

Chapter 3

Natural and Climate Change Mediated Invasions

Steve I. Lonhart

3.1 Introduction

Species distributions are constantly in flux. Biological and physical factors continually influence the rates of range expansions and contractions, altering the distribution of species in space and through time (MacArthur 1972; Brown 1995; Brown et al. 1996). Ranges expand as individuals colonize new areas and contract as populations become locally extinct. Understanding how organisms respond to environmental changes and describing the underlying mechanisms are key research components in the fields of ecology and biogeography. Knowing where populations occur—and where they are absent—provides insights into the ecological and physical factors that regulate patterns of density and distribution (see also Chap. 2, Carlton).

Historically, biological responses were due to natural processes and often occurred over long (geological) time scales. More recently, anthropogenic (i.e. human-mediated) processes have played an increasingly important role in driving patterns of density and distribution. In this chapter I will present biological invasions in the context of geographic range shifts, explore range shifts due to natural, anthropogenic, and artificial processes, and consider how climate change is already affecting species distributions.

3.2 The Geographic Range of a Species

The geographic range of a species is commonly defined as the known spatial extent of the species. Field guides often display range information as a map with polygons or shading to indicate species presence. Since species distributions are dynamic, a truly accurate assessment of the geographic range is nearly impossible. Instead, range maps represent estimates of distribution based on limited, often incomplete data and thus provide a general view of where a particular species occurs (Brown et al. 1996). Range limits, with the exception of

a few species, are likely either under- or over-estimates of the actual geographic range. This combination of historic, recent, and anomalous range records is not likely representative of a species' current range extent (Gaston 1994). For the majority of species, most of which receive little scientific attention, geographic ranges are likely underestimated due to inadequate sampling near range limits.

A suite of biological and physical factors regulates the distribution and density of each species. Physiological tolerance limits set thresholds beyond which an individual cannot reproduce, grow, or survive, and ecological interactions (e.g., competition, predation, mutualism) further modify these limits. Physical barriers can also prevent species from dispersing to all suitable habitats. For marine species, such barriers are often land masses, such as continents. For example, since completion of the Suez Canal in 1869, over 200 marine species have invaded the Mediterranean Sea from the Red Sea (Rilov et al. 2004; Chap. 27, Ferreira et al.). Similarly, the open ocean can act as a barrier to intertidal organisms with limited dispersal distances. In addition, there are numerous and often interacting environmental and physical factors driving individual and population-level responses that lead to local and regional fluctuations in density and spatial distribution. These natural responses make it nearly impossible to know the actual geographic range of a species at any given point in time.

3.3 Range Shifts

Understanding the causes and consequences of geographic range shifts assumes that new range records can be compared to existing range data that are both accurate and complete. Currently there are no widely accepted criteria used to determine what constitutes a range shift, let alone standard methods to measure and describe the geographic range of a species (Gaston 1996, 2003). Range shifts encompass contractions due to local extinction at the range edge and expansions as individuals invade beyond former range limits. But how long must a population be absent from a range edge to be considered locally extinct, warranting a range contraction? Conversely, when an individual is observed beyond its range limit, does that constitute a range expansion?

3.3.1 *Factors that Influence our Understanding of the Geographic Range and Range Limits*

“I am never sure whether to be general or more detailed with distributions, as animal distribution records often tell us as much about the distribution of biologists as they do about the geographical range of a species.” Dr. Bill Rudman, <http://www.seaslugforum.net/>

The geographic range of a species is dynamic, representing a moving target. In addition to the variation derived from environmentally driven and anthropogenic changes, there are also logistical constraints that limit our ability to describe effectively the geographic range of a species. Gaston (1994) noted that measures of geographic range are inaccurate or problematic for the following reasons: (1) the quality of data varies across the entire range since it is impossible to sample all areas equally; (2) the magnitude of error estimating the range varies as a function of true range size; (3) there is no standard way to deal with anomalous occurrences or transient or migratory species; and (4) the need to distinguish between historical and current range sizes.

Collecting new range data is not trivial and there are few biogeographic studies focused on detecting the range limits of marine species (Sagarin and Gaines 2002a). Instead, new range records are often collected serendipitously as a result of monitoring programs or surveys designed for other purposes. If we consider the most studied and accessible marine habitat—the rocky intertidal—we are still confronted with significant logistical barriers. For example, selection of rocky intertidal study sites is typically nonrandom and biased toward areas adjacent to marine laboratories or with relatively easy access. Sampling effort within and between sites may be unequal due to differences in exposure and available habitat. In addition, few sites are selected a priori as part of a study design focused on describing the range limits of a species (but see Gilman 2005).

With the exception of a few narrowly distributed species, comprehensive sampling of the entire geographic range is rarely feasible. This obstacle is reduced somewhat for intertidal species since the range is essentially linear (Sagarin and Gaines 2002b), but this is true only for intertidal obligates—many intertidal species also occur in the shallow subtidal. Surveys near range limits require intensive sampling effort to detect what should be a relatively rare occurrence. As such, these organisms are commonly undersampled at or near the range limit and therefore underestimate their spatial extent (Sagarin and Gaines 2002a). Spatial variation in abundance within the rocky intertidal makes it difficult to sample for certain species (Sagarin 2002). If the species is small or otherwise cryptic, the likelihood of detecting it declines. Furthermore, since distributions change over time, sampling the range requires repeated surveys on a regular basis. Such extensive on-site efforts are rarely undertaken for most species (but see Sagarin and Gaines 2002b; Gilman 2005).

Determining whether a new range record represents a “true” range expansion is difficult, requiring additional evidence. For example, it is not always possible to determine whether an extralimital range record represents a natural range expansion, a human-mediated invasion, or is a sampling artifact. The context of the discovery (i.e. species dispersal capabilities, site characteristics, and sampling history) provides additional information to evaluate the status of a new range record. Such records may not indicate that a species recently expanded into a new area, but instead may have been observed for the first time due to increased sampling effort or exploration of a new area. Without long-term, intensive sampling at a particular site, it is difficult to separate real range shifts from sampling artifacts.

There are also analytical issues that hinder accurate descriptions of geographic range. Existing range data can have multiple shortcomings. A range limit can be based either on a single, anomalous extralimital range record or the presence of a well-established population. As discussed earlier, anomalous, extralimital range records should not be used to determine geographic range. Conversely, an extralimital, well-established, self-sustaining population provides strong evidence of an expanded geographic range. There are also new range records that go unreported. During a search of several museum collections, Lonhart and Tupen (2001) discovered several “new” (i.e. unpublished) range records that exceeded recent field observations. However, unless sufficient metadata are included with museum voucher materials, it is difficult to differentiate extralimital range records from true range expansions. Furthermore, museum collections also represent a time-integrated view of the geographic range. Compiling range records that span decades, if not centuries, can be problematic when describing the current geographic range of a species.

Marine ecologists working in the field may lack the taxonomic expertise and natural history background to recognize extralimital species, and thus many potential new range records go unnoticed. In contrast, when taxonomic experts undertake expeditions to remote locations, it is not surprising that numerous new range records are reported (e.g., Vermeij et al. 1990; Bertsch et al. 2000). Ideally, coastlines would be systematically sampled, but this is not practical. Instead, targeted areas are sampled, and these are selected in a non-random manner. Thus the clustering of range limits at a particular site may be more indicative of where experts sampled than of the true limit of any particular species. Moerman and Estabrook (2006) describe a pattern where university botanists in North America have, in general, spent more time in investigating areas near their university, resulting in higher local species richness than in counties more distant from their home institution, a phenomenon they call the ‘botanist effect.’

Range maps may use some or all of these data to generate distribution polygons, and must extrapolate between the relatively few known data points (Gaston 1994; Brown et al. 1996). Thus, with the exception of a few species that have extremely limited distributions along the intertidal, the geographic range of a marine species cannot be known in great detail and is instead estimated using available information. While this level of detail is sufficient for biogeographic analyses that cluster endpoints at 1° latitude scales or larger (e.g., Roy et al. 1995), it may be insufficient to track invasions or ecological responses to climate change.

3.3.2 Natural Range Shifts

Natural range shifts require the establishment of extralimital populations without direct mediation by human activities. There are key spatial and temporal components to defining the validity of a proposed range shift, where a ‘shift’ may include

range contraction and/or expansion. In the case of a range expansion, the new range record must occur beyond the known geographic range limits of the species. This is typically verified by consulting a field guide or other published reference that contains the spatial extent of the species in question. The second component, which receives little attention, is to determine whether the new range record represents an anomalous occurrence, or is part of a well-established population. If the new range record is based on one or a few individuals, temporarily found beyond the species' range limit, then the observation should be considered an extralimital range record. Relative to the geographic range of a species, extralimital range records should not constitute a basis for expanding the geographic range. To be considered a "true" range expansion, these extralimital individuals should be part of a self-sustaining, multi-generational and well-established population persisting beyond the previously known range limit.

This restrictive definition of range expansion excludes marginal-population that persist beyond the edge of the range for only a short period of time ('relict populations') or are sustained by external propagules ('sink-population'). Relict populations persist beyond their range limit for a single generation but fail to reproduce successfully, ultimately leading to local extinction. Such populations represent ephemeral range shifts. In contrast, sink populations persist beyond range limits, sustained by propagules derived from source populations within the established range limits. Although sink populations can persist for multiple generations, should dispersal from the source population cease, the sink population will become locally extinct.

Published geographic ranges may include data from anomalous extralimital range records and marginal populations. Without clear definitions for valid range records and criteria for including or excluding data from estimates of the geographic range, natural variation and sampling error may obscure our view of species' geographic ranges and their dynamics.

History and time Species range shifts occur for a number of reasons. Over the evolutionary history of a species, there are three general phases: initial expansion, equilibrium, and decline to extinction (Gaston 1996). During the initial expansion phase, a species invades new, suitable habitats. Expansion may be rapid or very slow, depending on the dispersal capabilities of the species and suitability of habitats. This is followed by a period of dynamic equilibrium, when the spatial extent of the species is stable and near its maximum. Finally, as the species declines and approaches global extinction, its range size diminishes by either contracting along the entire range towards the center or creating a patchwork of shrinking, isolated populations. Since these phases are not synchronous across taxa, each of the three phases is currently represented by a multitude of species. While these changes naturally take place at geologic time scales, anthropogenic processes have hastened the pace of species decline (e.g., habitat loss, pollution, over-fishing) and global spread (e.g., intentional and accidental introductions).

Response to natural changes Range shifts are also expected as species respond to natural changes in climatic conditions. Climatic external forcing occurs at

various time scales, from seasonal to millennial (Root and Schneider 2002). Individuals and populations can respond to changes in weather and season, but these shifts are fine-scale and ephemeral, making them hard to detect and track. Furthermore, such shifts likely have little impact on general estimates of geographic range. Interannual shifts due to large-scale atmospheric and oceanographic changes, such as El Niño Southern Oscillation (ENSO) and North Atlantic Oscillation (NAO) events, can alter species distributions significantly (Harley et al. 2006). Although many of these range shifts are temporary some can be lasting (Lonhart and Tupen 2001). At decadal scales, regime shifts such as the Pacific Decadal Oscillation (PDO) can dramatically alter patterns of species density and distribution (Chavez et al. 2003; McGo wan et al. 2003). At millennial scales, paleontological records indicate shifts in species ranges in response to geologic processes and glacial-interglacial periods (Valentine and Jablonski 1993). These large-scale, low-frequency climatic changes lead to long-term, broad-scale range shifts.

3.3.3 Human-mediated Range Shifts

The pace and extent of species spread has rapidly accelerated as human modes of transportation (e.g., ships, planes) have increased in number, speed and distance traveled. Humans are moving species either intentionally or accidentally to all parts of the world. This accelerated global redistribution of species has led to a phenomenon termed ‘biotic homogenization’, where community assemblages in different regions are becoming more similar to one another through the addition of cosmopolitan species (McKinney and Lockwood 1999).

Intentional species introductions occur for a variety of reasons (Chap. 5, Minchin et al.; Chap. 6, Hewitt et al.). In terrestrial systems, many species are brought to new environments for economic reasons (e.g., agriculture, silviculture), while other species are introduced as biocontrol agents to combat invasive pests. In aquatic systems, species are intentionally introduced for aquaculture, and in freshwater systems for commercial and recreational angling (Rahel 2000; Kolar and Lodge 2002). There is also increasing evidence that the release of pets from aquariums may be a significant source of species introductions (Semmens et al. 2004).

Not all introductions are intentional. Many species are accidentally introduced by human activities. In North America, Ruiz et al. (2000) conservatively estimate that just over half of the nearly 300 invasive species studied were introduced by shipping. Species can be transported on the hulls of vessels, in cargo, or in ballast tanks, either suspended in ballast water or in the tank’s sediments. Hitchhikers are also found associated with commercially important species, such as oysters and abalone, whose shells serve as habitats for a myriad of invertebrates and algae (Culver and Kuris 2000; Wasson et al. 2001).

3.4 Climate Change and Range Shifts

The Intergovernmental Panel on Climate Change (IPCC) recently reported on observed climate changes to (1) atmospheric concentrations of greenhouse gases and aerosols, (2) the Earth's surface temperature and precipitation, (3) snow cover, sea and river ice, glaciers, and sea level, (4) climate variability, and (5) extreme climatic events (IPCC 2007). These changes are the result of natural, internal processes (e.g., El Niño Southern Oscillation, Pacific Decadal Oscillation), natural external forcing (e.g., Milankovitch cycles), and human-mediated external forcing (e.g., elevated CO₂ levels) (Beaugrand and Reid 2003). Describing the patterns and understanding the mechanisms that drive existing and predicted biological responses to climate change are active areas of research in the fields of ecology and biogeography.

Predicted and observed biological responses to global warming include changes in physiology, morphology, patterns of density and distribution, phenology, species interactions, and population genetics through local adaptation (Hughes 2000; McCarty 2001; Sagarin 2002; Beaugrand and Reid 2003; Helmuth et al. 2006; Parmesan 2006). A dynamic model of community response to climate change suggests species will respond individually rather than as a tightly linked species assemblage (Graham and Grimm 1990). Shifts will occur at the level of individuals, populations, and species—not at the level of communities—and will be limited by life history characteristics and phylogenetic constraints. Responses may be further limited by species interactions. For example, depending on coevolutionary relationships, the rate of range expansion for some species (e.g., parasites, mutualists, habitat specialists) will be limited by the rate of spread for an obligate host or habitat.

3.4.1 Observed Biological Responses to Climate Change

Organisms respond to climatic changes at various temporal scales. Many marine apex predators undergo seasonal migrations to forage in ephemeral but highly productive areas, to find mates, or give birth. Geographic range maps usually capture these temporary changes in distribution. At longer time scales (i.e. interannual, interdecadal, millennial), changes in distribution represent actual range shifts. The evidence for responses at these longer time scales is growing and several examples are presented below.

At interannual scales, atmospheric and oceanic processes act at large, basin-wide scales. In the Pacific Ocean, El Niño Southern Oscillation events, which persist for several months and occur every 2–7 years, increase sea surface temperature (SST) and alter equatorial and coastal current patterns (McGowan et al. 1998; Chavez et al. 1999). From coastal California there are multiple examples of new northern range records, spanning several taxa and nearly a century, that

coincide with ENSO events (e.g., Hubbs and Schultz 1929; Glynn 1961; Richards and Engle 2001; Engle and Richards 2001). Poleward flow of coastal currents along the northeastern Pacific entrains the adults and larvae of subtropical and warm temperate species, depositing them well beyond their typical northern range limits. As ENSO conditions wane and SST drops, few of these extralimital individuals survive, although some may establish relict populations (Lonhart and Tupen 2001).

If SST serves as a key driver of change in coastal marine species, then during ENSO events populations of cold temperate species near their southern range limit should respond by either declining in abundance locally or contracting poleward. A recent study of the giant kelp, *Macrocystis pyrifera*, along the northeastern Pacific coast reported delayed recovery at its southern range limit in response to an ENSO event (Edwards and Hernández-Carmona 2005). During the 1982–1983 ENSO, high wave action, high SST and low nutrients decimated kelp populations at the southern limit. At these same areas the southern sea palm, *Eisenia arbor ea*, persisted during the 1982–1983 ENSO and quickly recruited at high densities into habitats devoid of *Macrocystis*. By coupling long-term monitoring data and field experiments, Edwards and Hernández-Carmona (2005) showed that the southern range shift of *Macrocystis* over a 20-year period was due to increased mortality and recruitment failure of *Macrocystis* after the ENSO event and the ability of the understory kelp *Eisenia* to competitively exclude *Macrocystis*.

Interdecadal regime shifts, a term used to describe significant and sustained changes in ecosystems responding to climate change (Hays et al. 2005), add yet another layer of complexity. The Pacific Decadal Oscillation occurs in the Pacific Ocean, lasts for 20–30 years, and is more pronounced at high latitudes (Mantua and Hare 2002). Long-term data sets are needed to track decadal changes, and in southern California the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program has organized cruises to collect physical and biological data since 1949 (McGowan et al. 2003). During the winter of 1976–1977 there was an abrupt shift from the cooler ‘anchovy regime’ to the warmer ‘sardine regime’ (see Chavez et al. 2003). Following this regime shift, the offshore species composition and abundance of calanoid copepods changed, zooplankton phenology shifted, and the abundance and proportion of larval fishes changed (summarized in McGowan et al. 2003). Pelagic tunicates, significant members of zooplankton communities, also responded to the PDO regime shift (Lavaniegos and Ohman 2003). Of the 10 species studied, 4 were present in both cool and warm phases of the PDO, while 4 dropped below the limits of detection after the regime shift. During the warm phase, dramatic changes in biomass were not solely due to declines in abundance, but also to decreases in the size of individual zooids and colonies (Lavaniegos and Ohman 2003).

In the nearshore waters of southern California, Holbrook et al. (1997) documented substantial changes to the assemblages of reef fishes after the 1976–1977 regime shift and slight increase in SST (nearly 1 °C). At the two sites that were

studied, species richness fell by up to 25% and dominance shifted from cold water to warm water species. In central California, Barry et al. (1995) re-sampled rocky intertidal invertebrates along a transect that had been initially sampled from 1931 to 1933. By locating the original bolts, they were able to replicate the original study and quantitatively compare abundances over the 60-year interval. Changes in abundance occurred for 32 of the 45 species analyzed, indicating a significant shift in community structure. When species were categorized by geographic range (i.e. southern/warm water, northern/cold water, or cosmopolitan), eight of nine southern species increased in abundance while five of eight northern species decreased significantly (Barry et al. 1995). Climate change was considered the primary driver of change, while alternative mechanisms such as habitat changes, anthropogenic effect, species interactions, ENSO events and upwelling variation were not considered as important (Sagarin et al. 1999). An unintended “experiment” on the California coast demonstrated how warming of seawater by the thermal outfall of a power-generating station caused dramatic changes in intertidal community structure through apparently cascading responses to changes in abundance of several key taxa, particularly habitat-forming foliose red algae (Schiel et al. 2004).

In the northeastern North Atlantic marine organisms have expanded northward concordant with warm water regime shifts and the North Atlantic Oscillation (NAO) (Hays et al. 2005). From 1960 to 1999 calanoid copepods (crustaceans) shifted up to 10° latitude northward as SST increased in part due to the NAO and climate change (Beaugrand et al. 2002). Physical and biological data suggest the northeastern North Atlantic is currently in a warm water dynamic regime and concomitant changes in the abundance, distribution, and diversity of phytoplankton and zooplankton communities may have contributed to the recent decline of Atlantic salmon stock (Beaugrand and Reid 2003). Southward et al. (1995) also report range shifts and population-level responses of plankton and intertidal barnacles and mollusks to increased SST in the western English Channel. During warm water phases, warm water species increased in abundance and expanded northward; the reverse was true during cool periods. Using 20 species with range limits in the North Sea, Perry et al. (2005) reported that during a period of increased SST half of the ranges shifted northward for warm water species and half of the ranges contracted for cold water species.

Prior to the acceleration of global change mediated by human activities (e.g., habitat loss, pollution, introduced species, and overfishing), changes in species-level distributions were relatively slow. Studies of the fossil record have added to our understanding of biological responses to climate change. During the Pleistocene, eastern Pacific marine mollusks indicate species range shifts and redistributions were common and driven by climatic changes associated with glacial-interglacial cycles (Valentine and Jablonski 1993; Roy et al. 1995, 1996). In fact, fossil evidence shows that species additions, deletions, and substitutions within marine communities are the rule rather than the exception (Valentine and Jablonski 1993).

3.5 Contrasting Natural Range Expansions and Biological Invasions

Range expansions as a result of natural processes (i.e. dispersal not aided by human activities) share many similarities with human-mediated biological invasions. Both result in the introduction of a species into a new habitat and expansion of the geographic range. However, there are also striking dissimilarities, and at least six have important ecological and biogeographic implications. First, the vectors and rates of transmission are very different. Biological invasions circumvent physical barriers to dispersal through human activities (e.g., shipping, aquaculture) and occur at an alarming and accelerating rate (Cohen and Carlton 1998). Natural range expansion of marine organisms often depends upon oceanic currents and occurs at longer, often geologic, time scales. Second, the rate of addition into communities is greater for introduced species than natives (Strauss et al. 2006). For example, marine biological invasion events often occur locally but at high frequencies, such as ships inoculating harbors on a daily basis (i.e. small spatial scale, high rate). In contrast, natural range expansions are driven by large-scale, low frequency climatic events (i.e. large spatial scale, slow rate). Third, many biological invasions fail because of very different environmental conditions between donor and recipient regions. Tropical species attached to the hull of a vessel are unlikely invaders of cold temperate regions. When a natural range expansion occurs, it is often because conditions in areas just beyond the current range limit change, becoming environmentally tolerable to the species in question. Fourth, invasive populations are disjunct from their native range in the donor region, often by very large distances. As a consequence, invasive populations can suffer Allee effects and become locally extinct unless there is a steady supply of new propagules. This is in contrast to natural range expansions, which are often contiguous with the main population. The 'rescue effect' (see Brown and Kodric-Brown 1977) may buffer extralimital populations from local extinction through immigration from the main, adjacent population. Fifth, responses to climate change will differ between native and invasive species (Carlton 2000), and the variation in response may be greatest for invasive species. As environmental conditions change in the recipient region, invasive species may increase or decline in abundance, depending on physiological tolerances. As SST increases due to climate change, selection by environmental conditions in the donor region will affect the ability of invasive species to persist in the recipient region: the abundance and distribution of warm water species should increase while cold water species could become locally extinct. Further, the likelihood of regional extinction is potentially higher for invasive species. Small and nascent invasive populations are more susceptible to the deleterious direct and indirect effects of climate change. For these vulnerable populations, a local extinction of an invasive population can also be a regional extinction. In contrast, native species responding to increasing SST may lead to poleward range expansions and range contractions away from the equator, but regional extinctions are unlikely. Finally, introduced species lack a co-evolutionary history with species in the recipient region (unless, by chance,

there are other invasive species from the same donor region). Species undergoing a range expansion are likely moving into habitats and communities that share many of the same species. In spite of these differences, the response of established invasive species to recent global warming mirrors native species: on the Pacific coast of North America, all nine of the invasive species that have apparently responded to recent global warming moved poleward (Carlton 2000). Comparative studies on the responses of both natives and invasive species to climate change will improve our understanding of the biological and physical processes driving geographic range shifts and the success or failure of invasive species.

3.6 Conclusions

Without human activities to overcome physical barriers to dispersal, the ability of invasive species to spread long distances is minimal. In contrast, natives have a long history of opportunities to invade nearby areas, and the inability to expand further is due primarily to biological barriers affecting survival (e.g., physiological tolerances, species interactions) and not physical barriers to dispersal. The rate of change for natural range shifts is typically slow, occurring over decades and centuries and covering tens to hundreds of kilometers. In contrast, human-mediated invasions are occurring at an unprecedented rate, with species moved hundreds or thousands of kilometers in a matter of hours to days. The threat of biotic homogenization is significant: while the rate of climate change might be altered by human production of CO₂ and other greenhouse gases, and habitat loss can be reduced or even reversed, invasive species, once established, are rarely eradicated and therefore pose an ongoing threat with potentially severe ecological consequences.

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