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Using rigorous selection criteria to investigate marine range shifts

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Abstract

We reassess whether range shifts in marine organisms are occurring in a direction predicted by causation due to climate using two different methods: a global meta-analysis and a regional analysis of museum records focussing on marine molluscs. Globally we used rigorous selection criteria to investigate studies describing range shifts in marine organisms, including exclusion of single-species studies and those that inferred range shifts through shifting abundance. For each species meeting these criteria (311 species from 13 studies), the distance in kilometres moved per year was calculated, and life history characteristics such as mobility, habitat, dispersal potential and trophic level were recorded to assess if these were linked to the shifts. We also examined the potential correlation between changing sea surface temperatures and range shifts. Regionally we analysed the intertidal mollusc collection of the Australian Museum and Museum of Victoria and consulted with mollusc experts to determine if museum records could be used to detect range shifts in marine invertebrates. The global meta-analysis showed that individual species shifted on average 8.9 km polewards per year. Range shifts were not significantly related to temperature change or life history characteristics with the exception of intertidal and nearshore subtidal fauna showing poleward shifts (6.8 and 14.3 km per decade, respectively) and shelf fauna showing a slight equatorial shift (2.7 km per decade). Our regional analysis showed that 54 of the 634 mollusc species examined shifted their range into or out of the well-surveyed Sydney region. However, closer examination by mollusc experts revealed that the evidence for these shifts was unreliable, and we conclude that caution is required when using museum records in range shift studies. Overall, our study supports previous research showing a poleward shift in response to climate change, although this is an order of magnitude less than values reported in the only other meta-analysis on marine range shifts, possibly owing to the strict selection criteria applied here.

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USING RIGOROUS SELECTION CRITERIA TO INVESTIGATE MARINE RANGE SHIFTS

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ABSTRACT

Marine range shifts associated with the effects of climate change have been described for well studied groups including fish, corals, zooplankton and macroalgae, but range shifts in most marine invertebrates remain unknown due to the complexities in determining species' distributions in the marine environment. In this study we reassess whether range shifts in marine organisms are occurring in a direction predicted by causation due to climate using two different methods; a global meta-analysis and a regional analysis of museum records focusing on marine molluscs. Globally we used rigorous selection criteria to investigate studies describing range shifts in marine organisms, including exclusion of single-species studies and those that inferred range shifts through shifting abundance. For each species meeting these criteria (291 species from 12 studies), the distance in kilometres moved per year was calculated and life history characteristics such as mobility, habitat, dispersal potential and trophic level were recorded to assess if these were linked to the shifts. We also investigated if changing sea surface temperatures were correlated to detected range shifts. Regionally we analysed the intertidal mollusc collection of the Australian Museum and Museum of Victoria and consulted with mollusc experts to determine if museum records could be used to detect range shifts in marine invertebrates. The global meta-analysis showed that individual species shifted on average 9.1 km polewards per decade. Range shifts were not significantly related to temperature change or life history characteristics with the exception of intertidal and nearshore subtidal fauna showing significantly different poleward shifts (7.0 and 14.3 km per decade, respectively) than shelf fauna showing a slight equatorial shift (2.7 km per decade). Our regional analysis revealed that 54 of the 634 mollusc species examined shifted their range into or out of the well-surveyed Sydney region. However, closer

examination by mollusc experts revealed that the evidence for these shifts was unreliable, and we concluded that caution should be used when using museum records in range shift studies. Overall, our study supports previous research showing a poleward shift in response to climate change, although on an order of magnitude less than values reported in the only other meta-analysis on marine range shifts, possibly owing to the strict selection criteria applied here.

1 INTRODUCTION

Range shifts are often cited as one of the most noticeable and likely effects of warming waters due to climate change (Barnes et al., 2009; Johnson et al., 2011; Wernberg et al., 2011), although the generality of this statement across regions has recently been questioned (e.g. eastern Australia in Polaczanska et al., 2011). Compared to terrestrial taxa (Parmesan and Yohe, 2003; Chen et al., 2011), there has been little broadscale investigation of modern range shifts due to warming waters in marine organisms, particularly invertebrates (Parmesan, 2006; Przeslawski et al., 2008, but see Sorte et al., 2010). In a recent global meta-analysis in which temperature was linked to general poleward expansion for the first time, marine invertebrates, including algae, accounted for only 9% of all studies and 6% of species responses (Chen et al., 2011), likely reflecting the comparatively limited studies on distributions of many marine organisms (Parmesan et al., 2005).

While many records exist for changing abundances due to temperature changes (e.g. Barry et al., 1995; Schiel et al., 2004; Licandro et al., 2006;), and temperature-associated nutrient levels (e.g. Billett et al., 2001), they tend to focus on only one site or narrow area, thus making the identification and quantification of true range shifts difficult. Results from such studies have been used to infer range shifts, based on the underlying assumption that abundance decreases from the range centre to its edge (e.g. Pitt et al., 2010; Sorte et al., 2010; and references therein). However, the validity of this assumption has been questioned at both regional and local scales (10s – 100s km) (Helmuth et al., 2002; Sagarin et al., 2006; Hidas et al., 2010), suggesting that the detection of range shifts must involve sampling at multiple locations overlapping the known range edges (Rivadeneira and Fernandez, 2005).

Despite the comparative lack of data quantifying true marine range shifts (as opposed to changing abundances or transient occurrences), studies in several regions have documented abundance or community changes that are potentially linked to warming waters (Sorte et al., 2011 and references therein). Excellent long-term time series studies in the Northeast Atlantic have revealed extensive changes in marine communities, with intertidal and zooplankton communities showing an increase of warm-water species and a decrease in cool-water species (Southward et al., 1995; Beaugrand et al., 2009), and similar shifts have been found in rocky intertidal invertebrates from the Californian coast (Barry et al., 1995, but see Helmuth et al., 2002). There is some indication of poleward shifts in temperate Australian fish communities (Last et al., 2011), and perhaps the best known range shift among Australian marine invertebrates has been the expansion of the sea urchin *Centrostephanus rodgersii* into Tasmanian waters (Ling, 2008). Laboratory studies suggest that range expansion is almost certainly due to warming waters, as this species has not undergone an adaptive shift to cooler waters nor a change in reproductive phenology (Ling et al., 2008).

A variety of physiological and ecological factors impact the likelihood of a species expanding or contracting its range (Sanford and Swezey, 2008). The duration of life cycles seems to be related to range expansions. Among demersal fish of the North Sea, range shifts have occurred among species with faster life cycles than non-shifting species (Perry et al., 2005). The dispersal potential of a species also seems likely to influence its ability to extend its range (Dunstan and Bax, 2007), with increased expansion linked to longer planktonic larval duration (Booth et al., 2007). In addition,

the habitat requirements and associated availability of required habitats will influence the capacity to shift ranges (Dunstan and Bax, 2007). Finally, the physiology of larval, juvenile, and adult stages will affect a species' likelihood to contract its range, particularly the thermal tolerance limits (Matson and Edwards, 2007).

Range shifts in individuals or small groups of species have previously been quantified using experimental studies (e.g. Southward et al., 1995; Stuart-Smith et al., 2010) or a combination of experimental and historical data (e.g. Rivadeneira and Fernandez 2005; Pitt et al., 2010). Although several regions have excellent data related to long-term time series (e.g. zooplankton from N Atlantic in Southward et al., 1995 and Beaugrand et al., 2009; rocky intertidal fauna from Britain in Mieszkowska et al., 2006 and Hawkins et al., 2008), most regions lack such long-term experimental data (Brown et al., 2011). Associated range shift studies are therefore reliant on museum records and other historical data (reviewed in Tingley and Beissinger 2009). At a broader scale, meta-analyses can identify regional or global patterns in range shifts (Parmesan and Yohe, 2003; Sorte et al. 2010; Chen et al. 2011). Regardless of the approach taken to quantify range shifts, a critical evaluation of the data used is crucial.

In this study, we investigate whether range shifts in marine organisms are occurring in a direction predicted by causation due to climate change using two different methods. First, we use a meta-analysis at the global scale with strict inclusion criteria (discussed below) to critically review range shifts of marine organisms reported in the literature and identify taxonomic and regional knowledge gaps. We also examine physiological and ecological factors that may be associated with demographic

responsiveness to warming waters associated with climate change. As shifts may be more pronounced in regions where water temperatures have warmed more in recent years, we also investigate the relationship between range shifts and the magnitude of warming. Previous meta-analyses have addressed range shifts (Table 1), but these are either focussed on terrestrial organisms (Parmesan and Yohe, 2003; Chen et al., 2011) or include comparatively relaxed selection criteria (e.g. inclusion of studies which inferred range shifts based on abundance or studies from only a single species (Sorte et al., 2010) which may result in publication bias of positive results (Csada et al., 1996; Gurevitch and Hedges, 1999).

Second, we assess whether museum records could be used to detect range shifts and potentially fill the knowledge gaps identified above. Museum collections are a valuable source of biodiversity information that can be used to study a broad range of topics (Graham et al., 2004). However, there are known inaccuracies and spatial biases in the coverage of museum records, which means they need to be used with caution (Ponder et al., 2001; Graham et al., 2004), particularly regarding detection of range shifts (Tingley and Beissinger 2009). Indeed, in any range shift study it is difficult to distinguish real range expansions from previously undocumented populations (Frey, 2009), and this is especially true with museum records as there are no documented absences. Therefore, an important aspect of this study is the examination of sampling effort across space and time and tailoring methods to suit the available data. In this study we examine a novel method for detecting range shifts, by examining whether species shift into or out of the best surveyed region in southeast Australia and then using recognised experts to review the data. Based on the results

of both the meta-analysis and analysis of museum records, we address important considerations, limitations and data gaps for future range shift studies.

2 METHODS

2.1 Gap identification and meta-analysis

Literature was searched in ISI Web of Science using the following search terms: ‘range shift’, ‘range expansion’, ‘range contraction’, ‘range reduction’, or ‘distribution change’, with root words used to expand results. We did not use ‘climate change’ in our search terms (e.g. Sorte et al., 2010; Chen et al., 2011) to avoid bias towards positive results, but we did not exclude studies with this term either. Search results were then confined to the topic of ‘marine and freshwater research’ as defined by the database. In addition, we compiled references from the three other meta-analyses on range shifts that include marine invertebrates (Parmesan and Yohe, 2003; Sorte et al., 2010; Chen et al., 2011). Where necessary, authors were contacted directly for data.

All studies included in the meta-analysis were required to present range boundaries from two time periods for marine metazoans; for those studies that included more than two time periods, only the oldest and most recent were used. This low temporal resolution precludes any patterns of variability in the interim years but is a trade-off for the higher number of species able to be included in the analysis and avoidance of temporal autocorrelation (Brown et al., 2011). Those studies that inferred range shifts from abundances were excluded, as they are based on early ecological theory that assumes abundance is normally distributed over a species range, whereas recent evidence suggests that many species have non-normal distributions of their abundance

(Brown et al., 2011; Hidas et al., 2009). In studies where range shift was shown only in maps and not recorded as distance per unit of time, this information was extracted in ArcGIS v 9.3. When a time period spanned multiple years, we used the average year (e.g. 1955 for 1950s). We excluded studies in which the authors concluded that apparent range shifts were actually an artefact of improved sampling (e.g. Goddard and Foster, 2002). In order to reduce bias associated with the publication of positive results (Csada et al., 1996; Gurevitch and Hedges, 1999), particularly those related to climate change, we only included those studies that examined multiple species because demographics that were static or unrelated to climate change predictions were more likely to be reported in such studies. This approach has been previously used in most other meta-analyses on range shifts (Parmesan and Yohe, 2003; Chen et al., 2011), but was not used by Sorte et al. (2011) in the only other study on marine species. We excluded studies in areas in which dramatic local anthropogenic changes had occurred (e.g. thermal changes from power plant in Schiel et al. (2004)) and those incorporating disparate or anecdotal data (e.g. Last et al., 2011).

For each study meeting these criteria, only marine or estuarine species that had either northern or southern boundaries within the study area were included as a data point in the meta-analysis. Species that were represented by more than one study were only included once based on the study that spanned the longest time period. We excluded species defined as invasive following Sorte et al. (2010), as well as those species where only a single individual was recorded, as these were not considered robust evidence of range shifts (Sorte et al., 2010).

Of the 12 studies included in our meta-analysis (see Appendix S1), four did not account for potential error among sampling times (Southward et al., 1995; Precht and Aronson, 2004; Rivadeneira and Fernandez, 2005; Wethey and Woodin, 2008). Five studies attempted to address this issue by maintaining similar methods in both the historical and recent surveys (Mieszkowska et al., 2006; Herbert et al., 2007; Hsieh et al., 2009; Pitt et al., 2010; Polocsanska et al., 2011). Lima et al. (2007) combined the use of similar methods among times with a split moving window technique to further reduce sampling bias. Only two studies were able to reduce sampling bias by maintaining the same research team and methods among both time periods (Ma et al., 2009, Stuart-Smith et al., 2010).

The effect size was defined as the distance in kilometres moved per year by a given species such that:

Effect Size = |range boundary shift (km) | / (Year 2 – Year 1), with poleward shifts denoted by a negative sign and equatorial shifts denoted by a positive sign.

Temperature change was adopted from values reported in the original study. Where this was not reported, we used SSTs from HadISST 1.1 Global sea-Ice coverage and SST (1870 – present) (Raynor et al., 2003) in which temperatures were extracted from the centre of the study area for each survey time and averaged over the survey year as reported in Supplementary Materials, as well as the preceding and subsequent years in order to account for error associated with short-term interannual fluctuations. The difference in average temperatures between the historical and modern surveys was standardised to give a value of temperature change per decade.

Analyses of range shifts were performed on two separate datasets: 1) Individual range shifts based on each species' response as per Parmesan and Yohe (2003) and Sorte et al. (2010) (Appendix S1), and 2) amalgamated range shifts based on the average shift for each combination of taxonomic group and regions as per Chen et al. (2011) (Appendix S2), the latter of which also addresses the potential issue of spatial autocorrelation (Brown et al., 2011). Adopting both approaches allows a more robust assessment of range extensions, facilitates comparisons with previous studies, and helps identify taxonomic and regional data gaps. Variances for most species were not available so analyses were not weighted. Data for individual species were not normally distributed, and a non-parametric Wilcoxon signed rank test was performed to determine if the mean range shift of all species differed from the null hypothesis that there was no mean boundary change. In order to identify life history characteristics (mobility, habitat, dispersal potential, trophic guild) that may be linked to range shifts, Kruskal-Wallis tests were also performed on this dataset, excluding those species for which a given life history characteristic was unknown or not applicable (see Appendix S1 in the Supporting Information). Data for combinations of taxonomic groups and region were normally distributed, and a one-sample *t* test was performed and compared with a mean shift of zero for those groups that included more than 2 species (Appendix S2). Correlation analyses were performed between temperature change (total and standardised) and the individual species dataset, as there were not enough regions in the amalgamated dataset for a robust analysis (4 regions, see Appendix S2). Statistical analyses were conducted in the R 2.13.0 statistical platform with $\alpha = 0.05$.

Wherever possible, life history characteristics were recorded for each species using online databases and references therein, field guides or journal publications (see Appendix S1). Categories were very broad due to the large number of species and limited information for many of them (see Appendix S1).

2.2 Southeast Australian museum records

We used marine molluscs of southeast Australia to determine if museum records could be used to detect range shifts in marine invertebrates. We selected this region because two Australian museums (Museum of Victoria and the Australian Museum) have extensive collections dating back to the late 1800s from this area as well as having relevant researchers able to provide expert opinions on identified patterns. Both institutions have archived a significant portion of their marine invertebrate collections in online databases. We initially also considered polychaetes, echinoderms and decapods but we rejected these groups due to limited collection time span.

We obtained 113 693 records of marine molluscs (5 167 species) from the databases maintained by the Australian Museum and Museum of Victoria for the area south of 22°S, east of 146°E and within 100 km of Australia (including Tasmania). Despite the fact we chose one of the best represented marine invertebrate groups from museum collections in Australia, only 207 of these species (4%) had more than 100 records and only 53 (1%) more than 200. There were also clear biases that are typical of museum collections (Ponder et al., 2001), with most records (41.5%) collected between 1967 and 1980, and 38.3% of the records collected in the Sydney region (defined as 34.5°S to 33.5°S in this study; Fig. 2).

Large sample sizes are needed to determine range boundaries accurately since populations are often patchy near range limits (Randin et al., 2006; Frey, 2009; Ashcroft et al., 2012). Given the low density of records outside Sydney (Fig. 2) and the low sample sizes for the majority of species (see above) we did not try to determine the actual limits for species' ranges. Instead, we focussed on the best surveyed region (Sydney) to determine if museum collections could show if any species had moved into or out of this highly-sampled region between the pre-1971 period and the post-1970 period. We restricted our analysis to those species that had at least ten records prior to 1971 (1860 to 1970), at least ten records after 1970 (1971 to 2010), and their known range spanned the Sydney region. There were a total of 634 marine molluscs (60 145 individuals) that satisfied these criteria. The 1970 cut-off was chosen to incorporate the increased rate in warming that has occurred over the last 60 years (Poloczanska et al., 2011) and to ensure similar numbers of records in both periods. A limit of 10 records was imposed to exclude species with very sparse data, but 10 records was sufficient to detect the majority of species in the Sydney region (see Results).

Although the Sydney region is a relatively densely populated region, it is the only region with sufficient data to possibly detect shifts. If we avoided populated areas, then we would not be able to detect shifts elsewhere because there are insufficient records to determine ranges (Fig. 2). The east-Australian region has experienced a temperature increase of $\sim 1.5^{\circ}\text{C}$ over the past 60 years, although this has not necessarily led to shifts in species' ranges (Poloczanska et al., 2011).

We assessed four possibilities: species that spanned the Sydney region prior to 1971, but were only found northward after 1970 (northern species shifting their trailing edge north contrary to climate change); species that spanned the Sydney region prior to 1971, but were only found southward after 1970 (southern species shifting their trailing edge south consistent with climate change); species that spanned the Sydney region after 1970, but were only found northward prior to 1971 (northern species shifting their leading edge south consistent with climate change); and species that spanned the Sydney region after 1970 but were only found southward prior to 1971 (southern species shifting their leading edge north contrary to climate change). In effect we tested both the leading and trailing edges of species ranges and tested for both poleward and equatorial shifts.

After we identified species that the data suggested had moved into or out of the Sydney region, we consulted collection managers and mollusc researchers at the Australian Museum to provide expert opinions on the results. They were asked to provide advice on whether the shifts for each species were plausible, or whether they reflected known sampling biases, taxonomic issues, or were inconsistent with their knowledge of the range of the species.

3 RESULTS

3.1 Meta-analysis

Suitable data were obtained for 291 species from 12 studies (Appendix S1), representing 8 taxonomic groups and 7 regions (Appendix S2). Of these, macroalgae and fish were represented by most number of species (97 and 90 respectively), although these each only originated from two study regions (Appendix S2). Molluscs

were the most well-represented taxonomic group regarding number of studies (5) and regions (3). Of the regions, eastern Australia and Tasmania were the most well-studied in terms of our selection criteria and included three studies and eight taxonomic groups (Appendix S2).

Results showed that organisms shifted polewards in both datasets, but at a faster rate in the individual species dataset (9.1 ± 3.3 km per decade) (mean \pm SEM) than the amalgamated dataset (3.9 ± 6.0 km per decade). Marine invertebrate species may be significantly shifting their ranges polewards on a global scale (individual dataset: $V = 8938$, $p = 0.0007$), although results from the amalgamated dataset were not significant ($t = 0.2697$, $p = 0.7951$), likely due to high variation and low sample size ($n = 9$ groups). 40% of species showed little to no range shifts (< 5 km per decade) (Figure 1), with $\sim 33\%$ shifting poleward and $\sim 27\%$ equatorial by more than 5 km per decade?

In the individual species dataset, geographic range shifts were not significantly related to adult mobility ($df = 2$, $\chi^2 = 2.8526$, $p = 0.2402$), vertical zonation ($df = 2$, $\chi^2 = 0.5546$, $p = 0.7578$), dispersal potential ($df = 2$, $\chi^2 = 3.9800$, $p = 0.1367$), or trophic level ($df = 4$, $\chi^2 = 2.6373$, $p = 0.6202$). However, range shifts were related to horizontal zonation ($df = 2$, $\chi^2 = 7.0167$, $p = 0.0300$), with both intertidal and nearshore subtidal fauna showing significantly different poleward shifts (7.0 ± 5.7 and 14.3 ± 4.7 km per decade, respectively) than shelf fauna which showed a slight equatorial shift (2.7 ± 7.0 km per decade). Numbers of species in groups were unequal based on classifications, particularly in classifications based on vertical zonations (benthic species accounted for 67% of species, benthopelagic 23.5%, pelagic 9.5%),

horizontal zonations (nearshore subtidal species accounted for 55% of species, intertidal 26%, shelf 19%) and dispersal potential (species with planktotrophic development accounted for 65% of species, direct or unknown development 35%) (Appendix S1).

There was no correlation between range shifts of individual species and total temperature change ($r = -0.0775$, $p = 0.1874$) or standardised temperature change ($r = -0.0685$, $p = 0.2442$).

3.2 Eastern Australian museum records

There were 60 145 records for the 634 selected species, with 33 398 records prior to 1971, and 26 747 records after 1970. Most species were observed in the Sydney region (34.5°S to 33.5°S) both before 1971 (97.3%) and after 1970 (91.8%). Of the species that had range changes into or out of the Sydney region, contrary to predictions under a warming climate, we found that more species shifted north (33 species) than south (21 species). In addition, more species shifted their ranges out of the Sydney region (42 species) than into it (12 species), which is consistent with the lower number of records and species from the post-1970 period.

The expert malacologists (Des Beechey, Winston Ponder Ian Loch, Mandy Reid from the Australian Museum) suggested that identified trends were likely to be unreliable for most of the species (50 out of 54; 93%). Reasons for discarding the species included taxonomic inconsistencies (10 species), biases in collection methods (15 species) and inconsistencies with known distributions (25 species) (see Appendix S2). For the remaining four species, two were northern species shifting north out of

Sydney and two were northern species shifting south into Sydney. The results for these species were attributable to 1-3 outlying observations, with the remaining records 400 km or further north. These species were also discarded as outlying individual observations provide weak inference of an overall change in range (Sorte et al., 2010).

The reduction in species records since the 1980s (Fig. 2) can be attributed to a reduction in fieldtrips by the experts and increasing regulations in collecting animals along the coast as marine parks and reserves are declared, as well as a declining number of amateur shell collectors. In addition, collecting was highly targeted at different times to the specific groups on which the experts were working on. Therefore, despite the fact we targeted the best surveyed area and a well-studied taxonomic group, we were unable to confidently detect range shifts using museum records for any of the species in our study.

4 DISCUSSION

4.1 Global meta-analysis

Our results support previous studies showing that marine invertebrate species are generally shifting poleward in response to climate change (Table 1), although the magnitude and generality of this pattern across regions is debatable (see Burrows et al., 2011). The meta-analysis in the current study reveals a poleward shift of 3.9 – 9.1 km per decade; this is an order of magnitude less than values recorded from the only other meta-analysis on exclusively marine range shifts (average of 190 km per decade in Sorte et al., 2010). The discrepancies between our study and Sorte et al., (2010) are most likely due to the inclusion criteria for the respective meta-analyses. We adopted

a stricter set of criteria, particularly the exclusion of studies considering only a single species (e.g. Parmesan et al. 2003, Chen et al., 2011) in order to avoid publication bias (Gurrevitch et al., 1999) or those inferring range shifts through changes in abundance to avoid uncertainty that may be associated with this approach (Sagarin et al., 2006; Hidas et al., 2010).

Most of the studies considered for our meta-analysis did not meet our criteria due to lack of empirical evidence of range extensions, a problem also encountered by Booth et al., (2011) for Australian fish. We also found that only 67% of the 12 studies we examined quantified the sampling bias sufficiently to exclude the alternative hypothesis that apparent range shifts were only due to increased sampling effort in poleward locations. While some studies attempt to address the issue, methods are often unsatisfactory. Poleward shifts may be occurring in response to climate change, but we cannot be confident of the magnitude or frequency until we exclude the effect of sampling effort on results.

Our meta-analysis revealed no correlation between changes in sea surface temperature and range shifts. These results are contrary to a previous meta-analysis which showed that poleward shifts were significantly greater in studies with higher levels of warming (Chen et al., 2011). However, most of the species (94%) included in Chen et al. (2011) were terrestrial and may have been exposed to more regionally homogenous temperatures than their marine counterparts. The majority of species in our meta-analysis inhabit the intertidal, either exclusively (25%) or at the edge of their predominantly nearshore subtidal range (55%) (Appendix S1). The intertidal is an environment defined by its boundary between terrestrial and marine, and quantifying

decadal temperature changes in such an environment is extremely challenging due to the need to account for both air and water temperatures. Moreover, the intertidal is renowned for highly heterogeneous habitats which likely lead to complex demography rather than simple range shifts (Helmuth et al. 2006). Fine-scale values associated with these micro-habitats were not included in the coarse measures of SST we used (e.g. HADISST1.1 at 1° resolution). Due to the high proportion of intertidal species included in our meta-analysis, a causal relationship between temperature and marine range shifts cannot be ruled out. Irrespective of the magnitude of global range shifts, the high variation found in both our study (Fig. 1) and Sorte et al. (2011) coupled with the decreased significance in the amalgamated dataset requires caution in making sweeping generalisations. Instead, it seems likely that a few species are responding to warming waters quite dramatically, but overall there is extremely high variation in both the direction and magnitude of range shifts among most other marine species.

Most life history traits in the current study yielded no clear relationship to shifting ranges based on the meta-analysis. Such results should be cautiously interpreted, however, as the broad categories used here may have precluded detection of any trends. Species with slower life cycles are already more vulnerable to anthropogenic pressures such as overfishing and may bear the brunt of climate change more than species with faster life cycles (Perry et al., 2005). In addition those species unable to successfully establish themselves in higher latitude waters due to competition or predation will also be at risk (Parmesan et al., 2005).

Nevertheless, horizontal zonation of habitat did have a significant effect on range shifts of species included in the meta-analysis, with intertidal and nearshore fauna more likely to shift ranges in accordance with climate change scenarios than shelf fauna. Last et al. (2010) found similar patterns, with the poleward extension of Tasmanian fish more prevalent among reef-associated species. This could be due to more extreme and changing conditions in shallow waters.

At the global scale, most regions did not have any data that met the inclusion criteria for our meta-analyses, and those that did were often limited to a single taxonomic group (Appendix S2). Most data used in the current meta-analyses originated in eastern Australia which included the broadest range of taxonomic groups, reflecting recent well-documented studies on range expansions in Tasmania (Stuart-Smith et al., 2010, Pitt et al., 2010) and the eastern mainland (Polocsanska *et al.*, 2011). This is likely due to disproportionate effects of key species (Ling, 2008) and comparatively rapidly warming waters (Lough, 2008). This is in contrast to terrestrial studies on range expansions in which most data originates from the United Kingdom and Western Europe (Parmesan and Yohe, 2003; Chen et al., 2011). The United Kingdom and Eastern Australia are by far the best-studied regions regarding marine range shifts based on our strict inclusion criteria, but most studies here are confined to intertidal or shallow waters (< 20 m). We have almost no information about range shifts for species inhabiting deeper waters, including the potential for migration of intertidal and nearshore species to deeper waters during periods of warming.

4.2 Eastern Australian museum records

Our results from southeast Australia suggest that museum records cannot be used to reliably infer range changes in marine invertebrates. While the databases we examined contained a large amount of data on many marine invertebrate species, there were few species with sufficient data to accurately quantify their current or past ranges. Given that we examined the best-surveyed area and probably the best-studied taxonomic group of marine invertebrates in Australia, it is unlikely that better results could be achieved with other groups. We suggest our results should act as a warning to those who unquestioningly use museum records to examine species' distributions without consulting the relevant experts.

There were a number of issues apparent in the analysis of museum records. Firstly, when data from multiple institutions are combined there is a risk that trends could be apparent due to different sampling biases at each institution. For example, Museum of Victoria conducted intense sampling in the 1970s, and an unquestioning look at the data might suggest that many marine molluscs shifted south during this period. However, this likely represents a surge in sampling off the Victorian coast than a real trend. Secondly, tropical vagrants are common in the Sydney area, and although most do not establish sustaining populations (Booth et al., 2011), such species are more likely to be collected for museums due to their novelty in the area. These unusual observations may make species' ranges appear to be much broader than they actually are, as we did not consider vagrants a reliable indication of range change. In the opinion of the malacologists we consulted they confident that such vagrants were isolated individuals not able to build up sustained populations. Thirdly, changes in collecting techniques and storage of specimens over time can influence results. For example, species from deeper water will only be sampled at times when the

appropriate equipment is available, and differences between dry and wet storage can affect whether species can be reliably identified.

The results of our analysis of museum records would be even less likely to identify range shifts if we reduced the dataset to narrower time intervals, examined poorer-studied taxa, or examined trends in more recent times to identify contemporary changes. Indeed, the lower sampling effort in recent times (Fig. 2) will result in less likelihood of detecting range shifts. Range shifts may be more likely to be detected using complete surveys of targeted locations, and indeed Pitt et al. (2010) have recently documented poleward range shifts for marine invertebrates in Tasmania using this approach. However, a similar approach was used by Poloczanska et al. (2011) on the east coast of Australia and failed to document shifts. One potential limitation of such approaches is that sites can be separated by maybe 50–100 km, and shifts over shorter distances are unlikely to be detected. In addition, detection is never 100%, and one erroneous observation could result in an apparent shift of 50–100 km to the next site. The variability introduced by imperfect detection may obscure the underlying trend.

Our study highlights the need to identify species which could be used for ongoing targeted surveys along the coast to detect range shifts. Such species need to be conspicuous, easy to collect and belong to groups where the taxonomy is fully resolved. It would also be useful to determine if specimens on the boundaries of their ranges are mature and breeding individuals rather than just strays.

Museum records may be most valuable to detect species distribution changes by using them in conjunction with recent alternative approaches to mapping range shifts. For example, Redmap is a new online database in which members of the general public report occurrences of species outside of their traditional ranges (www.redmap.org.au). It has been recently used to support experimental findings of fish population changes in eastern Tasmania (Johnson et al., 2011), with plans to expand to a national scale in late 2012 (Gretta Pecl, pers. comm.). Similarly, Reef Life Survey (RLS) is a collaborative program between scientists, managers, and recreational divers, in which divers are trained to a very high level and record fish and mobile invertebrate species at reefs throughout Australia and internationally (www.reeflifesurvey.com). Redmap, RLS, and similar programs have the capacity to provide a recent assessment of species distributions to complement historical museum records and expert knowledge, thereby detecting range shifts.

4.3 Recommendations & Conclusions

Based on the challenges and results associated with the global meta-analysis and analysis of museum records, we recommend the following considerations for future studies on marine range shifts:

- All studies aimed at detecting or quantifying range shifts should publish geographic data associated with individual species. In the meta-analysis we conducted, many studies were excluded due to lack of published latitudinal (Stebbing et al., 2002; Schiel et al., 2004) or species-level data (Beaugrand et al., 2009; Smith et al., 2006), and we were therefore unable to quantify the effect size (kilometres moved per year). Similarly, Brown et al. (2011) found that only 33% of distribution and phenology studies they compiled had

published metrics useful to meta-analyses. With the increasing availability of online supplementary material in journals, such data could easily be published and will greatly facilitate future reviews and meta-analyses of range shifts.

- Those studies incorporating historical data should solicit expert knowledge to ensure data integrity. In our analysis of museum records, most species with shifting ranges were ultimately deemed unsuitable for analysis based on expert opinion from the relevant taxonomists and curators. Without input from these experts, false range shifts would have been reported.
- For regions in which there is little historical data and no long-term datasets, data on species distributions should be collected now using clearly described methods that can be applied to future surveys. Key species should be targeted based on the proximity of their range edge as well as their ability to be easily identified. Such baseline information will facilitate future detection of range shifts in areas where this has previously not been possible.
- Those studies comparing modern distributions with historical records should quantify potential bias and apply appropriate statistical methods to allow unbiased comparisons between the two potentially disparate datasets (Tingley and Beissinger 2009).
- Species which show obvious range shifts should be targeted with experimental studies in order to understand processes by which changing environmental conditions may affect their physiology, survival, and reproduction (e.g. Ling et al., 2008) (see Wernberg et al., 2012 for review and suggestions on marine climate change experiments).

Despite evidence that overall marine species are globally shifting polewards, 40% of individual species show little indication of range shifts, even in regions that are showing definite signs of warming (Appendix S1). Importantly, this does not mean that these species are not affected by warming waters. Rather, they may be limited in their ability to disperse (e.g. Poloczanska et al., 2011). Alternatively, they may be unable to establish viable populations in new waters due to other abiotic factors besides temperature (e.g. lack of suitable habitat, Poloczanska et al., 2011) or due to biotic interactions such as competition or predation. For some species, range contractions due to local mortality or recruitment failure may not be predictable based on just physiology alone, and other biological factors such as increased predation and lowered nutrients and anthropogenic impacts such as harvesting must be considered (Last et al., 2011). Changing distributions of intertidal marine invertebrates may be particularly difficult to predict due to the high inter-annual variability within populations, larval dispersal and settlement success of new recruits in addition to complex variations in thermal stress due to climate, oceanography, and the timing of low tides (Helmuth et al., 2002).

Range shifts due to climate change do not seem to be as obvious in marine as in terrestrial systems. One explanation for this is the open nature of marine systems and the multiple scales at which environmental factors operate which may mask, exacerbate, or interact with climate change effects (Brown et al., 2011), thereby resulting in the complexities detected in the current study. For example, recent evidence on the eastern Australian coast suggests that biogeography of intertidal fauna here is driven by oceanography and geomorphology, not temperature (Poloczanska et al., 2011). In addition, thermal dynamics in marine systems are highly dimensional,

and temperature changes are often less pronounced in deeper waters (Hsieh et al., 2009). Temperature change alone may not be a suitable indicator of impact; instead, the velocity of change may be the most important factor driving climate change impacts (Burrows et al., 2011). Importantly, our results highlight the lack of empirical data for range shifts in most regions and taxa in the marine environment. Modelling range shifts has become increasingly common (e.g. Cheung et al., 2009), but empirical approaches are crucial not only to inform and validate models, but also to understand the complex variation in responses likely to occur in the marine environment.

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7 SUPPLEMENTARY DATA

Appendix S1: List of species included in the global meta-analysis of individual species responses.

Appendix S2: List of groups based on taxonomy and regions included in the global meta-analysis of amalgamated data.

Appendix S3: List of species that shifted their range in and out of Sydney.

8 GENERAL STATEMENT AND AUTHOR ROLES

Each member of the research team has a different area of expertise; first and second authors are marine benthic ecologists, the third author is a spatial analyst and the fourth author is a taxonomist with an in-depth knowledge of the Australian Museum collections. Author roles were as follows: R.P., P.H. and I.F. conceived the ideas; R.P., M.A. and I.F. collected the data; R.P. and M.A. analysed the data; P.H. spoke with the experts, and R.P. and I.F. led the writing. All authors have approved the final article for submission.

1 **TABLE 1: Compilation of global meta-analyses of latitudinal range shifts. Poleward shifts are denoted**
2 **with a (+).**

Source	Focus	No. Studies	No. species (groups)	% marine species	Mean range shift (km / decade)	Std Error	p-value	Shift relationship to temperature	S
Parmesan and Yohe, 2003	Terrestrial	3	99	0	-6.1	2.4	0.013	Not analysed	In w sl a la in w S
Sorte et al., 2010	Marine	55	129	100%	-190	38	<0.0001	Not analysed	E sl sp S
Chen et al., 2011	Both	9	764 ^a (23)	6%	-17.6 ^c	2.9 ^c	<0.0001 ^c	Significant relationship	A in re g ta re in w S
Current study	Marine	12	291 (16 ^b)	100%	-9.1, -3.9 ^c	3.2, 6.0 ^c	0.0007, 0.7951 ^c	No significant relationship	A in a re in w S

3 ^a 764 species responses were analysed and may include multiple species.
4 ^b Only 8 of these groups had sufficient species to be included in statistical analyses.

1 ^c Value from analysis of groups based on taxonomy and region

1 **Figure legends**

2

3 Figure 1. Frequency histogram based on range shifts of species compiled for meta-

4 analysis.

5

6 Figure 2. Combined number of mollusc records from the Australian Museum and

7 Museum of Victoria for the area south of 22°S, east of 146°E and within 100 km of

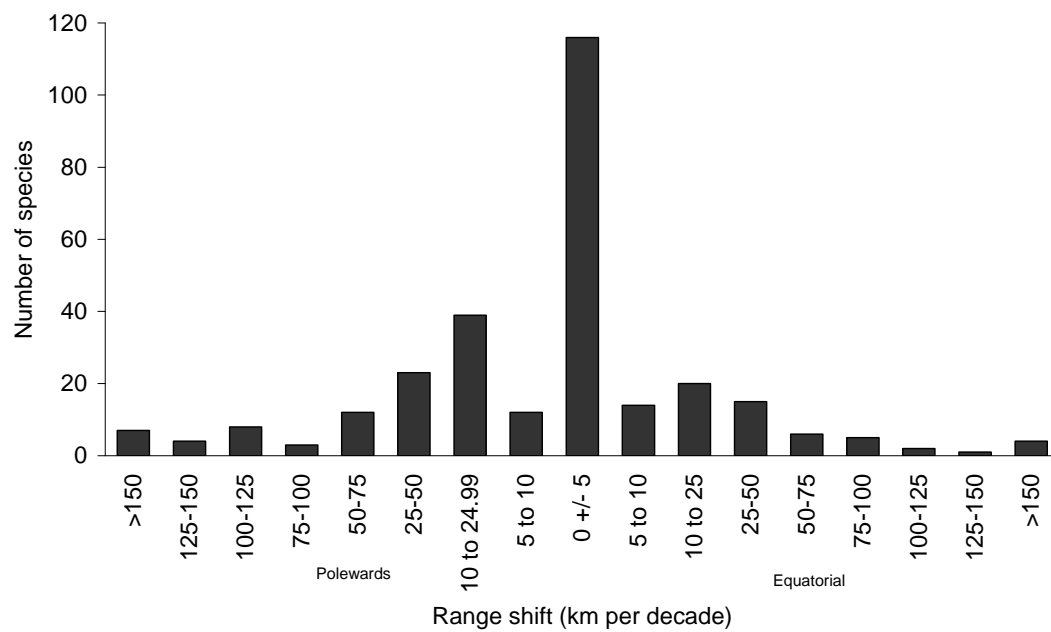
8 Australia (including Tasmania) from 1860 to present. Data is restricted to the 634

9 species with ten or more records in each time period and distributions that span the

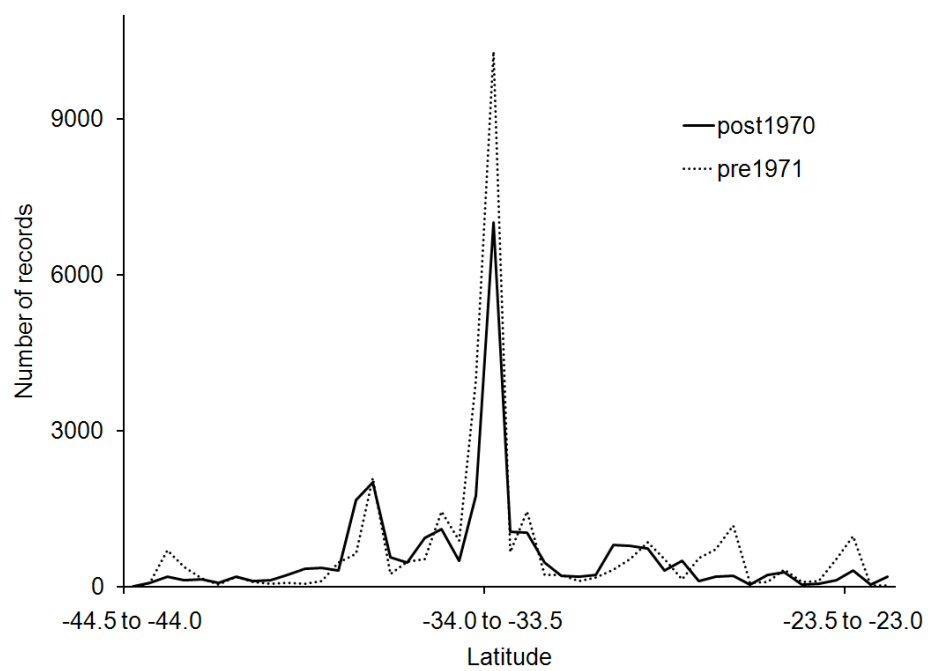
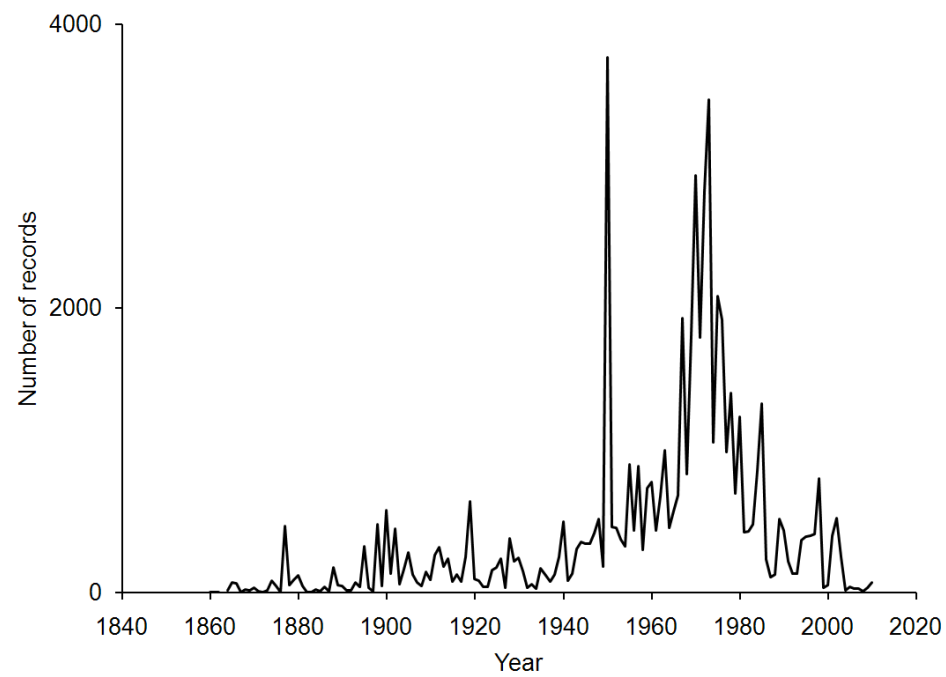
10 Sydney region.

11

1 Fig 1



2



1

2 Fig. 2