7 Interactions Between Climate Change and Species Invasions in the Marine Realm

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Abstract

Climate change and species invasions are prominent drivers of anthropogenic global change, contributing to biodiversity loss in marine systems worldwide. It is increasingly understood that these two processes might interact, with their combined impacts being more or less than the sum of their individual effects. Over the past two decades, 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 interactions between these two aspects of global change. 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. At the same time, it is becoming increasingly clear that not all interactions are synergistic: there are many documented cases of combined impacts of climate change and invasions being less than additive. There remain significant gaps in our understanding of responses to non-thermal factors (such as changes in ocean pH, dissolved oxygen and extreme events) and how species-specific idiosyncrasies will manifest in changes at the community level. Continued exploration of the interactions between climate change and species invasions will help us to incorporate another level of complexity: potential indirect effects mediated through responses of interacting invasive and native species.

Introduction

Both climate change and species invasions have been independently recognized as major drivers of biodiversity loss (Sala *et al.*, 2000; Cheung *et al.*, 2009; Mainka and Howard, 2010), but their total impact may be modified by interactive effects. There is increasing evidence that interactions between climatic change and species invasions are complex and could result in antagonistic, synergistic or additive effects, with these interactions increasing or decreasing the impacts of invasive species in marine systems (Fig. 7.1; Stephens *et al.*, 2019). For example, climate change could drive an increase in invasive species' abundances and, consequently, density-dependent effects on native prey species. At the same time, invasive predators could drive population declines of native prey and, therefore, decrease the potential of these native species to cope with climatic changes. As another, non-trophic, example, the combined stressors of warming and an invasive alga led to over 90% tissue necrosis of a native coral, whereas temperature alone had no effect on necrosis (Kersting *et al.*, 2015). On the other

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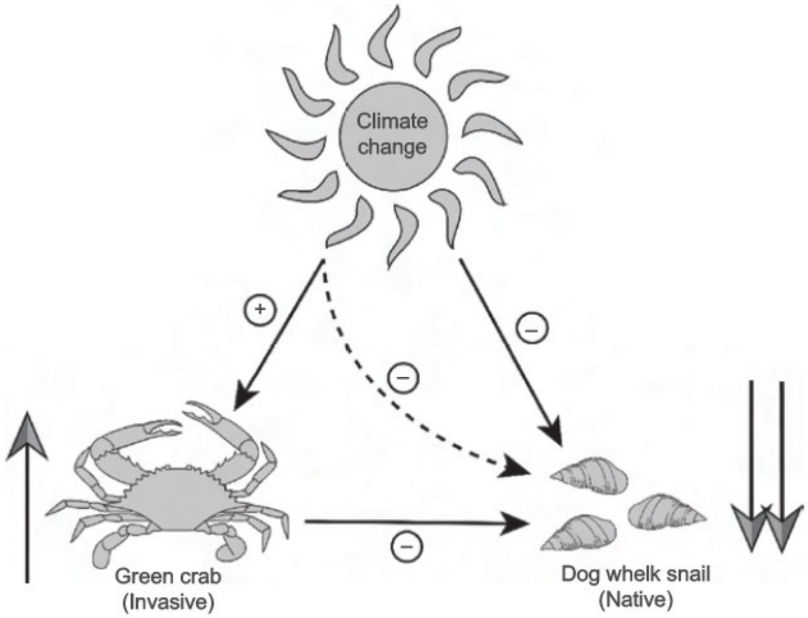

Fig. 7.1. Climate change can have both direct (solid lines) and indirect (dashed lines) effects on species. For example, if climate change has a positive effect (e.g. increased growth and survival) on the invasive green crab, then this will lead to an indirect negative effect on the crab's prey, the native dog whelk snail, by decreasing abundance. Green crabs can also decrease dog whelk foraging owing to a trait-mediated response to predation risk (Miller *et al*., 2014). Climate change may also have a direct negative effect on the dog whelk snail (e.g. increased metabolic costs), which will then lead to a doubly negative impact (via both direct and indirect effects) on the native species. While this example highlights a synergism, interactions between climate change and invasive species can alternatively be antagonistic: for example, when an invader serves as a predation refuge for a native species (e.g. Miranda *et al*., 2019). Finally, the absence of an interaction between climate change and invasions leads to additive effects of these two factors on native species. (Symbols are provided open-access with attribution from the Integration and Application Network, University of Maryland Center for Environmental Science: https://ian.umces.edu/media-library, accessed 7 July 2022.)

hand, an interaction between invasions and climate change could mitigate their individual effects on marine systems, such as by invasive species sheltering natives from climate extremes (e.g. Gestoso *et al*., 2016; Miranda *et al*., 2019).

Despite the critical need to understand and predict the combined effects of climate change and invasions on marine ecosystems, study of this interaction in marine systems still lags 5–10 years behind that in terrestrial systems (Fig. 7.2; for a review of this topic in freshwater systems, see Rahel and Olden, 2008). This discrepancy in publishing rate is despite evidence that marine systems appear, in some cases, to be more greatly threatened 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; Pinsky *et al*., 2019). Furthermore, previous studies have focused on only a few types of climate stressors and their interactive effects with species invasions. Warming has been, and remains, the most studied climate change factor; however, since 2011, increasing research has focused on the effects of acidification and hypoxia relative to invasions (Fig. 7.2). Given the vulnerability of marine systems and increasing threat of global change, it is crucial that we better understand the interactive effects of climate change and invasions in marine systems, including across different types of climate stressors.

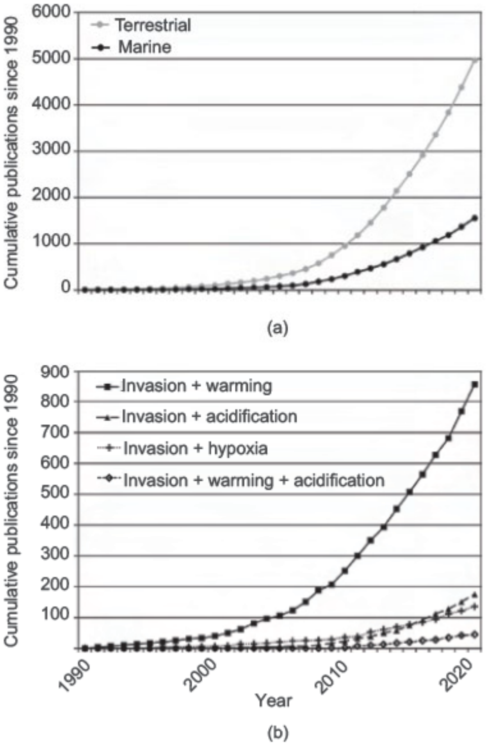

Fig. 7.2. (a) Studies on climate change and species invasions in marine systems (black) trail comparable studies in terrestrial systems (gray). (b) Most of the studies of climate change drivers and invasion in marine systems have focused on warming (squares), although studies incorporating acidification (triangles) and hypoxia (crosses), as well as both warming and acidification (diamonds), have increased substantially since the year 2010. Values are cumulative publications since the year 1990 and are based on a topics search using the International Statistical Insititute Web of Knowledge.

In this chapter, we first summarize recent and predicted alterations in the ocean associated with climate change as well as the hypothesis that these environmental alterations will impact invasive species less negatively than co-occurring native species. Second, we review the marine literature to assess whether our current understanding of climate change effects on invasive species conforms to the expectations of this hypothesis. Finally, we synthesize the literature to explore how responses of invasive species to climate change will, in turn, determine their future impacts on native species. Throughout this chapter, the term 'invasive' is used as synonymous with 'non-native' and/or 'exotic', although most 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). It is also important to note that discerning between the responses of native and exotic species may be made more difficult by the presence of cryptogenic species (species that are neither clearly native or exotic to a region) *sensu* (Carlton, 1996).

Climatic Changes in the Marine Realm

The oceans, which cover about 70% of the Earth's surface, have absorbed an estimated 31% of the excess carbon dioxide (CO_2) emissions (Gruber *et al.*, 2019) and more than 90% of the excess heat within the Earth system owing to anthropogenic greenhouse gas emissions (Cheng *et al.*, 2017b; Zanna *et al.*, 2019). Recent and future predicted increases in CO_2 levels and temperature feed back to influence other physical properties of marine systems (Table 7.1; Lee *et al.*, 2021). While an increase in dissolved CO_2 might be expected to fertilize 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.*, 2020). Increased temperature leads to a decrease in dissolved oxygen and can increase stratification, further preventing oxygen diffusion (Levin, 2018). Global warming also causes expansion of ocean water and melting of terrestrial ice, leading to sea level rise, while 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, including marine heatwaves. Although this chapter focuses on changes in climatic variables, particularly those that have been best studied

Table 7.1. Observed and predicted changes in the marine environment associated with climate change. Unless noted, values are from the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (Lee *et al.*, 2021) and are based on the SSP2-2.6 (shared socio-economic pathway) scenario when multiple projections were given. Changes observed to date and predicted by 2100 were calculated from values relative to the present day.

Physical factor	Past changes (observed)	Changes predicted by 2100
pH	↓ 0.1 units since 1980s	↓ 0.06 units
Sea surface temperature	↑ 0.88°C since 1850s	↑ 0.54°C
Dissolved oxygen	↓ 1.2–6.1 mmol/m³ since 1970s	↓ 2.4 mmol/m³
Salinity	No data	↑ ↓ depending on location
Sea level	↑ 0.2 m since 1901	↑ 0.3–0.5 m
Extreme climatic events	↑ frequency and intensity	↑ frequency and intensity

(i.e. climate warming; Fig. 7.2), it is important to note that other anthropogenic factors (e.g. pollution, nutrient inputs, fishing pressure and habitat modification) could also interact with climate variables and invasions to impact marine systems.

Why Might Climate Change Favor Invaders over Native Species?

Changes in marine climatic conditions are expected to favor invaders over native species owing to the overlap between traits associated with invasion success and traits that could facilitate persistence under future conditions. Specifically, both climate change ‘winners’ (species likely to benefit most or suffer least) and successful invaders are expected to (i) have life-history characteristics favoring fast growth, high reproductive rates and rapid utilization of available resources; and/or (ii) have relatively broad environmental tolerance ranges or tolerances that encompass future conditions.

Species differ in their physiological tolerances, with performance 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; Waldock *et al.*, 2019). Within this framework, then, climatic changes will or will not benefit a particular species based on whether conditions become more physiologically optimal or stressful, respectively (Bennett *et al.*, 2021). We note, however, that whereas we consider the species level for this discussion, tolerance also varies intra-specifically based on individuals’ differential histories of adaptation and acclimation, such as between broadly distributed native and invasive populations (Wesselmann *et al.*, 2020; Villeneuve *et al.*, 2021). Predictable responses to climate change have been associated with geographic affinity (see Helmuth *et al.*, 2006), and geographic range can be considered a proxy for environmental tolerance range. For example, Givan *et al.* (2018) examined fish species captured in the eastern Mediterranean and found that the relative abundance of native species declined over a 20-year period while the proportion of invasive species increased. Importantly, the invasive fish species observed tended to occur in geographic areas with greater mean sea surface temperatures than the areas inhabited by the native species. Although geographic affinity has been associated with responses to climate change, these patterns can 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 now compelling evidence that species with broad environmental tolerances have been more successful as invaders, as postulated by Dukes and Mooney (1999) and Kolar and Lodge (2001). Within taxonomic groups, invasive species tend to exhibit higher upper thermal thresholds than native species (Kelley, 2014), and in marine ecosystems, non-native species tend to outperform natives under warmer conditions (McKnight *et al.*, 2021; but see Stephens *et al.*, 2019). Studies have also demonstrated that invasive species tend to outperform natives when examining the relative impacts of both single (e.g. Atkinson *et al.*, 2020) and multiple (e.g. Bollen *et al.*, 2016) stressors on native and invasive species. Tolerance range could be related to invasion success because broad tolerances allow species to inhabit a wide native range, causing them to be more often transported, 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, when investigating whether invasive species will be favored under warmer and more acidic conditions in marine systems, all the studies included in the meta-analysis by Sorte *et al*. (2013) were conducted in relatively cool, temperate locations, whereas most invasive species considered had originated in warmer locations. However, studies comparing the relative effects of global change on native and invasive species typically examine closely related or competing species, so it is uncertain whether invasive species will be favored when considering interactions between trophic levels (i.e. predation). For example, when examining how increased temperatures affected two species of invasive oyster drill (*Urosalpinx cinerea* and *Ocenebra inornata*) and their native oyster prey (*Ostrea lurida*), Cheng *et al*. (2017a) found that both invasive drills had lower thermal optima than the oyster prey, suggesting greater susceptibility to warming in the invasive predators. As such, while invasive species may be generally favored over species within the same taxonomic group owing to broad physiological tolerances, determining the net effect of global changes on community compositions is complex and may not consistently favor invasive species after considering the interactions between invaders and organisms in the recipient communities.

'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 most efficiently use available resources, 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). Alexander *et al*. (2015) tested this resource capture hypothesis by comparing algal uptake of two invasive mussels (*Mytilus galloprovincialis* and *Semimytilus algosus*) and one native mussel (*Aulacomya atra*) across a range of temperatures, finding that *M. galloprovincialis* consistently consumed the greatest quantity of algal cells regardless of temperature. At the same time, climate change could increase resources either directly (e.g. via increased CO_2) or indirectly, when it acts as a disturbance freeing up food or space for resistant or newly colonizing species, favoring 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.

Finally, invasive species could be favored over native species if they generally display greater plasticity or adaptability in the face of a changing climate. In the marine realm, several recent studies have found that invasive species have the capacity for rapid adaptation to novel conditions, such as changing temperature (Han and Dong, 2020) or salinity (Green *et al.*, 2020), which may have allowed them to initially become invasive or may contribute to future spread. Invasive species, such as the European green crab *Carcinus maenas*, have also shown the ability to adapt to both warmer and cooler recipient communities (Tepolt and Somero, 2014; Wesselmann *et al.*, 2020), potentially improving the likelihood of their future persistence. However, knowledge about the relative strength of selection in native versus invasive species is still lacking (Moran *et al.*, 2014), limiting our ability to resolve whether invasive species generally hold an evolutionary advantage over native species.

Responses of Marine Invaders to Changing Climatic Conditions

Here, we review tests of the hypothesis that invasive species will be less negatively impacted by changing climatic conditions. To date, studies have primarily been constrained to easily manipulated species and the most accessible intertidal and shallow subtidal communities. 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 and hydrozoans) 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 *C. maenas* (see Fig. 7.1). Studies conducted in less accessible habitats or those examining vertebrates, however, remain rare.

Observed changes in invasive species prevalence

The earliest and most numerous studies to invoke climate change as a cause of increases in species invasion have been descriptions and time series observations. The responses of invasive species have been most thoroughly studied alongside changes in ocean temperature, though there has been increased focus on the effects of other changing factors (e.g. pH and hypoxia; Fig. 7.2b) on invasion, as well as whether the overall impact of multiple drivers is synergistic, additive or antagonistic. These studies report on shifts in abundance coincident with a change in climatic conditions along a temporal or spatial axis, such as an increase in invasive species as a particular location warms over time or across a geographic gradient of increasing salinity. Observing abundance changes across space and time, Carlton (2000) identified nine invasive species across five invertebrate phyla whose distributions have shifted northward concurrent with an increase in water temperature along the North American west coast.

However, as Carlton (2000) pointed out, it is difficult to ascribe causality from observational studies given that multiple factors may vary concurrently, limiting conclusions about the increase in introduction frequency or intensity that has occurred alongside accelerating climate change (Ruiz *et al*., 1997; Wonham and Carlton, 2005). Thus, for example, although it is tempting to attribute the ten-fold increase of invasive species cover in a California epibenthic community to local warming of ~1°C over 40 years, several of the most dominant invaders were introduced only in the latter 20 years of that time interval (Sorte and Stachowicz, 2011). Similarly, when two or more factors are at play, as with warming and changing salinity simultaneously affecting invasion on the coast of New Zealand (Floerl *et al*., 2013), the individual contribution of each driver may be difficult to parse.

Of the suite of climate change drivers which may affect species invasion, the relationship between climate warming and invasion has been the most thoroughly studied (Fig. 7.2b), and researchers have accounted for the limitations of observational data (Ruiz *et al*., 1997; Wonham and Carlton, 2005) 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 effects of extreme climatic events on invasive species across systems, and invasives were favored over natives in all marine studies included (see also Castro *et al*., 2021). For example, heatwave-related mortality was up to ten times higher for the native New Zealand mussel *Perna canaliculus* than the invasive Mediterranean mussel *M. galloprovincialis* (Petes *et al*., 2007). Second, researchers have endeavored to demonstrate 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 on the northeast coast of the United States. Temperature-focused studies have documented increases in: a suite of invasive epibenthic species in shallow subtidal communities in the northeastern United States (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).

Interactions between climate change and invasion have become particularly relevant in high-latitude and polar ecosystems (Mahanes and Sorte, 2019). Climate change is altering environmental conditions in these areas that have historically had low levels of invasion, making these areas more hospitable to invasive species and expanding the pool of potential invaders to include the more diverse set of species from temperate zones (Chan *et al.*, 2019; Goldsmit *et al.*, 2020). Additionally, climate change is indirectly affecting invasion in the Arctic by altering human behavior: increased ship traffic in the Arctic from newly passable trade routes (because of thawing sea ice); increasingly accessible mineral resources; and a booming Arctic tourism industry which is increasing propagule pressure in the Arctic (Seebens *et al.*, 2013). Though the Antarctic remains largely free of invasive species, likely owing to comparatively lower ship traffic and inhospitable, as well as highly seasonal, temperatures (Byrne *et al.*, 2016; McCarthy *et al.*, 2019), it may become increasingly vulnerable to invasion in the future.

Despite the consistent focus on warming, other aspects of climate change, including ocean acidification, changes in salinity and increasingly extreme weather are also affecting species invasion worldwide. Research by Hall-Spencer *et al.* (2008), capitalizing on natural pH variation near subtidal CO_2 vents in the Mediterranean Sea, found that invasive seaweeds were among the species most resistant to (i.e. for which abundances did not decline in the face of) high CO_2 and low pH. There is mounting evidence to suggest that invasive seaweeds may be facilitated by ongoing ocean acidification; one of the most widely invasive seaweeds, commonly referred to as killer algae (*Caulerpa taxifolia*), displays a faster growth rate in acidified conditions (Roth-Schulze *et al.*, 2017). Acidification may also alter interactions between invasive and native species. Sanford *et al.* (2014) showed that acidified conditions reduce the adult size of native Olympia oysters (*Ostrea lurida*) in California, United States, while increasing oyster predation rate of an invasive snail, the Atlantic oyster drill (*Urosalpinx cinerea*). Shifts in weather patterns, which can change salinity and cause disturbance via increased water flow, may also affect the success of invasive species. Minchinton (2002a) found that growth and fecundity of the invasive 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. Additionally, disturbance events associated with high water flow have caused disproportionate mortality of native species, favoring the invasive mussel *M. galloprovincialis* (Erlandsson *et al.*, 2006), the Asian clam (Nichols *et al.*, 1990) and invasive seagrass species (Steiner *et al.*, 2010).

Climate warming and other climate-related changes are affecting the proliferation of invasive species, and some studies suggest that interactions among multiple changing conditions (e.g. simultaneous shifts in temperature and salinity, or dissolved oxygen and pH) can produce complex, non-additive effects (Jackson *et al.*, 2016). The potential for synergism or antagonism (increasing or mitigating the overall impact, respectively) among multiple stressors complicates predictions for the impacts of global change (Côté *et al.*, 2016; Geraldi *et al.*, 2020). Synergistic interactions among multiple factors can accelerate the proliferation of an invasive species, as has been observed with the rayed erythrean mussel (*Brachidontes pharaonis*) in the Mediterranean Sea. Rising sea surface temperatures were the strongest driver of erythrean mussel invasion, but high salinity zones and nutrient input from urban centers also facilitated the spread of the mussel throughout the Mediterranean (Sarà *et al.*, 2018). The conventional wisdom has been that non-additive effects among stressors would generally be synergistic, as is the case with the rayed erythrean mussel, but recent meta-analyses concluded that most non-additive effects among global change drivers studied to date are antagonistic, resulting in a smaller overall impact than if each factor were acting independently (Côté *et al.*, 2016; Jackson *et al.*, 2016; Tekin *et al.*, 2020). Miranda *et al.* (2019) documented one such antagonistic interaction: warming increased grazing intensity on a native seaweed, the common kelp *Ecklonia radiata*, but in the presence of the invasive seaweed *Caulerpa filiformis*, herbivores preferentially grazed on the invader, reducing the climate-related increase in grazing pressure on the native kelp.

Interactions among multiple changing climate factors can also produce surprising patterns that further complicate impact forecasts. 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, United States. They found that abundance of the invasive mussel was positively related to salinity and negatively related 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 later in this chapter. Given that temperature and salinity co-vary negatively across sites, it seems that the abundance of this invasive mussel is more strongly tied to salinity than temperature. This example highlights the possibility that warming – although the best-studied environmental change (Fig. 7.2b) – is not always the most important driver of biological patterns.

These results from observational studies paint a complex picture of the relationship between climate change and species invasion, with incidences of synergistic, antagonistic or simply additive effects on native species (Jackson *et al.*, 2016; Geraldi *et al.*, 2020). 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 or more than non-natives (e.g. Sorte and Stachowicz, 2011; Sangil *et al.*, 2012) under climate change. Recent meta-analyses suggest that the overall trend favors antagonistic interactions, with climate change reducing the impact of invasives on native communities, despite expectations from their relative responses to climate change, suggesting that climate change could amplify the effect of invasions on native species (Tekin *et al.*, 2020). To better understand the drivers behind observed responses and inform attempts to forecast future ecological changes, researchers have increasingly turned to manipulative studies to better elucidate the mechanisms driving the relationship between changing climatic conditions and invasive species abundances.

Single-species studies in the lab and field

Results of controlled laboratory experiments and field 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. Using short-term laboratory and field experiments, several studies have demonstrated higher performance of recent invaders than co-occurring native species under altered conditions including: growth rates and photosynthetic performance of the invasive seaweed (*Sargassum muticum*) under warming (Atkinson *et al.*, 2020); high salinity tolerance of the Asian shore crab (*Hemigrapsus sanguineus*) in the northwestern Atlantic (Hudson *et al.*, 2018); 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).

Integration of both field and laboratory experiments may make conclusions even more representative of what we might expect under future climate change. As an example, Lagos *et al.* (2017) found that invasive epibenthic invertebrates (e.g. solitary ascidians, arborescent bryozoans) were more tolerant of low oxygen conditions than their native counterparts in Australia. Similarly, along the Israeli Mediterranean coast, increasing ocean temperatures have reduced the physiological performance of the native European purple sea urchin (*Paracentrotus lividus*) while invasive rabbitfishes have prospered (Yeruham *et al.*, 2020). Another interesting example is that of the mussels *Mytilus galloprovincialis* (in this case, the native species) and the invader *Xenostrobus securis* from the coast of Spain: acidification led to higher mortality in the native than the invasive species, although this effect was diminished when the native grew in mixed clumps with the invasive (Gestoso *et al.*, 2016). Overall, findings suggest that invaders have higher performance under changing climatic conditions, but these patterns can change with community context, as discussed in greater detail later in this chapter.

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). An example of subcellular climate change impacts uses the invasive tunicate *Diplosoma listerianum* as a model. This species has increased in abundance in an epibenthic community of California, United States, concurrent with ocean warming (Sorte and Stachowicz, 2011). A link between local ocean warming and this species' population growth is supported by 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 had a 24 h lethal temperature of ~28°C (Zerebecki and Sorte, 2011), which was nearly 10°C higher than the maximum 24 h temperature recorded locally during the preceding five years (Sorte, 2010). At the molecular level, Hsp70, a chaperone protein responsible for rescuing other 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; see also Somero, 2012). These two species are very similar in habitat, function and morphology – the latter so much so that they must be identified via genetic methods. Where they are non-native, the invasive Mediterranean mussel outcompetes native mussels by having faster growth rates, higher tolerance to air exposure and higher reproductive output (Branch and Steffani, 2004). 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 in California, United States, when the system shifted to a cold-phase period (Hilbish *et al.*, 2010; Lynch *et al.*, 2020). This invasive species tends to be more temperature tolerant than the related native species (Lockwood and Somero, 2011), although there is some evidence that upper tolerance limits are more plastic in native blue mussels than in the Mediterranean mussel (Lenz *et al.*, 2018) and that the invader's tolerance varies by habitat (Collins *et al.*, 2020). Overall, the invasive mussel tends to have higher survival (Schneider, 2008; Dowd and Somero, 2013), cardiac function (Braby and Somero, 2006b; Tagliarolo and McQuaid, 2015), and stress protein production and gene expression (Lockwood *et al.*, 2010; Fields *et al.*, 2012; Saarman *et al.*, 2017) as compared with native species. Nevertheless, given the consistency across experiments, these findings of high physiological tolerance to environmental variation help to explain the increasing success of the Mediterranean mussel as global temperatures increase. Across studies, there is support for the hypothesis that invasive species have higher tolerances than native species, although how invasives and climate change will interact under future conditions to impact native species is less well 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 less common. This follows the overall trend of climate-related publications focused on marine systems, in which most research is conducted at the species or population scales, and only 36% of the studies reviewed by McDonald *et al.* (2018) considered biological responses at the community level or higher. The explanation for this trend may be largely logistical, as communities vary in how amenable they are to experimental manipulation.

Although it is challenging to replicate realistic climatic changes in the field, researchers have had some success increasing temperatures with passive warming plates in intertidal habitats (Charles and Dukes, 2009; Gedan and Bertness, 2009; Lathlean and Minchinton, 2012; Kordas *et al.*, 2015), heaters deployed in tide pools (Sorte and Bracken, 2015) and heated substrata in shallow subtidal systems (Smale *et al.*, 2011; Smale and Wernberg, 2012; Loiacono, 2016; Ashton *et al.*, 2017), although invasive species have only been included in studies using the latter technique. On settlement panels deployed in Australian waters, Smale *et al.* (2011) found that the most common species was a relatively recent invader, the white crust tunicate (*Didemnum perlucidum*), which tended to be over twice as abundant on heated as on unheated panels. 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). A similar study conducted in central California found that both native and invasive fouling organisms grew faster in warmed communities, but that this increase in growth rate was greater for the invasive species (Loiacono, 2016). Finally, Bertocci *et al.* (2015) found that the invasive algae *Grateloupia turuturu* and *Sargassum muticum* benefited from variable, high-intensity disturbances (as would be associated with changes in storm events) but that when disturbances occurred more regularly, the richness of native species also increased. At present, manipulative experiments continue to be rare enough to prevent specific conclusions; however, results to date indicate that community interactions and ecosystem context are likely to significantly alter predictions of invader responses to climate change.

Despite previous hypotheses suggesting that invasive species may facilitate each other's likelihood of establishment or survival (Simberloff and von Holle, 1999), a meta-analysis by Jackson (2015) determined that, on average, interactions between invasive and native species in the marine realm results in reduced performance for both species. Climatic changes are known to modulate the direction and intensity of biotic interactions (Kordas *et al.*, 2011; Blois *et al.*, 2013), however, which may result in unexpected outcomes for population sizes of both invasive and native species in the future. Studies examining the epibenthic community provide examples of how community interactions may be altered by climatic changes. When growth rates were compared for invasive epibenthic species maintained in the lab as either species monocultures or as part of whole communities, the direction of warming effects switched from positive to negative for some species, and outcomes of simulation models differed greatly when interactions were included in the parameterization (Sorte and White, 2013). Similar complexities were described in a manipulative study that compared how the patterns of overgrowth competition between broadly distributed invaders (such as the tunicates *Botrylloides violaceus*, *Botryllus schlosseri*, *Diplosoma listerianum*, *Didemnum vexillum* and the bryozoan *Watersipora subtorquata*) changed with temperature along US coastlines (Lord and Whitlatch, 2015). Specifically, populations in the northern portions of species' ranges tended to benefit from warming, indicated by increased growth rates and competitive ability, whereas populations in the southern portions of species' range tended to be negatively impacted by increased temperatures, with competitive outcomes varying greatly between species pairs. A follow-up study demonstrated that, in addition to being impacted by climatic changes such as increased temperature, the outcome of competitive interactions involving invasive species may also be influenced by resource availability (Lord, 2017a). Together, these studies demonstrate how it is possible for invasive species to be both 'winners' and 'losers' of global changes, including via mechanisms involving community interactions.

Integrative Forecasts of Invader Impacts under Climate Change

The importance of the interaction between climate change and invasions is typically described in the context of understanding the impacts of these processes on native species. Parker *et al.* (1999) defined the impact of invasive species 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 more strongly impact their native compatriots 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, p. 540), recent studies have attempted to integrate emerging results into specific predictions for a number of invasive species. Forecasting and measuring 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.

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; Lord, 2017b), 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; Lord, 2017b; Roth-Schulze *et al.*, 2018; Atkinson *et al.*, 2020; Nguyen *et al.*, 2020). 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 nine- and 62-fold increases in percentage 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. They detected likely increases in population growth rate 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 population growth rate of this species based on demographic rates measured across four locations and did not find a direct effect of temperature.

Impacts may depend on the invaded community composition and spatial factors. Using stage-based matrix models, Denley *et al.* (2019) found that the effects of near-future temperatures on invasive bryozoan *Membranipora membranacea* abundance is likely to vary spatially in relation to availability of kelp substrate. Though growth rates increase with warmer water, the impacts were mediated by climate-induced changes to the structure of the habitat through indirect effects on algal hosts. Spatially explicit demographic models could increase the accuracy of predictions by incorporating habitat suitability, dispersal and source–sink dynamics (Mellin *et al.*, 2016). In addition, machine-learning models can generate predictions using temporal datasets, which could predict outbreaks of invasive species such as crown-of-thorns starfish (Matthews *et al.*, 2020) but may not directly measure climate impacts. Generally, invasive species likely to increase in abundance with future climate change are those for which environmental changes have been consistently (i.e. across multiple responses) found to drive increases in historical population sizes and in demographic rates.

Furthermore, although this chapter has primarily focused on direct effects of changing climate on invasive species, climate-driven decreases in native species can also lead indirectly to increases in, or complex effects on invasive species. Given that resource availability is directly related to invasion success (Davis *et al*., 2000), climatic conditions that increase mortality of native competitors could also lead to an increase in invasive species. For example, declines in a native seagrass have been implicated in allowing the spread of the invasive seaweed *Caulerpa taxifolia* in the Mediterranean (Ceccherelli and Cinelli, 1999; Occhipinti-Ambrogi and Savini, 2003). Similarly, 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 invasive *Phragmites australis* (Minchinton, 2002b). In rare cases, antagonistic effects between climate change and invasive species may mitigate impacts on native species. Warming led to increased grazing on the macroalga *Ecklonia radiata*, which caused Australian subtidal reefs to become dominated by the invasive alga *Sargassum muticum*; however, grazing of *E. radiata* was mitigated by the presence of a chemically defended invader *Caulerpa filiformis* (Miranda *et al*., 2019). There are, thus, direct and indirect pathways by which climate change may increase the abundance and, by extension, modify impacts, of many invasive species.

Will ranges expand?

Whether or not climate change will drive 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 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 single or few threshold values, such as limits to survival, germination, photosynthesis, growth or reproduction (e.g., Carlton and Cohen, 2003; Loebl *et al*., 2006), and have overwhelmingly predicted future range expansions. Species distribution models have increased in use for marine species (Robinson *et al*., 2011; Martínez *et al*., 2015; Canning-Clode *et al*., 2017), and increases in future ranges have been predicted for dozens of invasive marine organisms using climate envelopes based on species' current ranges (de Rivera *et al*., 2011; Zhang *et al*., 2020; de la Hoz *et al*., 2019; Beca-Carretero *et al*., 2020). 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 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). Invasive lionfishes *Pterois miles* and *Pterois volitans* are physiologically limited by cooler northern and inshore temperatures (Barker *et al*., 2018), and are predicted to increase their range with warmer water in several regions (Grieve *et al*., 2016; Poursanidis *et al*., 2020). 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 southeastern

United States 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?

The impact of invasive species per individual (i.e. per capita effect) on native species has been assessed for the minority of marine invaders, and, for these, 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 in the Ponto-Caspian region (Cuthbert and Briski, 2021), and for Indo-Pacific lionfish in the Caribbean (Côté and Green, 2012). However, for the lionfish, this per capita effect was predicted to be minor in comparison with the density-dependent effects of continuing local population growth. Höffle *et al.* (2012) conducted a factorial manipulation of temperature and presence of the invasive mud snail and found that impacts on a native seagrass were additive, not synergistic. Climate change has been shown to alter invasive host–pathogen dynamics in complex ways as each interactor may respond differently to changes in environmental variables (Byers, 2021; Costello *et al.*, 2021), subsequently altering per capita effects. 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 impact studies are undertaken.

Conclusions and Route Forward

The literature review in this chapter provides several lines of evidence that climate change has influenced and will continue to influence 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 most visible, easiest to observe and manipulate and, potentially, most impactful. Thus, there is still much research needed to evaluate whether – and when – climate change and invasive species will impact native species in a way that is more or less than the sum of the individual effects of these global change drivers.

The clearest gaps in our current knowledge are related to (i) the mechanisms underlying species' often 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 – tolerance ranges across species' life histories, geographic ranges and inhabited environmental gradients. 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 directly associated 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 processes underlying 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 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 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*., 2013) in which climate change will be disproportionately detrimental to invasive species, which presents intriguing opportunities for restoration (Bradley and Wilcove, 2009). Overall, the great majority of marine invasive species remains understudied, and increased research effort and coordination between the global network of invasion biologists will allow us to draw broader conclusions about the role of climate change in determining the outcome of species invasions.

In conclusion, although invasive species have long been recognized as threats to intact marine systems (e.g. Thompson *et al*., 2002), concern about their potential impacts has, in some cases, been overshadowed by studies focused on 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 be altered under changing climate conditions, with consequences for native species that may already be vulnerable to accelerating climate change.

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