



# 7 Synergies between Climate Change and Species Invasions: Evidence from Marine Systems

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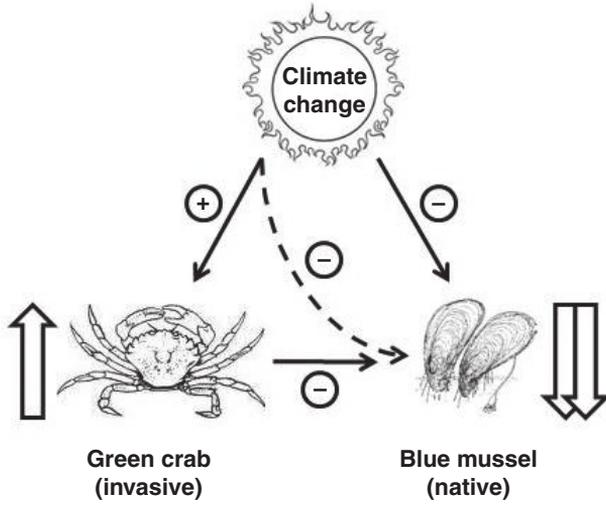
## **Abstract**

The hypothesis that climate change will facilitate species invasions has recently received increasing focus in studies of marine systems. Over the past decade, approaches to testing this hypothesis have shifted from time-series observations of concomitant increases in both processes to experimental tests that are beginning to reveal the mechanisms underlying the synergies between these two aspects of global change. The results of many studies conform to expectations that under climate change, invasive species' abundances, ranges and per capita effects – collectively indicative of invader impacts – will increase. However, there remain significant gaps in our understanding of responses to non-thermal factors (such as changes in ocean pH, dissolved oxygen and storm events) and how species-specific idiosyncrasies will manifest in changes at the community level. Continued exploration of the synergies between climate change and species invasions will help us to anticipate potential indirect effects (mediated through the responses of interacting invaders) on native species, which may themselves also be directly affected by climate change.

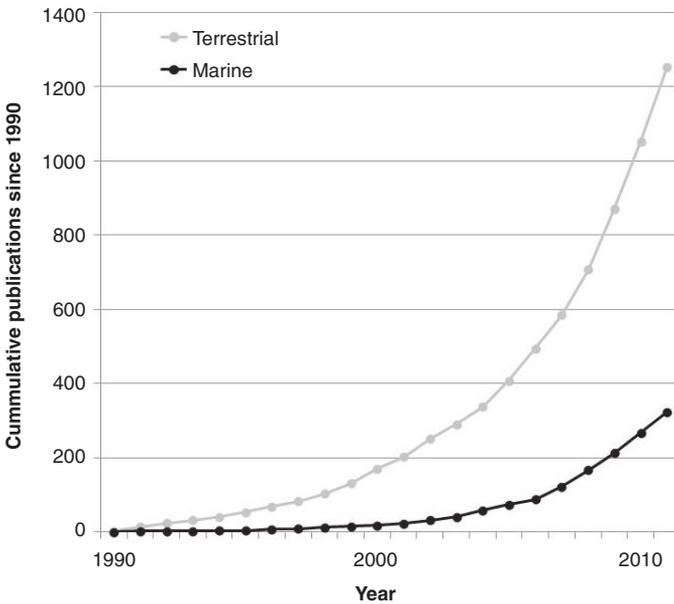
## **Introduction**

Both climate change and species invasions have been recognized independently as

major drivers of biodiversity loss (Sala *et al.*, 2000), and their total impact could be compounded by synergistic effects (Brook *et al.*, 2008). For example, climate change could drive an increase in invasive species' abundances and, consequently, density-dependent effects on native prey species (Fig. 7.1). On the other hand, invasive predators could drive population declines of native prey and, therefore, decrease the potential of these prey species to cope with climatic changes. Despite the likelihood that such reciprocal interactions will increasingly threaten the Earth's systems, a decade ago, few experimental studies had 'investigated the responses of different plant species to global warming in an ecosystem context, and none [had] examined the response of biological invaders' (Dukes and Mooney, 1999). Furthermore, although the terrestrial literature now contains in excess of 1000 papers discussing the topic, study of the interaction between climate change and species invasions in marine systems lags about a decade behind that in terrestrial systems (Fig. 7.2; cf. Rahel and Olden, 2008, for a review of freshwater systems). This discrepancy in publishing rate is despite evidence that marine systems appear, in some cases, to be threatened more greatly by climate change, invasions and their interaction than their terrestrial counterparts (Cohen and Carlton, 1998; Sorte *et al.*, 2010a, 2013; Burrows *et al.*, 2011; Sunday *et al.*, 2012).



**Fig. 7.1.** Climate change can have both direct (solid lines) and indirect (dashed line) effects on species. For example, if climate change has a positive effect (e.g. increases the growth and survival) on the invasive green crab, then this will lead to an indirect negative effect on the crab's prey, the native blue mussel. Furthermore, if climate change also has a negative direct effect on the blue mussel, then this will lead to a doubly negative impact (via both direct and indirect effects) on the native species.



**Fig. 7.2.** Terrestrial (grey) and marine (black) studies on climate change and species invasions. Values are cumulative publications since 1990 and are based on a topics search using ISI Web of Knowledge.

This chapter first summarizes recent and predicted alterations in the ocean associated with climate change, as well as the main hypotheses for why these environmental

alterations are predicted to impact invasive species less negatively than co-occurring native species. Second, the marine literature is reviewed to assess whether our current

understanding of climate change effects on invasive species conforms to the expectations of these hypotheses. Finally, the chapter synthesizes the literature to explore how the responses of invasive species to climate change will, in turn, determine their future impacts on native species.

### Climatic Changes in the Marine Realm

The oceans, which cover about 70% of the Earth's surface, have absorbed an estimated 26% of the excess CO<sub>2</sub> (Sabine *et al.*, 2004) and 84% of the increased heat held within the Earth system via greenhouse warming (between 1955 and 1998; Levitus *et al.*, 2005). Recent and future predicted increases in CO<sub>2</sub> levels and temperature feedback to influence other physical properties of marine systems (Table 7.1; Meehl *et al.*, 2007). While an increase in dissolved CO<sub>2</sub> might be expected to fertilize the growth of oceanic primary producers, it also drives decreases in pH (i.e. ocean acidification) and shifts in carbonate saturation states that can impede calcification (Doney *et al.*, 2012). Increased temperature leads to a decrease in dissolved oxygen and can increase stratification, further preventing oxygen diffusion (Keeling *et al.*, 2010). Global warming also causes the expansion of ocean water and melting of terrestrial ice, leading to sea level rise, while the melting of sea ice and changes in evaporation rates are associated with changes in ocean salinity. At the same time as average conditions are shifting, extreme climatic events are and will be increasing in

frequency and intensity. Although global warming has been best studied, each of these environmental alterations has the potential to affect invasive species and their impacts.

### Why Might Climate Change Favour Invaders over Native Species?

Changes in marine climatic conditions might be expected to favour invaders over native species because some of the same species' characteristics that could facilitate persistence under future conditions are those associated with invasion success. Specifically, both climate change 'winners' (species likely to benefit most or suffer least) and successful invaders are expected to (i) have environmental tolerance ranges that are either relatively broad or encompass future conditions, and/or (ii) have life-history characteristics favouring fast growth, high reproductive rates and rapid utilization of available resources.

Species differ in their physiological tolerances, with functioning being optimal over a small range of conditions, declining as conditions become increasingly suboptimal and ceasing completely (eventually leading to mortality) outside of tolerance limits (Monaco and Helmuth, 2011). Within this framework, then, climatic changes will or will not benefit a particular species based on whether conditions become more physiologically optimal or more stressful, respectively. I would note, however, that whereas considering the species level is appropriate for this discussion, tolerance

**Table 7.1.** Observed and predicted changes in the marine environment associated with climate change. Unless noted, values are from the Fourth Assessment Report of the Intergovernmental Panel on Climate Change and are based on the A1B scenario, when multiple projections were given (Meehl *et al.*, 2007).

| Physical factor                      | Past changes (observed)                    | Changes predicted by 2100 |
|--------------------------------------|--|---------------------------|
| pH                                   | ↓ 0.1 unit since pre-industrial time       | ↓ 0.25 units              |
| Sea surface temperature              | ↑ 0.4°C between 1955 and 1998 <sup>b</sup> | ↑ 1–4°C                   |
| Dissolved oxygen                     | ↓ in several regions <sup>c</sup>          | ↓ 1–7% <sup>c</sup>       |
| Salinity                             |  | ↓↑ depending on location  |
| Sea level                            | ↑ 0.08 m between 1961 and 2003             | ↑ 0.35 m                  |
| Extreme climatic events <sup>a</sup> | ↑ frequency and intensity                  | ↑ frequency and intensity |

Notes: <sup>a</sup>Extreme heat events and storms creating high waves; <sup>b</sup>Levitus *et al.*, 2005; <sup>c</sup>Keeling *et al.*, 2010.

also varies intra-specifically, based on individuals' differential histories of adaptation and acclimation. Several marine studies, although not focusing directly on species invasions, have shown predictable responses to climate change associated with geographic affinity (see Helmuth *et al.*, 2006), and geographic range can be considered a proxy for environmental tolerance range. For example, when researchers from a field station in California, USA, compared abundances of coastal marine species between the early and late 20th century, they found that local ocean warming was associated with an increase in more warm-adapted species, a decrease in more cool-adapted species and no significant change in cosmopolitan (widely distributed and therefore likely to be broadly tolerant) species (Barry *et al.*, 1995; Sagarin *et al.*, 1999). However, patterns related to tolerance characteristics may sometimes be obscured or overshadowed by other factors, such as indirect effects via increases or decreases in key (e.g. foundation) species (Schiel *et al.*, 2004).

There is some evidence that species with broad environmental tolerances have been more successful as invaders (see Dukes and Mooney, 1999; Kolar and Lodge, 2001). Tolerance range could be related to invasion success because broad tolerances allow species to inhabit a wide native range, causing them to be transported more often, as well as increasing the probability that species will survive and establish in an introduced habitat (Theoharides and Dukes, 2007). Furthermore, invaders may enjoy greater success under shifting environmental conditions when they have been transported from a source location more similar to the future climate in their introduced habitat. Thus, the colder an introduced habitat, the more likely that invasive species have come from relatively warmer locations and are more temperature tolerant than the local native species, suggesting that study location should be acknowledged as a possible factor modifying the strength of this pattern. For example, in a recent meta-analysis, which indicated that invasive species would be favoured under warmer

and more acidic conditions in marine systems, all of the studies included were conducted in relatively cool, temperate locations, whereas most of the invasive species considered had originated in warmer locations (Sorte *et al.*, 2013).

In addition to the relative breadth of physiological tolerances, 'pioneering' life-history characteristics (see Sakai *et al.*, 2001) could underlie both invasion success and the ability to capitalize on changing climates. Invasive species that can use available resources most efficiently, grow and mature quickly, and produce large numbers of offspring may be best able to colonize, establish and spread in their introduced habitat (Theoharides and Dukes, 2007). At the same time, climate change could increase resources either directly (e.g. via increased CO<sub>2</sub>) or indirectly, when it acts as a disturbance, freeing up food or space for resistant or newly colonizing species, favouring marine species with high resource-use efficiencies. Together, this reasoning leads to the expectations that physiological tolerance and resource-use characteristics will partly determine the success of species, both as invaders and under climate change.

### **Responses of Marine Invaders to Changing Climatic Conditions**

Whether the relative responses of invasive and native species to changing climatic conditions conform to these expectations has been examined primarily by comparisons focused on a subset of the most accessible intertidal and shallow subtidal communities and easily manipulated species. Foundation species from temperate communities are best represented, which, in contrast to terrestrial systems where foundation species are predominantly plants, include filter-feeding animals (e.g. bivalves) in addition to primary producers (seagrasses and seaweeds). There have also been a number of studies conducted in the epibenthic 'fouling' community, a highly tractable system of primarily sessile species including tunicates (sea squirts) and bryozoans (moss animals) that colonize submerged substrata such as

docks, boat hulls and natural rocky reefs. Well-studied consumer species include several snails and crustaceans such as the green crab, *Carcinus maenas*. Here, the term 'invasive' is used synonymous with 'non-native', although the majority of non-native species used as examples have had demonstrated impacts on native species and communities. Native species undergoing range expansions are not considered invasive, although there may be cases where expanders and invaders are difficult to differentiate (such as for pelagic species) or where a 'new' invader was previously overlooked (see Nehring, 1998).

### Observed changes in invasive species prevalence

The earliest and most numerous studies to invoke climate change as a cause of increases in invasive species have been descriptions and time series of observations. Such studies report on shifts in abundance coincident with a change in climatic conditions along a temporal or spatial axis, including an increase in invasive species as a particular location warms over time or across a geographic gradient of increasing temperature. Invasive species' responses observed concurrent with ocean warming are best represented. These have included increases in a suite of invasive epibenthic species in shallow subtidal communities on the north-east coast of the USA (Harris and Tyrrell, 2001), several species of non-native phytoplankton, zooplankton and fishes in the North Sea (Nehring, 1998; Beare *et al.*, 2004; Johns *et al.*, 2005), the proportion of alien species in the zooplankton and benthos of estuaries in Finland (Ojaveer *et al.*, 2011), the abundance and range of an introduced cordgrass in northern Europe (Loebl *et al.*, 2006; Nehring and Hesse, 2008) and a green alga invading the Canary Islands from across the Atlantic (Sangil *et al.*, 2012). Observing abundance changes across space and time, Carlton (2000) identified nine invasive species across five invertebrate phyla whose distributions had shifted northward concurrent with an increase in water tem-

perature along the North American west coast.

However, Carlton (2000) also pointed out the difficulty of ascribing causation from observational studies, given that multiple factors may vary concurrently, limiting conclusions about the increase in introduction frequency or intensity that has occurred at the same time as accelerating climate change (Ruiz *et al.*, 1997; Wonham and Carlton, 2005). Thus, for example, although it is tempting to attribute the tenfold increase of invasive species cover in a California epibenthic community to local warming of  $\sim 1^{\circ}\text{C}$  over the past 40 years, several of the most dominant invaders have only been introduced in the past 20 years (Sorte and Stachowicz, 2011). In order to resolve the relationship between climate change and invasions, researchers have partly circumvented these limitations of observational data in two ways.

First, an interaction between climate change and invasions is best supported when changes in the two are tightly linked in time, such as when abrupt shifts in invasive species abundances are associated with pronounced changes in climate. Diez *et al.* (2012) reviewed the effects of extreme climatic events on invasive species across systems, and invasives were favoured over natives in all marine studies included. For example, heatwave-related mortality was up to ten times higher for the invasive Mediterranean mussel, *Mytilus galloprovincialis*, than a native New Zealand mussel (Petes *et al.*, 2007). In addition, disturbance events associated with water flow have caused disproportionate mortality of native species, favouring *M. galloprovincialis* (Erlandsson *et al.*, 2006), the Asian clam (Nichols *et al.*, 1990) and invasive seagrass species (Steiner *et al.*, 2010). Temperature regime shifts have, in general, also been related to a 150% increase in invasions within the eastern Mediterranean (Raitsos *et al.*, 2010; Pancucci-Papadopoulou *et al.*, 2012; also see Galil, 2008).

Second, researchers have endeavoured to demonstrate the causal relationships between invasive species' abundances and environmental conditions across non-linear

time series, such as when warmer and cooler years are interspersed over time. Using interspersed time-series data, Stachowicz *et al.* (2002) showed that invasive epibenthic species recruited earlier and in higher numbers during years of warmer winter temperatures in Connecticut, USA. Positive relationships between temperature and invasive species recruitment were subsequently demonstrated among epibenthic species in California, USA (Sorte and Stachowicz, 2011), and Nova Scotia, Canada (Saunders and Metaxas, 2007), as well as for the cordgrass, *Spartina alterniflora*, in Washington, USA (Buhle *et al.*, 2012). Similarly, Minchinton (2002a) found that the growth and fecundity of the common reed, *Phragmites australis*, increased during a year of high precipitation (leading to decreased salinity stress) relative to the low precipitation years before and after. Finally, capitalizing on variation in pH across a portion of the Mediterranean containing subtidal CO<sub>2</sub> vents, Hall-Spencer *et al.* (2008) found that invasive seaweeds were among the species resistant to (i.e. for which abundances did not decline in the face of) high CO<sub>2</sub> and low pH.

Incorporating variation across both space and time, Braby and Somero (2006a) related abundance of the invasive Mediterranean mussel and a native congener to temperature and salinity conditions across years and sites in California, USA. They found that abundance of the invasive mussel was related positively to salinity and related negatively to temperature, whereas the opposite patterns held for the native species. Their results, however, are surprising in light of surveys finding the invader to be more prevalent in warmer microhabitats (Schneider and Helmuth, 2007), as well as the evidence for high thermal tolerance discussed below. Given that temperature and salinity covary negatively across sites, it seems that the abundance of this invasive mussel is tied more strongly to salinity than to temperature. This example highlights the possibility that warming – although the best-studied environmental change – is not always the most important driver of biological alterations.

Overall, results from observational studies conform to expectations and largely support a facilitative effect of climate change on species invasions. However, there are exceptions to this general pattern, and observations including multiple species also highlight the idiosyncrasy of individual invaders' responses, including across climate drivers within a single species. In a survey of epibenthic species in estuaries of Australia, abundance patterns of only one of six invasive species were related to environmental variables in a manner suggesting an increase with climate change, whereas three species declined in warmer or acidic conditions (Dafforn *et al.*, 2009). There are several other reports of invasive species that have not increased (e.g. Ojaveer *et al.*, 2011) and native species that have increased as much as, or more than, non-natives (e.g. Sorte and Stachowicz, 2011; Sangil *et al.*, 2012) under climate change. To better understand the drivers behind the observed responses and to inform attempts to forecast future ecological changes, researchers have turned increasingly to manipulative studies to elucidate the mechanisms driving the relationship between changing climatic conditions and invasive species' abundances.

### Single species studies in the laboratory and in the field

The results of controlled laboratory experiments provide more rigorous support for hypotheses linking invasive species' responses to changing environmental conditions. Importantly, for informing attempts to forecast future ecological changes, they have also allowed researchers to test the effects of likely future conditions across a broader range of conditions than are observed – at least predictably – in present-day climates. Using short-term laboratory experiments, several studies have demonstrated the higher performance of recent invaders than co-occurring native species under altered conditions, including survival and growth under osmotic stress (i.e. reduced salinity) for the tunicate, *Didemnum vexillum*, in the UK (Gröner *et al.*, 2011),

survival under hypoxia and increased temperature for a gammarid amphipod in Finland (Sareyka *et al.*, 2011) and prey capture under increased temperature for the green crab, *C. maenas*, in Newfoundland, Canada (Matheson and Gagnon, 2012). Some of these studies have included a number and range of treatments sufficient to assess invasive species response curves. Such studies indicate the range of conditions that are optimal (where survival is 100%), stressful (survival <100%) and lethal (0% survival), as well as the rate of decline in survival across a change in conditions. For example, lethal temperature response curves indicate that in a California epibenthic community, declines in survival will be relatively abrupt for Didemnid tunicates relative to, for example, two co-occurring bryozoans (Zerebecki and Sorte, 2011), and populations of these species on the east and west coasts differ not only in their thermal limits but also in their likely rate of response to climate warming (Sorte *et al.*, 2011).

Beyond lethal tolerance limits and demographic rates of survival, growth and fecundity, responses of interest have also included subcellular modifications that, themselves, underlie patterns of organismal physiology (see Somero, 2012). To illustrate this reductionist approach, I work 'backwards' through processes by which climate change could impact the invasive tunicate, *Diplosoma listerianum*, a species which has increased in abundance in the epibenthic community of Bodega Harbor, California, concurrent with ocean warming (Sorte and Stachowicz, 2011). A link between local temperature increase and this species' population growth is supported by the results from field observations, indicating a positive correlation between recruitment rates and temperature (Sorte and Stachowicz, 2011). Furthermore, laboratory experiments showed increased growth and no change in mortality at increased temperature (Sorte *et al.*, 2010b), and the species has a 24-h lethal temperature of 27.9°C (Zerebecki and Sorte, 2011), which is almost 10°C higher than the highest 24-h temperature recorded locally over the previous 5-year period (Sorte, 2010). At the

molecular level, Hsp70, a molecular chaperone responsible for rescuing cellular proteins that have started to denature under stress, was present at higher levels in the cells of this species than in a related native species that was less thermotolerant, potentially indicating a subcellular mechanism of enhanced tolerance in this invasive species (Zerebecki and Sorte, 2011).

The physiological mechanisms of responses to climatic change have been particularly well studied in the invasive and native species of *Mytilus* mussels, to the point that they have already been the subject of their own review (Lockwood and Somero, 2011; also see Somero, 2012). The two species are very similar in habitat, function and morphology, the latter so much so that they must be identified via genetic methods. The invasion of the Mediterranean mussel appears to have been facilitated by increased temperatures (Hilbish *et al.*, 2012), a relationship that is also supported by an observed range contraction when the Pacific Decadal Oscillation shifted to a cold-phase period (Hilbish *et al.*, 2010). This invasive species is more temperature tolerant than the related native species in all comparisons (Lockwood and Somero, 2011), including of survival (Schneider, 2008) and cardiac function (Braby and Somero, 2006b), as well as stress protein production and gene expression (Lockwood *et al.*, 2010; Fields *et al.*, 2012). Given their consistency across experiments, these findings of high physiological tolerance to environmental variation clearly help to explain the increasing success of the Mediterranean mussel as global temperatures increase. Across studies, there is support for the tolerance hypothesis, although whether invasive species have broader tolerances or tolerances shifted in the direction of future climates is more rarely known.

#### **Studies incorporating community and ecosystem context**

Compared to the number of correlative observations and single-species experiments describing climate change impacts on

invasive species, manipulative studies at the community level are exceedingly rare. This follows the overall trend of climate-related publications focused on marine systems, in which only 20% of studies have considered biological responses at the community level or higher (Harley *et al.*, 2006). The explanation for this trend may be largely logistical, as species vary in how amenable they are to experimental manipulation. However, the results available to date indicate that realistic predictions for species abundances and community composition are very sensitive to the effects of species interactions. When growth rates were compared for invasive epibenthic species maintained in the laboratory as either species monocultures or as part of whole communities, the direction of warming effects switched from positive to negative for some species, and the outcomes of simulation models differed greatly when interactions were included in the parameterization (Sorte and White, 2013).

Although it is challenging to replicate realistic climatic changes in the field, researchers have had some success increasing temperatures with passive warming chambers in intertidal habitats (Charles and Dukes, 2009; Gedan and Bertness, 2009) and heated substrata in shallow subtidal systems (Smale *et al.*, 2011; Smale and Wernberg, 2012), although invasive species have only been included in studies using the latter technique. The most common species on heated settlement panels was the white crust tunicate, a recent invader in Australian waters, which tended to be over twice as abundant on heated than on unheated panels (Smale *et al.*, 2011). A subsequent experiment found a significant increase in this invasive colonial tunicate on heated panels, whereas an invasive bryozoan was more abundant on unheated tiles, and an invasive solitary tunicate showed contrasting responses between two sites (Smale and Wernberg, 2012). Finally, Incera *et al.* (2010) tested the effects of disturbance intensity and variability (as would be associated with changes in storm events) on the invasive seaweed, *Caulerpa racemosa*, by manipulating the presence of cobbles in tide

pools, and they found that under high disturbance, *C. racemosa* fronds were smaller and less dense, whereas the number and cover of native species was increased. At present, manipulative experiments are so rare as to prevent specific conclusions, but the results to date indicate that community interactions and ecosystem context are likely to significantly alter predictions of invader responses to climate change.

### **Integrative Forecasts of Invader Impacts Under Climate Change**

Forecasting the impacts of invasive species under climate change requires integrating knowledge gained from both field observations and manipulative experiments designed to test the mechanistic underpinnings of invaders' responses. Parker *et al.* (1999) defined impact as a function of local abundance or population size, geographic range and per capita effect on native species. Thus, any climatic change that drives invasive species to increase in abundance, expand their ranges or impact their native compatriots more strongly would be predicted to increase their overall impacts. Although just a few years ago there were 'few good predictions of which invasive species will have greater effects under climate change' in any system (Hellmann *et al.*, 2008), several recent studies have attempted to integrate emerging results into specific predictions for a number of invasive species.

#### **Will abundances increase?**

Increases in future population sizes at a single site are likely when climatic changes are related to increases in invasive species' demographic rates, such as fecundity or recruitment (e.g. Stachowicz *et al.*, 2002; Saunders and Metaxas, 2007; Sorte and Stachowicz, 2011; Buhle *et al.*, 2012), survival (e.g. Gröner *et al.*, 2011; Sareyka *et al.*, 2011) and growth (e.g. Minchinton, 2002a; Stachowicz *et al.*, 2002; Sorte *et al.*, 2010b). Fully parameterized population models are even more reliable because

results from unmeasured responses could be contradictory, with, for example, negative effects on survival balancing positive effects on growth (e.g. Sorte *et al.*, 2010b). Saunders *et al.* (2010) parameterized an individual-based population model for an invasive bryozoan using empirical estimates of temperature effects on recruitment and growth rates. Their model results, which were relatively consistent with historical, sampled values at ambient temperatures, projected 9- and 62-fold increases in per cent cover upon warming of 1°C and 2°C, respectively. Similarly, Cockrell and Sorte (2013) developed stage-based population models for three invasive species at ambient and increased temperatures, which involved field surveys and laboratory mesocosm experiments to quantify the temperature dependence of seven transitions between three life stages. Likely increases in population growth rate were detected for the tunicate, *Botryllus schlosseri*, but not an invasive bryozoan or the tunicate, *Botrylloides violaceus*. These findings for *B. violaceus* were consistent with those of Grey (2011), who projected the population growth rate of this species based on demographic rates measured across four field sites and did not find a direct effect of temperature. Thus, species likely to increase in abundance with future climate change are those for which environmental changes have been found consistently (i.e. across multiple responses) to drive increases in historical population sizes and/or in demographic rates.

Furthermore, until now, I have focused primarily on the direct effects of changing climate on invasive species; however, climate-driven decreases in native species can also lead to the indirect facilitation of invasive species. Given that resource availability is related directly to invasion success (Davis *et al.*, 2000), climatic conditions that increase the mortality of native competitors could also lead to an increase in invasive species. For example, declines in particularly a native seagrass species have been implicated in allowing the spread of the invasive seaweed, *Caulerpa taxifolia*, in the Mediterranean (Ceccherelli

and Cinelli, 1999; Occhipinti-Ambrogi, 2003). Similarly, the mortality of a native cordgrass initially increases wrack (i.e. dead plant material), which facilitates invasion spread by smothering marsh turf and increasing colonization by the invasive *P. australis* (Minchinton, 2002b). There are, thus, both direct and indirect pathways by which climate change should increase the abundance and, by extension, impacts of many invasive species.

### Will ranges expand?

Whether or not climate change will drive the continued spread of an invasive species depends on whether that species has already expanded to fill its climate space and, if not, whether there is another, non-climate factor limiting its distribution. For example, based on lethal temperature and salinity tolerances, an invasive caprellid amphipod does not inhabit its full climate space (Ashton *et al.*, 2007); thus, it should continue to spread unless it is currently limited by non-climate factors. Similarly, the ability of the Japanese eelgrass to sustain growth at temperatures beyond the limits of its current habitat has been invoked to infer the potential for range expansions (Shafer *et al.*, 2008). Range projections have been made based on a single, or a few, threshold value(s), such as limits to survival, germination, photosynthesis, growth or reproduction (e.g. Carlton and Cohen, 2003; Loeblich *et al.*, 2006), and overwhelmingly have predicted future range expansions. In addition, although species distribution models have been underutilized in marine studies (Robinson *et al.*, 2011), increases in future ranges have also been predicted for four invasive marine invertebrates using a climate envelope technique based on the species' current ranges (de Rivera *et al.*, 2011). However, the ranges of many of these invaders are not currently in equilibrium with (i.e. extending to the limits of) habitat climatic conditions, limiting the applicability of species distribution models (Jones *et al.*, 2010), and forecasted range expansions would require that the species have either

the ability or the opportunity to spread under their own power or via transport vectors.

There are a few species for which current conditions have been demonstrated as setting contemporary range boundaries, suggesting that changing conditions could facilitate range shifts. For example, whereas cold-water temperatures appear to limit the population growth – and thus range expansion – at the poleward-range boundary of the invasive slipper limpet in northern Europe (Thieltges *et al.*, 2004), ocean warming is linked to increased reproductive success of this species and could facilitate its expansion (Valdizan *et al.*, 2011). Initially, as global mean temperatures increase, a concurrent increase in the frequency of extreme cold events could continue to limit invasive species' abundances. Severe population declines and range contractions associated with episodic or periodic cooling have been observed for the Asian green mussel (Firth *et al.*, 2011; also see Urian *et al.*, 2011) and an invasive porcelain crab (Canning-Clode *et al.*, 2011) in the south-eastern USA and for the Mediterranean mussel (Hilbish *et al.*, 2010) and green crab (Behrens Yamada and Kosro, 2010) along the US west coast. However, it is also clear that there are invasive species essentially 'lying in wait' for climatic conditions to change and, from the physiological perspective, improve (e.g. Diederich *et al.*, 2005; Witte *et al.*, 2010) in order to allow population growth and continued spread.

### **Will per capita effects on native species be strengthened?**

Per capita effects on native species have been assessed for a small minority of marine invaders and, for these, the effects on native species tend to be negative (Sorte *et al.*, 2010a). A global review of introduced seaweeds, for example, found that impacts had been studied for only 17 of 277 species, and negative effects (found in almost 50% of studies) were three times as common as positive effects (Williams and Smith, 2007;

also see Thomsen *et al.*, 2009). Even fewer studies have detected alterations in per capita effects under changing climatic conditions. Temperature-dependent predation has been demonstrated for an invasive gammarid amphipod in Poland (Van der Velde, 2009) and the Indo-Pacific lionfish in the Caribbean (Côté and Green, 2012), although for the latter, this per capita effect was predicted to be minor in comparison to the density-dependent effects of continuing local population growth. Höffle *et al.* (2012) conducted a factorial manipulation of temperature and the presence of the invasive mud snail, and found that the impacts on a native seagrass were additive, not synergistic. Thus, the evidence for climate-related changes in per capita effects remains equivocal, and whether the lack of a general pattern is driven by low data availability will be unclear until more impacts studies are undertaken.

## **Conclusions and Route Forward**

The literature review above provides several lines of evidence that climate change has increased and will continue to increase the impacts of many invasive species in marine systems. However, only a handful of the total marine invaders have been studied, and this handful likely contains primarily species that are the most visible, easiest to observe and manipulate, and potentially also most impactful. Thus, there is still much research needed to evaluate whether – and when – responses to climate change will be more often and more strongly positive for invasive than for native species.

The clearest gaps in our current knowledge are related to (i) the mechanisms underlying species' seemingly idiosyncratic responses to climate change and (ii) the complexity inherent in forecasting biological changes. Mechanistically, we have made some progress in comparing physiological tolerances between invasive and native species, although a better understanding would require ecophysiological studies spanning – and reporting – species' complete tolerance ranges. Hypotheses regarding

resource use and related life-history characteristics should be increasingly testable as marine biologists shift focus from the impacts of solely climate warming to other changes associated directly with resource availability such as ocean acidification. Furthermore, as invasive–native comparisons accrue in the literature, there will be more adequate studies for comparing life-history traits as van Kleunen *et al.* (2010) have done for plants.

An ultimate goal of understanding the processes underlying the responses to climate change is to inform attempts to predict future species abundances and community structure. This is a daunting prospect, particularly given that responses will integrate across multiple climatic factors, demographic responses and interacting species. To identify climatic drivers eliciting the strongest responses, as well as interactive effects between these drivers, marine biologists, again, need to increase efforts focused on non-temperature factors such as ocean pH, hypoxia and salinity. Researchers should continue to embrace complexity by conducting studies incorporating multiple demographic responses, life stages and species – both in seclusion and in a community context. Targeted studies should also test the degree to which climate change would be expected to cause population growth and the spread of already problematic, noxious species versus species that are currently relatively restricted (and perhaps have not advanced beyond a lag phase; Witte *et al.*, 2010). There may also be cases (e.g. see Sorte *et al.*, 2010b) in which climate change will be disproportionately detrimental to invasive species, which presents intriguing opportunities for restoration (Bradley and Wilcove, 2009). Overall, there remains a paucity of work documenting the interaction between climate change and invasions in marine systems, and an increase in studies across species and locations will allow us to draw broader conclusions about the cases in which invaders are likely to be favoured in future climates.

In conclusion, although invasive species have long been known as threats to intact

marine systems (e.g. Thompson *et al.*, 2002), concern about their potential impacts has recently been overshadowed by climate change (Williams and Grosholz, 2008). Invasions deserve continued and increased consideration, given building evidence that invader abundances, ranges, and thus impacts, are likely to increase under changing climate conditions. The indirect effects of climate change on invasive species therefore have the potential to deliver a ‘double whammy’ to native species already experiencing direct negative effects of climate change.

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