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Defining and observing stages of climate-mediated range shifts in marine systems

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ABSTRACT

Climate change is transforming the structure of biological communities through the geographic extension and contraction of species' ranges. Range edges are naturally dynamic, and shifts in the location of range edges occur at different rates and are driven by different mechanisms. This leads to challenges when seeking to generalize responses among taxa and across systems. We focus on warming-related range shifts in marine systems to describe extensions and contractions as stages. Range extensions occur as a sequence of (1) arrival, (2) population increase, and (3) persistence. By contrast, range contractions occur progressively as (1) performance decline, (2) population decrease and (3) local extinction. This stage-based framework can be broadly applied to geographic shifts in any species, life-history stage, or population subset. Ideally the probability of transitioning through progressive range shift stages could be estimated from empirical understanding of the various factors influencing range shift rates. Nevertheless, abundance and occupancy data at the spatial resolution required to quantify range shifts are often unavailable and we suggest the pragmatic solution of considering observations of range shifts within a confidence framework incorporating the type, amount and quality of data. We use case studies to illustrate how diverse evidence sources can be used to stage range extensions and contractions and assign confidence that an observed range shift stage has been reached. We then evaluate the utility of trait-based risk (invasion) and vulnerability (extinction) frameworks for application in a range shift context and find inadequacies, indicating an important area for development. We further consider factors that influence rates of extension and contraction of range edges in marine habitats. Finally, we suggest approaches required to increase our capacity to observe and predict geographic range shifts under climate change.

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1. Introduction

In order to persist in the face of environmental change, species cope, adjust in situ or shift their geographical distribution (Maggini et al., 2011). Understanding this trade-off has inspired decades of research addressing the implications of long-term responses of populations, communities and biodiversity to global change, with species redistribution receiving significant research effort (Root et al., 2003; Hickling et al., 2006; Hawkins et al., 2008, 2009; Wernberg et al., 2011; Bellard et al., 2012; Cahill et al., 2012; La Sorte and Jetz, 2012; Parmesan and Yohe, 2003). Climate change has altered the spatial distributions of species by changing the balance between colonization and extinction, leading to geographic shifts in the location of species' range edges (Gaston, 2003; Sinervo et al., 2010; Cheung et al., 2013; Poloczanska et al., 2013). The rapid pace of climate change means that range shifts are expected to be the dominant impact on ecosystem function and structure (Dawson et al., 2011; Doney et al., 2012), and thus range shifts are the focus of this contribution.

Geographic shifts have been well documented at range peripheries, and in particular, at the leading edges of latitudinal and elevational ranges (Hickling et al., 2006; Sunday et al., 2012). For example, when range edges are limited by a species' cold tolerance, warming is expected to increase organismal performance (e.g., activity, growth and immune response), survivorship and fecundity (Pörtner and Farrell, 2008), and ultimately lead to population increase. With ongoing warming, locations that were historically too cold for survival will become increasingly suitable for colonists. Range extension can be a direct response to physical parameters, such as temperature, and on land, precipitation and soil moisture (Bonebrake and Mastrandrea, 2010; Chen et al., 2011a). Extension can also be facilitated by indirect processes, for instance the arrival of a critical habitat-forming species that subsequently facilitates colonization by individuals of a dependent species (Yamano et al., 2011). By contrast, range contractions at trailing range edges are driven by population decline from areas of a species' historical range (Helmuth et al., 2006). Sub-lethal and lethal effects of high temperature in populations at range edges occur when physiological thresholds are exceeded as environmental temperature increases, and are well-documented (e.g., Beukema et al., 2009; Jones et al., 2010; Smale and Wernberg, 2013). Indirect drivers (although less studied), such as declining food availability, have also been implicated in geographic contractions, but do not appear to be more important than temperature (Cahill et al., 2012, 2014).

Species with cold range edges that are presently limited by habitat availability will be particularly vulnerable to reductions in their environmental niche caused by climate change (Burrows et al., 2011, 2014; Mair et al., 2014). Examples include species that are currently threatened or constrained by habitat availability, including species from polar or alpine habitats, isolated islands or the edges of continents (Pörtner et al., 2009; Wernberg et al., 2011; Cahill et al., 2012). However, for many species, climate change will lead to both positive and negative population-level effects, as determined by local climate across their range, presenting complexities at community scales that are challenging to anticipate.

Predicting how species' ranges will respond to climate variability is limited by our capacity to observe and establish mechanisms for both geographic extensions and contractions. This is in part because evaluating range shifts comes with at least four practical challenges. First, preliminary stages of range shifts occur as a progressive sequence that can resemble or be confounded by the stochastic dynamics of range edges (Sexton et al., 2009). Attributing shifts to long-term climate trends is difficult if historical data are inadequate to quantify the portion of variability in the observed location of the range edge due to processes unrelated to climate change. Second, what constitutes a range shift can be difficult to define – range shifts can occur for different life history stages, such as larvae or adults, and new or remnant peripheral populations may represent viable self-recruiting or immigration-dependent populations. Third, the mechanisms setting range edge boundaries differ among species and therefore rates of range shift responses will also vary among species (Brown et al., 1996; Gaston, 2003; Sexton et al., 2009; Doak and Morris, 2010). Fourth, extension and contraction processes are underpinned by evolutionary, physiological, and demographic processes (Lenoir and Svenning, 2013). Such detailed biological information is rarely available at the community level and tracking distributions through time remains elusive for many species, limiting our power to predict range shifts from climate data alone.

Theoretical understanding of biological responses to climate change has been developed for terrestrial systems (e.g., Bellard et al., 2012; Lenoir and Svenning, 2013). We seek to translate this understanding to develop a framework for categorizing marine range shifts into discrete stages. We focus primarily on warming-related range shifts because the distributions of marine species generally correspond more closely to their environmental niche and have been directly responsive to climate warming (Sunday et al., 2012). In fact, the primary role of temperature in setting distributional limits has long been recognized for marine species (Hutchins, 1947). A notable example comes from 70 years of abundance data from intertidal invertebrates and plankton from the western English Channel. Periods of range extension by warm-water species corresponded with periods with warmer ocean temperatures, and contraction in these same species occurred during cooler periods, while the reverse occurred for cold affinity species (Southward et al., 1995). Indeed, temperature has been implicated as a pervasive driver of geographic range extension and contraction in diverse marine fauna and flora, e.g., seaweeds (e.g., Root et al., 2003; Tanaka et al., 2012; Smale and Wernberg, 2013; Nicastro et al., 2013), invertebrates (e.g., Sagarin et al., 1999; Helmuth et al., 2006; Mieszkowska et al., 2006), and fishes (e.g., Perry et al., 2005; Dulvy et al., 2008; Last et al., 2011). For these reasons, marine systems provide the opportunity to examine the progression of range shifts in species that span large-scale environmental gradients, where many species have been, and will continue to be, highly responsive to ocean warming (Cheung et al., 2013).

Here, we present a generalized framework for defining successive stages of geographic extension and contraction at range edges. We next consider differences in our capacity to observe these stages, and how limitations may be influencing our understanding of climate-mediated range shifts. Each range extension and contraction stage can be integrated within a confidence framework that considers the type and amount of evidence, and consensus among diverse lines of evidence, to provide an overall confidence score. We also explore how different biological traits and extrinsic factors can influence how quickly populations at range edges may transition through extension and contraction stages. Finally, we identify pragmatic directions for testing, observing and predicting range shift mechanisms and dynamics in marine systems.

Formulating range extensions and contractions as a series of well-defined stages facilitates: (1) the use of different types of data, (2) application across diverse species, (3) appropriate quantification of range shift rates so that early extension stages are not compared to late contraction stages, and (4) data objectives for monitoring programmes that will improve the capacity to make globally comparable assessments of community changes in response to warming.

2. Stages of range extension and contraction

Identification of range extension and contraction stages can be used to advance comparative analyses so that rates of change across systems and regions are standardized. A large body of research on range dynamics indicates that range extension can be compared to the final three stages of an invasion pathway, where non-native species move long distances to a novel geographic location, colonize, establish and spread (Theoharides and Dukes, 2007; Sorte et al., 2010). Similarly, range extensions can be classified in three successive stages of arrival, population increase, and persistence. The first stage, *arrival* (Fig. 1), is initiated by the presence of one or more individuals in a new geographic region. Once a species has reached a new location, the second stage of range extension occurs as *population increase* via migration and/or self-recruitment (Stage 2, Fig. 1). For instance, the red mullet recently returned to the southern North Sea, and its abundance has markedly increased over the last decade (Beare et al., 2005). Similarly, following local extinction after an extreme cold winter an intertidal barnacle has not only re-colonized its former English Channel range with warming, but also extended further north by 55 km displaying synchronous increases in abundance (Mieszkowska et al., 2007). With ongoing warming, range extending populations remain demographically stable and achieve the final stage of extension, *persistence* (Stage 3, Fig. 1). This progressive sequence not only applies to space, but also in the temporal dimension. In migratory, pelagic or planktonic species, an increase in the extent of seasonal occupancy or the frequency of occupation can be defined as a range extension. Indeed, many species are found throughout the year in what were traditional summer habitats as winters become increasingly mild (Bellard et al., 2012; Last et al., 2011).

Similarly, range contraction can also be conceptualized as three stages: performance decline, population decrease and local extinction, each occurring as thermal thresholds for optimum performance, survival and population growth rate are exceeded. The first contraction stage, *performance decline* (Stage 1, Fig. 1), can be indicated by negative impacts at the individual level such as reduced growth, condition, or reproductive potential (Helmuth et al., 2006; Sinervo et al., 2010). Performance decline has the potential to manifest at a population level, impacting rates of reproduction, mortality (Cahill et al., 2012), or emigration as individuals leave or avoid formerly occupied regions. When reproduction or immigration rates are insufficient to replace those individuals lost due to mortality or emigration (resident populations), or individuals no longer use traditionally occupied habitat (migratory populations), a decrease in occupancy is observed. Therefore, a sustained decrease in abundance and/or occupancy characterizes the second preliminary stage of contraction, *population decrease* (Stage 2, Fig. 1). The protracted absence of populations from previously occupied habitats at a range boundary defines the third stage of a range contraction, *local extinction* (Stage 3, Fig. 1). Populations of a mudflat clam, *Macoma balthica*, have followed these three stages of contraction. This example is particularly compelling as transplant experiments provided causal evidence that exposure to temperatures >30 °C led to multiple performance declines (elevated maintenance costs, condition loss, and starvation) that was linked to population decrease and ultimately local extinction at the range edge (Jansen et al., 2007).

3. Variability in range edge locations

A key challenge to classifying species and events with this extension and contraction framework is the risk of misclassifying events due to background variability in distribution and abundance patterns that arise, for example, in species with vagrant individuals or species undergoing distribution change due to confounding human activities (Helmuth et al., 2006; Sexton et al., 2009; Fenberg and Rivadeneira, 2011). Moreover, in cases where species range boundaries are at equilibrium with climate, edge populations may be demographically unstable, displaying highly variable survival and reproduction rates due to natural climate oscillations and frequent exposure to extreme environmental factors (Wethey et al., 2011). Thus it is possible that populations in initial stages of extension may retreat, while contracting edge populations may recover.

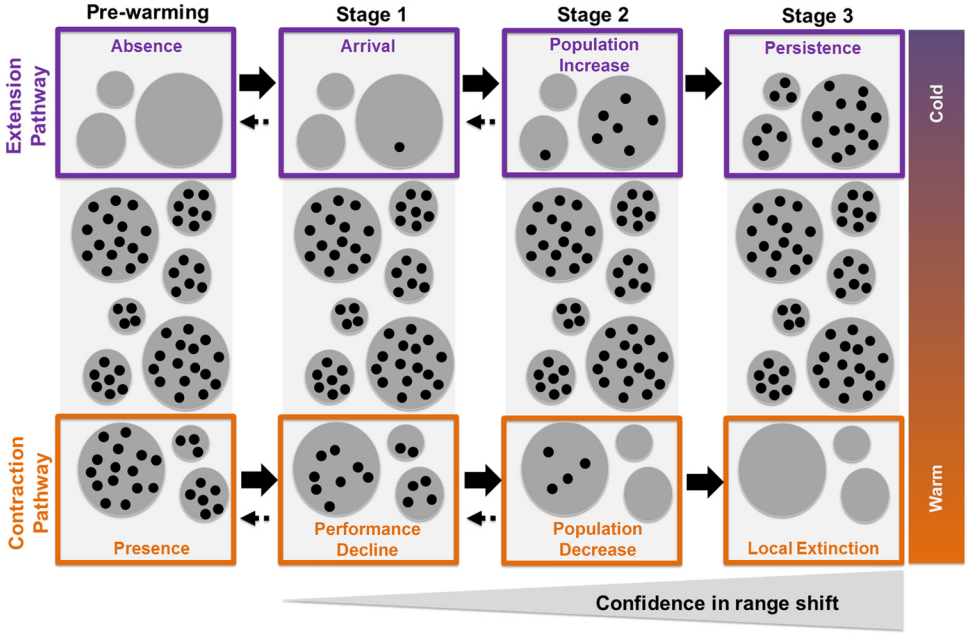

Fig. 1. Stages of geographic range extension and contraction. Grey circles represent suitable habitats spanning a temperature gradient; individuals are indicated by black circles. Range extension and contraction can be considered as a progression from a historical state that, under climate change, is expected to transition through three stages of range change (indicated by black, filled arrows). At preliminary stages, there is a probability of transitioning to a former stage (dotted arrows). Hence the highest confidence that a range change has occurred arises in cases where establishment (extension) or local extinction (contraction) is detected as transitioning through these stages, and is stable.

The stages of range extension and contraction can therefore be considered as observable states with increasing confidence with each subsequent stage (Fig. 1). Framing range shifts as a stage-based process allows observations, such as the new sighting of a species outside its historical range, to be considered with the appropriate level of confidence (e.g., the appearance of blue mussels on the shores of Iceland after being absent for a century; Berge et al., 2005). Such confidence assessments can be incorporated into statistical frameworks by using weighting terms in linear models in an approach that may be useful for meta-analytic studies (Bird et al., 2014). Confidence could also be integrated into Bayesian priors for parameter estimation and can dramatically improve models (McCarthy and Masters, 2005). To our knowledge, confidence scores in combination with range shift stages have not been incorporated into global analyses, thus representing a novel and potentially significant step forward in improving the inferences and applications derived from these approaches.

4. Multiple sources of evidence for range shifts and confidence classification

The pragmatic use of multiple evidence sources for assessing range shifts generally represents the best approach, at least until biological monitoring programmes are implemented at the spatial resolution and sampling frequency to accurately capture range dynamics. For example, changes in a range boundary over two or more time points may provide information on the distance a range boundary has shifted; but even greater understanding can be gleaned from information on the life-history stages present at each location and time step, and the seasonality of occupation patterns (Last et al., 2011).

Evidence for range shifts comes from anecdotal accounts, expert evaluation, fishery catch statistics, museum collections, volunteer-generated data and long-term systematic surveys, each with different inherent biases that may require different statistical approaches and/or careful interpretation (examples are highlighted in Table 1). Rare species, for example, may be over-represented in anecdotal reports by nature enthusiasts but remain undetected in systematic surveys. A further challenge is that many of the data sources providing historical baselines, such as trawl survey indices for fishes, have been designed for purposes other than detecting range shifts (Nye et al., 2009; Blanchard et al., 2008). As a result, surveys very likely offer biased information on changes in the true location of geographic range edges. Multiple converging lines of evidence may therefore have the highest potential to provide confidence in a particular range shift (Last et al., 2011). The challenge is how to compare and integrate diverse sources of information.

In assigning confidence that an observed range shift represents a stable change in a species' distribution consistent with that expected under climate change, the first step is to determine which extension/contraction stage has been observed. For instance, fishes found far outside their normal range may not necessarily be indicative of the first stage of a range extension (Booth et al., 2011; Last et al., 2011). An isolated unusual out-of-range sighting would therefore be scored as providing evidence weighted with "low confidence" in support of a climate change-mediated range shift.

The second step is to evaluate the reliability of the evidence for a particular observation. To facilitate this step, we have further developed the Intergovernmental Panel on Climate Change (IPCC) confidence assessment framework (Mastrandrea et al., 2010). The IPCC framework scores evidence by type, amount, quality and consistency, however evidence 'quality' (type and robustness) and 'amount' can work independently of each other. Here we separate these two evidence factors (Fig. 2). This separation means that given sufficient amount and consensus of data, even if the data are of low quality (such as anecdotal accounts from fishers' log books), a range shift could be scored with high confidence.

Applying this framework to the long-spined sea urchin, *Centrostephanus rodgersii*, which has moved progressively polewards in southern Tasmania over decades (Fig. 3) illustrates how multiple evidence may yield a high confidence assessment. The urchin has been detected beyond its known historical range in areas of southeast Australia at both adult and larval stages in fisheries and scientific surveys and by citizen scientists. In addition, its poleward expansion has been linked to the appearance of large urchin barrens, where it has established highly persistent populations, and thus its spread is associated with significant and observable ecological impacts (Johnson et al., 2011). These diverse lines of evidence, which all point to a range extension in conjunction with the urchin's continued occupation increased density within its new range in association with winter warming, provide an example of a "high confidence" range shift. By contrast, an example of a "low confidence" shift is the apparent northward extension of the North Sea redfish (*Sebastes viviparous*). The evidence supporting this shift is limited to catch surveys, and as discussed in the next section, these data suffer from spatio-temporal variation in effort (Table 1). Specifically, low sampling effort (poor sampling at the high latitudes of the North Sea) and changes in the distribution of effort through time (shifting survey distribution over time) likely contribute high variability in the observed distribution of this species (Dulvy et al., 2008).

5. Observing range shifts

One of the key complicating factors in climate change ecology is that many species have not undergone range changes or have moved in the opposite direction to isotherm shifts. Some of these non-shifting species may be falsely classified as responding to climate change while other shifting species may appear stable.

Table 1
Classes of data and their usefulness to the reconstruction of historical species distributions, in increasing order of robustness (from 1 to 4) for inferring range change.

Data type	Example	Comments	Example references
1. Anecdotal testimony	Interviews	• Often not quantitative • Low confidence	Johnson et al. (2011) and Last et al. (2011)
2. Natural history records	Museum collections and citizen science data	• Presence-only data • Variable effort in time and space • Potential location and taxonomic bias	Last et al. (2011) and Wernberg et al. (2011)
3. Non-targeted survey data	Fishery catch, port surveys for invasive species	• Often long time series • Usually restricted to species of interest • Potential reporting issues	Dulvy et al. (2008), Perry et al. (2005) and Hayes et al. (2005)
4. Direct re-surveys	Monitoring programmes	• Quantitative • Rarely available • Usually short-term (<30 years) • Spatially restricted • High confidence	Crisp and Southward (1958), Southward et al. (1995), Lima et al. (2007), Pitt et al. (2010), Poloczanska et al. (2011), Stuart-Smith et al. (2010) and Simkanin et al. (2005)

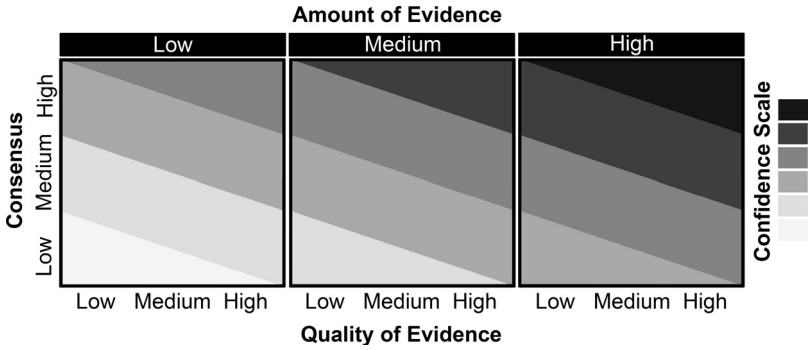

Fig. 2. Modification of the IPCC guidelines for assessing confidence in an observed stage of a range extension or contraction. The highest confidence is indicated by dark grey. Here we modify the IPCC guidelines to permit and facilitate explicit treatment of both the 'amount' of evidence and 'quality' of evidence, which are each independently important to our ability to assign confidence (Mastrandrea et al., 2010). Thus we add to the IPCC guidelines by highlighting that in cases where abundant, low quality evidence is strongly concordant, reasonable confidence for a given stage of range change can be assigned. Even so, the highest confidence score is limited to those cases in which extensions and contractions are detected with high confidence, persist through time, and are supported by multiple lines of evidence having high consensus, while the opposite is true for the lowest confidence score.

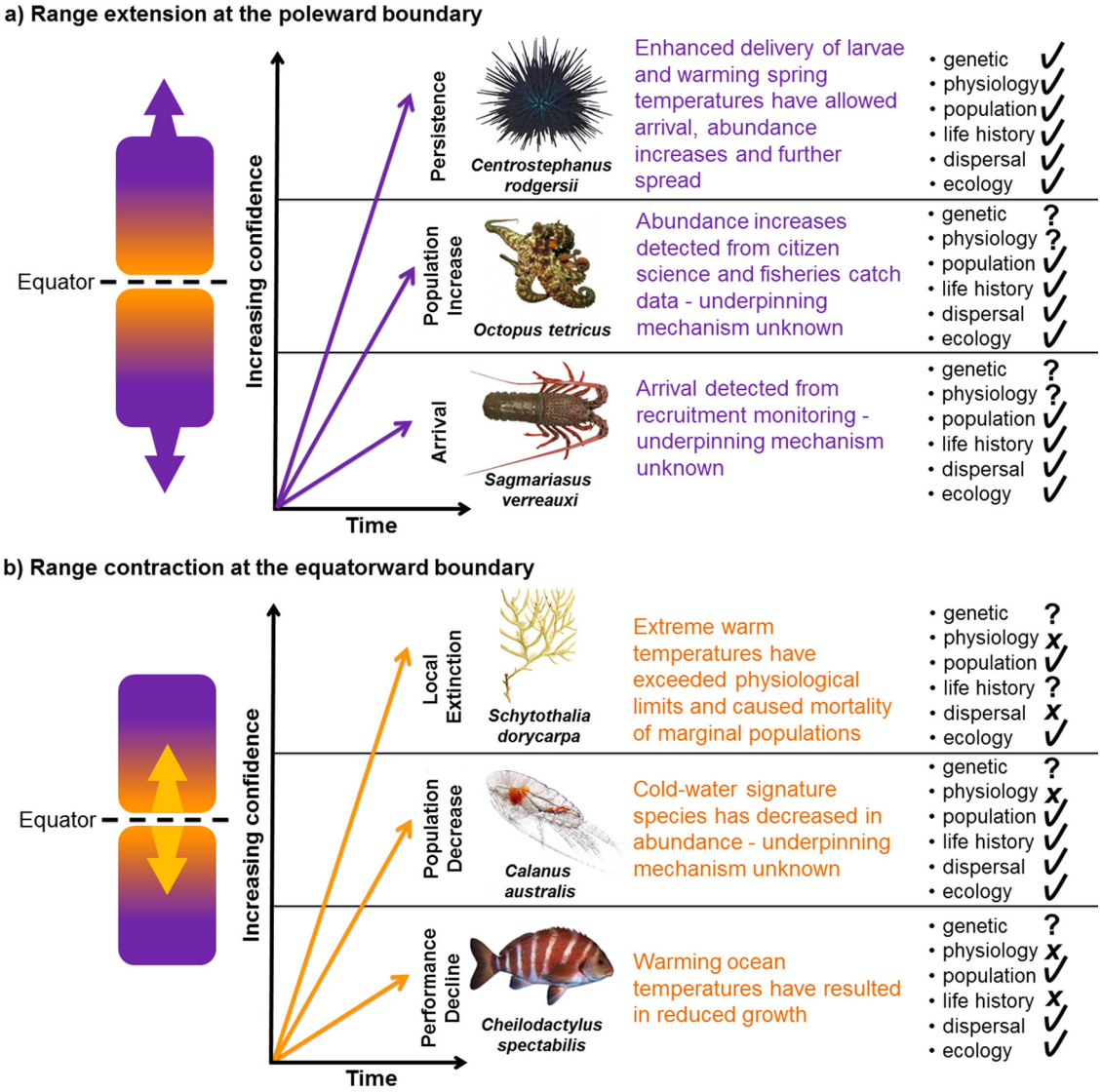

Fig. 3. Regions that are rapidly warming provide 'canaries in the coalmine' that can advance our understanding of biological responses to climate change. Six Australian marine species, selected to represent diverse taxa illustrate that, for a given period with uniform warming, species will be at different stages of range extension and contraction. For each species, biological traits with greater expected adaptability or acclimatory capacity are indicated with a check-mark, those with limited expected adaptability are indicated with an X, and those for which adaptability is unknown are indicated with a question mark. Traits were parameterized from the authors' knowledge of these species and the literature (Ling et al., 2008; Pecl et al., 2009; Johnson et al., 2011; Last et al., 2011; Neuheimer et al., 2011; Foo et al., 2012; Smale and Wernberg, 2013).

Here we discuss three general issues of detectability that may result in misclassifications of range shift stages and may hinder recognition of patterns of change that are important for attribution studies: paucity of observations, burden of proof, and sampling challenges.

A fundamental limitation in many situations is that baseline data are either lacking or were not collected at a spatial and temporal resolution designed for detecting changes in the edges of geographic ranges (Przeslawski et al., 2012). In particular, abundance data are sparse, especially in the ocean, where observations are logistically challenging and often limited to commercially important species (Brown et al., 2011; Richardson and Poloczanska, 2008). The paucity of data is a major constraint (although see Poloczanska et al., 2013) and one that will continue to hamper our understanding, particularly in the early documentation of range contractions (Cahill et al., 2012; Przeslawski et al., 2012). While abundance data for the majority of ocean-dwelling species are lacking, such information may be critical for developing a mechanistic understanding of range shift ecology (Mair et al., 2014).

The second challenge is based on the difference in the level of proof required for determining range extensions in comparison to contractions (Thomas et al., 2006). Given similar occupancy, detecting the arrival of new individuals (i.e., establishing their presence) requires less sampling effort than to reliably conclude that a species is no longer present (Hampe and Petit, 2005). So, while simply measuring species presence or abundance is adequate to detect early stages of range extensions and to document the final stage of a range contraction, the first stage of a range contraction may be overlooked if only abundance data are available. This pattern was reported for kelp in Western Australia, where density of the canopy did not change towards the warmer and presumably more stressful end of the distribution, but ecological performance declined (less recruitment, and recruit growth), such that the canopy became more vulnerable to local disturbance and extinction following an extreme heat event (Wernberg et al., 2010, 2013). Monitoring parameters such as individual growth rate, condition, or demographic rates may serve as important indicators of impending range contraction (Jansen et al., 2007; Neuheimer et al., 2011; Wernberg et al., 2010; Doak and Morris, 2010).

Third, sampling is complicated by the three dimensions (latitude, longitude, and depth) within which isotherms shift in the ocean, and in turn, determine the scale and shape of expected distribution change in marine species (Burrows et al., 2011). For example, the heating of surface waters by direct solar radiation can lead to both a deepening and polewards movement of isotherms expected to deform species' geographic ranges (Fig. 4). At the extending range edge, populations take advantage of warming and will therefore be observed first in relatively shallow-water locations where temperature is increasing more rapidly than at depth (Fig. 4). Because it is easier for humans to access and monitor high intertidal and shallow-water sites, climate-induced range extensions may be more easily observed than shifts into deeper waters. On the other hand, at the warm range edge, surface populations exposed to heat beyond their physiological tolerance thresholds become locally extinct (Helmuth et al., 2006; Weinberg, 2005; Dulvy et al., 2008; Smale and Wernberg, 2013). Populations may persist by shifting to cooler water at depth (for species without depth limitations), especially in the Tropics where isotherms level off (Fig. 4). If only shallow areas are sampled at the contracting range edge, a latitudinal contraction or local extinction will be inferred, while a 'deepening' response would be overlooked.

Issues related to both uneven sampling effort and variation in species detectability also arise (Hassall and Thompson, 2010). When historical sampling effort is less than contemporary effort, range extensions will be over-estimated and range contractions will be under-estimated, and vice versa when historical data are sampling with greater effort than contemporary data (Shoo et al., 2006). It is therefore important to recognize that unequal sampling effort and unreliable historical data lead not only to inaccurate estimates of range shifts, but also to differences in the detection of extending and contracting edges that will depend upon where the temporal focus of sampling effort lies, and on the underlying error structure of the data (Shoo et al., 2006). Correction for such biases is possible, and is increasingly attempted, for example, to understand historic changes in fish abundance as a result of fishing (e.g., Ferretti et al., 2013).

In addition, the ability to identify particular range shift stages depends upon where sampling is conducted relative to the range

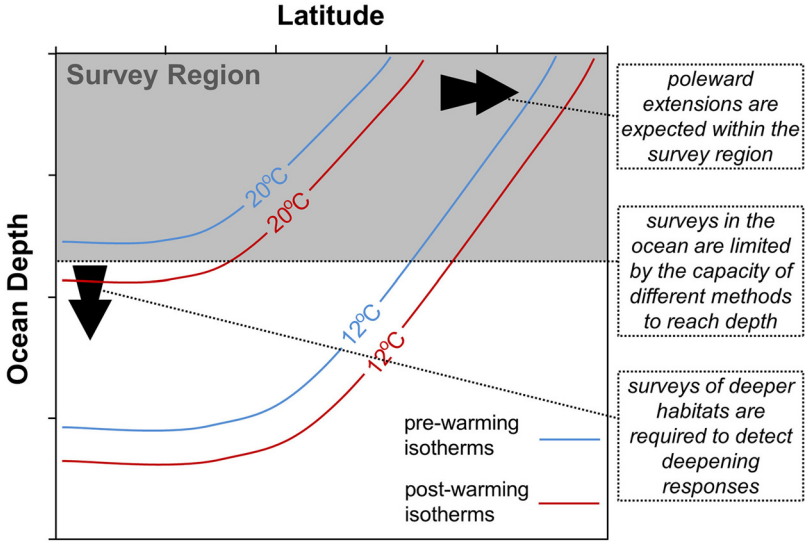

Fig. 4. Schematic depiction of a cross section from the equator to the pole showing historical and contemporary isotherms with increasing depth across latitude. Isotherms show the levelling-off of the latitudinal gradient of temperatures in the Tropics. For species with wide latitudinal ranges that occupy shallow marine habitats, populations nearer the Equator can move deeper to avoid rising environmental temperatures, in which case the latitudinal position of the range edge will not change, and a shift in depth will be missed if survey efforts are limited to the ocean surface. By contrast, in cases where warm water species are extending polewards, an increase in occupancy is predicted at the ocean's surface where warming is occurring at the fastest rate, and will therefore be more easily detected (e.g., by scuba divers).

edge. When sampling encompasses both historical and contemporary range edges, distance shifted (change in the location of the range edge boundary) or rate of change (distance shifted over time) is typically reported (Poloczanska et al., 2013; Sorte et al., 2010). When survey efforts do not span the range edge itself, but lie on the periphery of the range, change in abundance or patch occupancy has been used as evidence for extension and contraction. As highlighted in Fig. 1, these different types of responses represent different range shift stages and have different strengths and weaknesses that should be considered when assigning confidence to range shift data (Table 1). For instance, abundance data may be confounded in species with highly seasonal abundances, such as planktonic species. In such cases, distance shifted may not change with progressive transition to the second and third stage of our extension framework. By comparison, during a range contraction, a distance change in the range edge boundary is observed only following local extinction – that is, in the third contraction stage. Direct comparisons of the incidence of species within communities where range edges are expected to extend or contract will therefore be confounded if the stage of extension and contraction are not explicitly considered.

6. Are range extending and contracting species distinguished by their traits?

Some marine species have displayed stable distributions or shifted in a direction opposite to isotherms (Lima et al., 2007; Przeslawski et al., 2012), even in ocean warming hotspots (Last et al., 2011; Pitt et al., 2010; Poloczanska et al., 2011, 2013). While this lack of range shift may be due in part to the challenges associated with accurately measuring changes in geographic location of range edges, as discussed earlier, an open question is whether species displaying similar responses to climate change can be distinguished on the basis of their biological traits and life-history (Pinsky et al., 2013).

Risk (invasion) and vulnerability (extinction) frameworks are a pragmatic attempt to circumvent the requirement for detailed mechanistic understanding and to paint likely scenarios for different species upon which decisions can be made. In considering range extension, whether the traits of species displaying high invasiveness, rapid establishment, and spread following colonization in novel locations are similar to species undergoing rapid range extension is of interest. Although there are many species which fall outside expectations for invading species, some generalities emerge (Gurevitch et al., 2011; Weir and Salice, 2011). Traits of invasive species commonly used in risk frameworks associated with rapid range expansion include traits typical of 'r-strategists', such as short generation times, high abundance, early reproduction and smaller body sizes. Higher than average abundance, for example, is a trait associated with range-shifting North Sea fishes (Dulvy et al., 2008; Perry et al., 2005).

Broad physiological tolerances, phenotypic plasticity, the ability to overcome dispersal barriers and ecological generalism are expected pre-requisites for colonization and spread into new areas (Angert et al., 2011; Keith et al., 2011; Weir and Salice, 2011; Bates et al., 2013; Knutsen et al., 2013). Physiological tolerance and the capacity for physiological adjustment is especially important as a suite of physical parameters in addition to temperature (e.g., storm frequency, precipitation, ice melt, pH and deoxygenation (IPCC, 2007)) are expected to continue to change with ongoing climate forcing. These multiple stressors have the potential to influence the dynamics of species' geographic ranges (Helmuth et al., 2006; Lima et al., 2006). Ocean acidification, for instance, may further play a primary role as a stressor for some species in future decades, although more work in this area is required (e.g., Guinotte and Fabry, 2008; Munday et al., 2013). Dispersal will also likely be impacted by change in the strength of ocean currents which can facilitate or impede colonization, alter recruitment dynamics and carry organisms across geographic barriers (Herbert et al., 2009; Keith et al., 2011; Ling et al., 2008; Reid et al., 2007; Sorte, 2013; Wu et al., 2012). Overall, generalist species capable of thriving in diverse habitats are also likely to display population increases following arrival in new areas. For example, while species with specialized requirements, such as dependence on host plants (e.g., butterflies: Betzholtz et al., 2013), undergo rapid range extension, evidence is accumulating that species with more flexible behaviours, habitats and diets rapidly extend their range and display greater population persistence (Betzholtz et al., 2013; Weatherhead et al., 2012). Three range extending species from Australia that have responded to shifting isotherms display genetic, population, life history, dispersal and ecological traits consistent with these expectations (Fig. 3).

With regard to range contraction, extinction risk assessment frameworks such as those used to produce the IUCN Red List (Butchart, 2003; Foden et al., 2009) suggest that species with longer generation times, limited population connectivity, and restricted dispersal may undergo higher rates of local extinction and range contraction. In particular, species with environmental triggers or narrow temporal windows for reproduction, breeding, metamorphosis or sex determination may be particularly sensitive under climate change (Both and Visser, 2001; Cahill et al., 2012; Harley et al., 2006). The inability to persist under short periods of unfavourable or extreme climate may also be an important factor exacerbating range contraction (Early and Sax, 2011). This response has been recently observed for a habitat-forming seaweed, *Scytothalia dorycarpa* (Fig. 3), which contracted 100 km in less than a year in response to an extreme heat event that exceeded the upper thermal threshold of this species (Smale and Wernberg, 2013). Similarly, species with specialized habitats and diets, such as those dependent upon foundation habitats (e.g., coral reefs) or obligate symbionts may be disadvantaged in a future climate (Yamano et al., 2011) in cases where habitat mismatches occur. Variation in adaptive or acclimation potential may also play a role in range contractions – species with greater adaptive potentials may potentially adjust to new temperature regimes rather than contract at their warm range boundaries. Even so, a disproportionate level of genetic diversity may be held by trailing populations, such as Northern North Atlantic species as a result of recolonization patterns following the Quaternary ice age. Depending upon their phylogeography, range contracting species may face scenarios of genetic erosion that will limit their future evolutionary adaptive capacity (Nicastro et al., 2013; Provan, 2013). While studies of evolution at contracting range edges are scarce, this is an arguably important area of research for setting conservation priorities (Hampe and Petit, 2005; Munday et al., 2013).

Linking biological traits to invasion success and extinction vulnerability have been a long-standing goal of conservation biology, yet many species displaying occupancy changes consistent with range extensions (e.g., Przeslawski et al., 2012) and contractions (Fig. 3) do not always possess traits consistent with predictions from theory. In fact, some range contracting species, such as the cold-water copepod (*Calanus australis*), have biological traits that are inconsistent with theoretical predictions, and explanations for such inconsistencies are limited by lack of information (indicated by question marks in Fig. 3). Such observations therefore strongly suggest that acquiring adequate understanding of range shift ecology in the marine environment, a field that has been dominated by theory developed from terrestrial systems, is required to tailor assessment frameworks for geographic extension and contraction, and the stages of each. New tools, such as presented here, are needed to advance our capacity to make management decisions.

7. Why have so few species responded in the same direction as isotherms?

While biological traits of species will presumably shape the sensitivity of species to environmental change, in some cases extrinsic factors may exacerbate or constrain extension or contraction processes (Helmuth et al., 2006).

Here we highlight, among many, four mechanisms that are commonly explored in the literature (e.g., Gaston, 2003; Svenning and Skov, 2004; Sunday et al., 2012).

First, in many species, the current range edge may not be at equilibrium with climate and may even temporarily move in an opposite direction to isotherms. Long lag times from past climatic events (e.g., Pleistocene glaciations) and rebound effects from decadal-scale environmental variability provide two examples for range disequilibrium (Berge et al., 2005; Early and Sax, 2011; Gaston, 2003; Gaston et al., 2009; Hilbish et al., 2010; Sexton et al., 2009). Second, physical mechanisms that may restrict range extension include the availability of suitable habitat (e.g., light availability in photosynthetic species, substratum type) and presence of dispersal barriers, such as hydro-dynamic barriers (Keith et al., 2011; Poloczanska et al., 2011). Third, specifically in the case of range contraction, demographic compensation may prolong the process of change in the location of the range edge. Indeed, populations at equatorward edges in plants have experienced lower survival and recruitment but higher growth during warmer growing seasons, resulting in range edge stability in spite of warming (Doak and Morris, 2010). Forth, natural enemies and the presence (or release) of strong competitors have the potential to alter range shift trajectories (Cahill et al., 2012; Pimm, 1989). Thus indirect effects arising from climate change, such as changes in the sign and strength of species interactions, may also play a role in setting rates of range shifts (Helmuth et al., 2006; Urban et al., 2012), a research area presently gaining momentum in marine systems (Grigaltchik et al., 2012).

Concentrating on locations where communities are comprised of a subset of species undergoing extension and contraction at their range edges (such as at the boundaries of biogeographic regions) may be important areas of research focus to provide mechanistic insights to advance the field of range shift ecology. Such regions may also indicate how ecosystem structure and function are likely to change due to species' redistribution (Hawkins et al., 2008, 2009; Johnson et al., 2011).

8. Recommendations for a future in which range shifts can be observed and predicted with high confidence

Increasing our power to identify the underlying drivers of distribution change will advance our forecasting capacity. Given the potential impacts of range shifts, including significant changes to global resources and ecosystem services, identifying mechanisms for distribution change and developing predictive capacity are vital for conservation and management. Here, we identify approaches for monitoring, assigning confidence, and modelling range shifts that will contribute to a future with a greater capacity for observing species redistribution.

8.1. Cost-effective monitoring strategies for observing range shifts

Changes in population size, trajectory and distribution have the potential to impact ecosystem structure and function. Thus abundance surveys across life stages (e.g., Doak and Morris, 2010) will be vital in developing our understanding of the redistribution of species with climate change and the follow-on ecological consequences (Mair et al., 2014).

While laboratory and small-scale field experiments typically consider only acute effects, ongoing research surveys have proven invaluable in developing our understanding of climate change impacts in the ocean (Southward et al., 1995; Helmuth et al., 2006; Hawkins et al., 2009; Poloczanska et al., 2013). Thus, long-term monitoring programmes need to be secured (e.g., the UK Celtic Sea ground-fish survey: Blanchard et al., 2005). Data from historical monitoring programmes should also be archived securely and sites revisited (Chen et al., 2011b; Hawkins et al., 2013).

As all species cannot be monitored everywhere, creative solutions, such as engaging volunteers in citizen science to collect data, presents a cost-effective and increasingly recognized approach for global conservation efforts (Hochachka et al., 2012; Stuart-Smith et al., 2013; Bird et al., 2014). Identifying priority ecosystems and species will also be important in focusing resources, and those that have been developed for invasion and extinction could also be tailored for range-shifting species (Butchart, 2003; Leung et al., 2012; Keith et al., 2013). Additionally, new, targeted monitoring programmes need to be devised for areas undergoing rapid change, such as in rapidly warming regions where more comprehensive programmes may be justified and allow generalizations from high-quality baseline environmental and biological data to other regions (Hobday and Pecl, 2013). Strategic cost-benefit and risk-based approaches will also ensure the efficacy of on-going programmes. For example, a first sighting might prompt rapid scientific monitoring if a species that is newly identified in a particular area is considered a potential threat.

Concurrent monitoring of biological responses and environmental parameters will necessitate the expansion of programmes currently underway as well as the development of new programmes to detect environmental variability and trends. Regional (Pauli et al., 2012) and global (Richardson et al., 2012) collaborative efforts will allow for linkages between the biophysical and socio-economic arenas to develop innovative assessment and management options (Hannah et al., 2002). Interdisciplinary research and coordinated efforts provide the information required for anticipating the redistribution of species and the impacts of climate change.

8.2. Building capacity to detect and attribute biological responses to climate change

While species responses to natural climate variability can develop our understanding of the mechanistic processes setting range boundaries, attributing species range responses to climate change impacts caused by anthropogenic greenhouse gas emissions is more challenging. Attribution depends in the first instance upon accurate detection of range shifts at scales linked to human-driven climatic change. Well-structured and carefully-designed monitoring programmes are vital to achieving this goal, capturing the spatial and temporal scales corresponding to both climate processes and target species responses. Approaches such as coordination of the timing, areas of coverage, and methods of sampling will allow for greater understanding of process and a higher level of confidence in observed biological responses, while major advances will likely require global collaborative efforts (Richardson et al., 2012). Accounting for detectability using approaches such as mark-recapture and occupancy models will improve the identification, modelling and prediction of both current and future range shifts (MacKenzie and Royle, 2005; Wintle et al., 2012; Garrard et al., 2013). Where possible, field surveys should include some capacity to model the observed process itself, such as repeat sampling of sites, and include metadata describing collection variables so that these sources of variability can be accounted for at analysis stages (Sexton et al., 2009; Tingley and Beissinger, 2009).

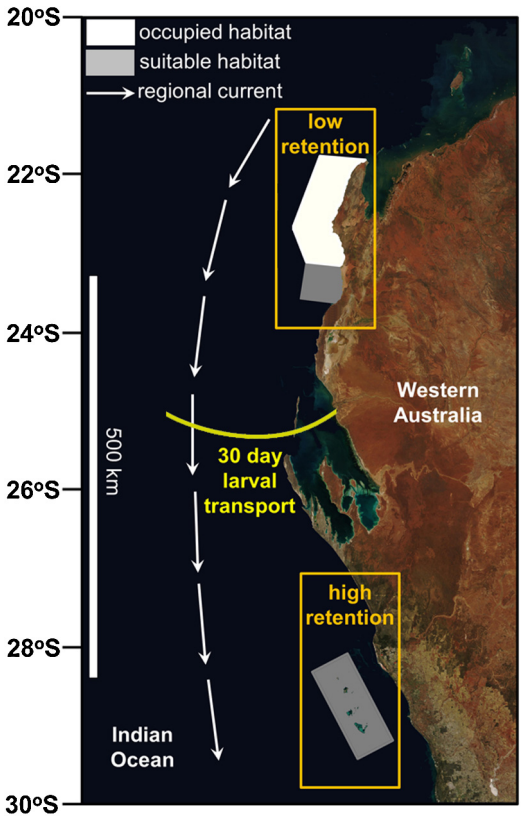

Fig. 5. Map of the Western Australia coastline indicating diverse coral reef assemblages (occupied habitat) that form a species larval pool for poleward transport to areas of known coral reef (suitable habitat), as indicated by the regional ocean current direction. The shelf south of ~24°S presents a potential geographic barrier because it is not conducive to the formation of extensive reefs, except for the shallow Abrolhos island group between 28° and 30°S. A long-duration larval dispersal phase is required to transport viable larvae across the gap to areas of suitable habitat, while those species with shorter dispersal windows will be unlikely to reach suitable habitat via ocean transport, as indicated by particle mobility experiments (e.g., 30 day larval transport distances are inadequate; Feng et al., 2010). For those species that manage to arrive in isolated habitats, factoring in larval retention time to predict local recruitment potential following colonization is also critical for accurate predictions of the longer term establishment potential (Aiken et al., 2011). Satellite image courtesy of NASA.

8.3. Improving models as predictive tools

Modelling approaches that can accommodate diverse types of data incorporate confidence scores, and that are developed in conjunction with ongoing monitoring will provide an important means to identify likely range shift pathways of focal species. Conceptualizing range shifts as stages, identified by occupancy and abundance data, can be incorporated into models of stochastic processes (e.g., Hanewinkel et al., 2014). It is also possible to constrain the stages of range shifts as multiple observable states, such as a reversible Markov chain, an approach that has been taken for invasion pathways (Hui et al., 2011). The probability of transitioning between the various stages of range extension and contraction can be described in matrix form and parameterized using field survey data on abundance (Hanski, 1994). Moreover, because the pathways of range extension and contraction can be understood in terms of demographic rates and occupancy, population models are useful for predicting the trajectories of range dynamics, particularly for parameterizing the transition probabilities among the range shift stages. Vital rates, such as reproduction and survival, will translate to changes in species occupancy and alternatively can be successfully coupled with correlative species distribution modelling (SDM) techniques to provide novel insights into how population persistence changes at both range boundaries under environmental variability (Early and Sax, 2011). Dynamic range models (DRMs) have also recently been developed to statistically estimate both range dynamics and the underlying environmental response of demographic rates from species distribution data (Schurr et al., 2012). Spatially explicit transport and dispersal models can also be combined with species distributions models to offer an important step in predicting range shifts (Fig. 5) (Cheung et al., 2010). Efforts to advance modelling techniques for the description of range shift pathways will develop our predictive capacity and ability to test some of the hypothetical links between range shifts and biotic or abiotic factors.

9. Conclusions

The underlying mechanisms of range shift processes are multi-layered, but can be classified into sequential steps. Species' responsiveness to climate change involves all levels of biological organization and interactions with various biotic and abiotic factors (Cahill et al., 2012; Grigaltchik et al., 2012; Kordas et al., 2011). A consistent framework to define and assess range shifts will therefore facilitate global comparisons of species at each stage of range change and should advance predictive capability. In particular, the processes that allow species to adjust and persist in a variable climate should be considered at each different stage of extension and contraction, and the importance of different processes, as well as both intrinsic and extrinsic factors, may differ among stages. Developing the potential to detect and predict range shifts will rely on the use of diverse information sources and careful interpretation of data to accurately quantify which species are at equilibrium with climate in regions undergoing rapid change. Yet a major limitation in the field of range shift ecology is the inadequacy of our present capacity to observe range shifts in order to obtain information needed to parameterize models and to predict how species will transition through extension and contraction pathways. A future with greater observing power will require new strategies to reduce the cost per observation and the implementation of monitoring programmes that meet known challenges in detecting range shifts and combine diverse evidence sources to appropriately evaluate confidence in observed changes. Without a concerted effort to invest in on-going and intensive monitoring, our understanding of the natural variability in the location of range edges and the observations of range-shifting species at early stages will continue to be obscured by limited data and misdiagnoses as we act on conclusions drawn from incomplete understanding. A future with both adequate data resolution and reliable predictive power can provide the foundation the implementation of sound conservation and management strategies during the global redistribution of species.

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