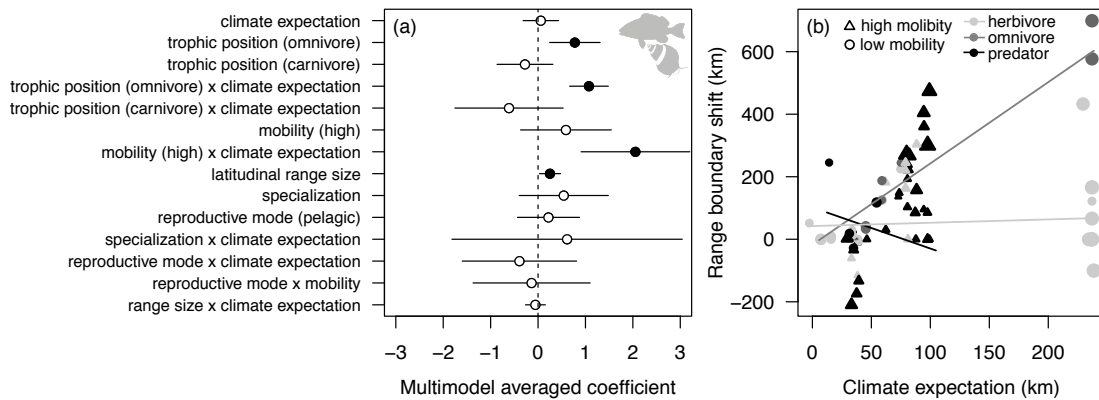
Fig. 3. Traits explaining variation in range shifts of marine fishes only. (a) Multi-model

average parameter estimates for each species trait; lines indicate 95% confidence

intervals; units are in standard deviations of each trait upon standard deviation of range

shifts. Black points indicate data 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,c) Lines represent multi-model average coefficients

and point size represents duration of study from 14 (smallest point) to 29 years.

(a)

(b)

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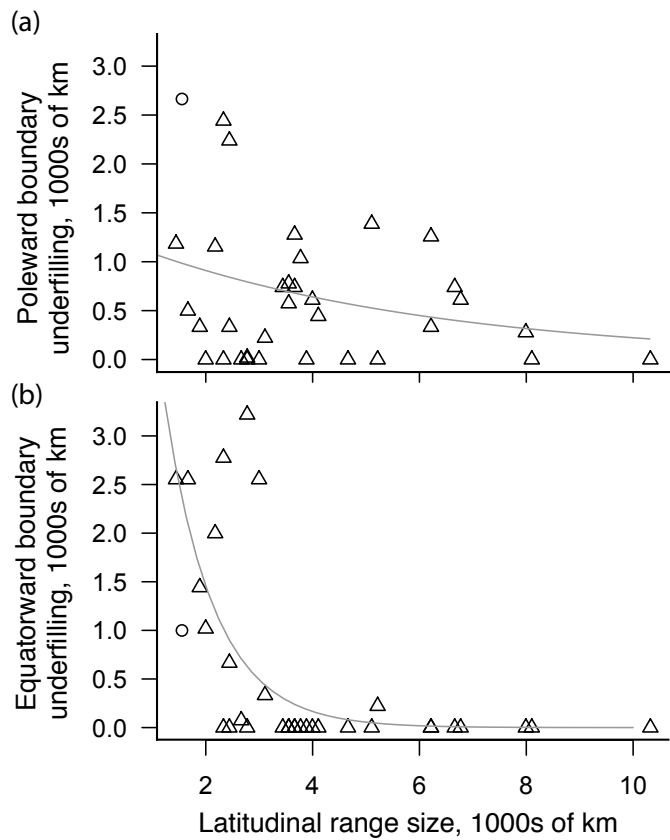
Fig. 4. Underfilling of the potential thermal latitudinal range as a function of latitudinal

range size in marine organisms from Sunday *et al.* (2012). Best-fit regression lines for

zero-bound data indicates the trend: species with larger latitudinal ranges are more likely

to 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.

759