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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.